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evolutionary biology of ostracoda

its fundamentals and applications

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    EVOLUTIONARY BIOLOGY OF OSTRACODA, ITS FUNDAMENTALS AND APPLICATIONS

Developments in Palaeontology and Stratigraphy, 11

evolutionary biology of ostracoda

its fundamentals and applications

Proceedings of the Ninth International Symposium on Ostracoda,
held in Shizuoka, Japan, 29 July-2 August 1985

edited by

Tetsuro Hanai

Professor Emeritus, University of Tokyo, Japan

Noriyuki Ikeya

Institute of Geosciences, Faculty of Science, Shizuoka University, Shizuoka, Japan

and

Kunihiro Ishizaki

Institute of Geology and Palaeontology, Faculty of Science, Tohoku University, Sendai, Japan

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Preface

At the general meeting of the Houston symposium, when we proposed to invite the next symposium to Shizuoka, Japan, someone asked us about the theme of the upcoming symposium. We replied that we intended to focus attention on the evolutionary biology of Ostracoda, its fundamentals and applications. On second thought, however, we felt that this theme would be inappropriate because evolutionary biology is a nomothetic science, whereas the study of Ostracoda adopts a more or less idiographic approach. Thus it was realized that our intention comprised two general approaches.

One fundamental approach is expressed in the words "evolutionary biology" and is especially intended to extend evolutionary biology into the geological past utilising Ostracoda. Taking advantage of their ideal characteristics for evolutionary research, it is possible to determine palaeobiologically significant events and develop theories. Recent progress in evolutionary biology seems to have been mainly based on studies of experimental organisms suitable for genetic research, with hardly any fossil evidence. Furthermore, theoretical syntheses in the field of evolutionary biology have recently advanced rather rapidly without sufficient palaeontological evidence. We believe that Ostracoda are one of the most useful organisms for studies intended to overcome difficulties originating from these circumstances. Understanding evolutionary process can doubtless be achieved through the cooperation of biologists and palaeontologists. This ostracod research group, which has been assembling every two or three years since 1963, is in a good position to conduct such studies.

Another traditional approach may be expressed by the two words, "of Ostracoda". In spite of the complaints about idiographically oriented methodology, which employs a little classification and generalizes on the descriptive level, if we trace the history of this methodology back into the time of Linnaeus and consider that our knowledge of Ostracoda was virtually nil at that time, our present knowledge is unexpectedly vast in both space and time; it also includes aspects from many fields of biology and other related sciences, as anyone who has studied Ostracoda knows. This knowledge of Ostracoda has been strengthened by generalizations on the descriptive level in the same manner as generalities have known as 'laws' in evolutionary biology. Even if we defer to the criticism of a strongly idiographic approach, the addition of the words "of Ostracoda" will, at least, still prevent studies from becoming mere intellectual exercises in the nomothetic and evolutionary disciplines.

Our other aim is to learn of fundamental studies which can be of vital importance, especially for biostratigraphy and palaeobiogeography, and therefore in the exploration for petroleum resources. Studies made by petroleum palaeontologists may even be able to relate evolutionary changes in ostracod fauna to the temporal influx of sea water flowing into the continents and to the movement of the plates.

As this was the first time this symposium was held outside of America or Europe, its results will aid and influence future ostracod studies in the Asian area. We wish to thank all our contributors and discussion participants for helping to promote a productive and well attended symposium. Chinese ostracodologists kindly agreed to receive an excursion to visit fossil localities in China.

For advice, assistance, and help in surmounting the language barrier, we are grateful to many of our colleagues. Professor John W. Neale and Dr. Heinz Malz prolonged their stays in Japan and gave us invaluable advice, assistance and support. Dr. J. F. Babinot, Dr. P. Carbonel, Dr. Thomas M. Cronin, Dr. P. O. Ducasse, Professor Gerhard F. Hartmann, Professor Joseph E. Hazel, Dr. Yasuaki Ishiwada, Professor Roger L. Kaesler, Dr. Takahiro Kamiya, Dr. R. E. L. Schallreuter, Dr. I. Gregory Sohn, and Dr. Robin C. Whatley also gave us valuable advice and helped us in innumerable ways. We are deeply indebted to all of these people for their unstinting help and encouragement both during the symposium and in the editing of these proceedings.

Tetsuro HANAI,
Noriyuki IKEYA and
Kunihiro ISHIZAKI

List of Contributors

A

Abe, K., Tokyo, Japan 367, 919
Adamczak, F.J., Stockholm, Sweden 275
Athersuch, J., Sunbury, England, U.K. 1187
Ayress, M., Aberystwyth, Wales, U.K. 739

B

Babinot, J.F., Marseille, France 823
Bentley, C., Canberra, Australia 439
Bismuth, H., Tunis-Belvédère, Tunisia 1087, 1261
Bodergat, A.-M., Villeurbanne, France 413
Bonaduce, G., Naples, Italy 375, 449, 1087

C

Carbonel, P., Talence, France 341, 353, 1003
Chen, D.-Q., Nanjing, P.R. China 797
Choe, K.-L., Seoul Korea 121, 367
Christensen, O.B., Stavanger, Norway 1269
Colin, J.-P. Bégles, France 823
Cronin, T.M., Reston, Virginia, U.S.A. 39, 871, 927

D

Danielopol, D.L., Mondsee, Austria 375, 485
Dehler, D., Purchase, New York, U.S.A. 597
Denver, L.E., Lawrence, Kansas, U.S.A. 671
Dewey, C.P., Mississippi, U.S.A. 685
Dias-Brito, D., Rio de Janeiro, Brazil 467
Dingle, R.V., Cape Town, South Africa 841
Donze, P., Villeurbanne, France 1261
Droste, H.J., Amsterdam, Netherlands 721
Ducasse, P.O., Talence, France 939, 1003

F, G

Farmer, M., Talence, France 1003
Finger, K.L., LaHabra, California, U.S.A. 1101
Foster, D.W., Lawrence, Kansas, U.S.A. 207

Geiger, W., Mondsee, Austria 485
Gerry, E., Ramataviv, Israel 659
Gou, Y.-S. Nanjing, P.R. China 797
Gramm, M.N., Vladivostok, U.S.S.R. 159
Guan, S.-Z. Beijing, P.R. China 1147

H

Hanai, T., Tokyo, Japan 17
Hao, Y.-C., Beijing, P.R. China 1163
Hartmann, G.F., Hamburg, F.R.G. 699, 787
Hartmann-Schröder, G., Hamburg, F.R.G. 699
Hayashi, K., Tokyo, Japan 557
Hazel, J.E., Baton Rouge, Louisiana, U.S.A. 39
He, J.-D., Nanjing, P.R. China 1153
Hoibian, T., Talence, France 353
Honigstein, A., Tel-Aviv, Israel 659
Hoose, E.M., Purchase, New York, U.S.A. 597
Hou, Y.-T., Nanjing, P.R. China 235

I, J

Ikeya, N., Shizuoka, Japan 319, 413, 891

Jones, P.J., Canberra, Australia 259

K

Kaesler, R.L., Lawrence, Kansas, U.S.A. 207, 671
Kamiya, T., Kanazawa, Japan 303
Keen, M.C., Glasgow, Scotland, U.K. 967
Keyser, D.A., Hamburg, F.R.G. 177
Khalaf, S.K., Mosul, Iraq 1113
Khosla, S.C., Udaipur, India 93, 105
Kielbowicz, A.A., Florencio Varela, Argentina 1125
Kontrovitz, M., Monroe, Louisiana, U.S.A. 187
Kornicker, L.S., Washington, D.C., U.S.A. 243

Krstić, N., Beograd, Yugoslavia 1063

L

Lee, E.-H., Seoul, Korea 541
Lété, C., Talence, France 939, 1003
Li, Y.-G., Beijing, P.R. China 1173
Li, Y.-W., Chengdu, P.R. China 1245
Li, Z.-W., Gansu, P.R. China 1293
Lord, A.R., London, England, U.K. 63, 855
Lundin, R.F., Tempe, Arizona, U.S.A. 145, 1051

M

Maddocks, R.F., Houston, Texas, U.S.A. 219, 637
Malz, H., Frankfurt am Main, F.R.G. 57, 63, 75
Mascellaro, P., Naples, Italy 1087
Masoli, M., Trieste, Italy 449
Maybury, C., Aberystwyth, Wales, U.K., 569
McCalla, D., Purchase, New York, U.S.A. 597
McKenzie, K.G., Wagga Wagga, Australia 29
Moguilevsky, A., Aberystwyth, Wales, U.K. 293
Moura, J.A., Rio de Janeiro, Brazil 467, 1207
Myers, J.H., Monroe, Louisiana, U.S.A. 187

N

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Neale, J.W., Hull, England, U.K. 3, 81, 709
Nohara, T., Okinawa, Japan 429

O, P

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Paik, K.-H., Seoul, Korea 541
Peypouquet, J.-P., Talence, France 1003
Pugliese, N., Trieste, Italy 449

R

Reyment, R. A., Uppsala, Sweden 987
Rosenfeld, A., Jerusalem, Israel 659
Rousselle, L., Talence, France 939
Ruggieri, G., Palermo, Italy 1087
Russo, A., Modena, Italy 1087

S

Schallreuter, R.E.L., Hamburg, F.R.G. 1041
Scharf, B.W., Mainz, F.R.G. 501
Schmidt, N., Tucson, Arizona, U.S.A. 927
Schornikov, E.I., Vladivostok, U.S.S.R. 195, 951
Shi, C.-G., Nanjing, P.R. China 1293
Siddiqui, Q.A., Halifax, Canada 533
Singh, P., Dehra Dun, India 81, 619
Sohn, I.G., Washington, D.C., U.S.A. 243
Steineck, P.L., Purchase, New York, U.S.A. 597
Su, D.-Y., Beijing, P.R. China 1173
Swain, F.M., Newark, Delaware, U.S.A. 1153

T

Tabuki, R., Okinawa, Japan 429
Terrat, M.-N., Metz, France 485
Titterton, R., Gwynedd, Walse, U.K. 759
Tölderer-Farmer, M., Talence, France 341
Tsukagoshi, A., Shizuoka, Japan 891

U, V

Ueda, H., Shizuoka, Japan 319

Van Harten, D., Amsterdam, Netherlands 721
Van Nieuwenhuise, D.S., Tulsa, Oklahoma, U.S.A. 1153

W

Wang, P.-X., Shanghai, P.R. China 805
Watson, K., Aberystwyth, Wales, U.K. 399
Whatley, R.C., Aberystwyth, Wales, U.K. 293, 399, 569, 739, 759, 1021
Wilkinson, I.P., Keyworth, England, U.K. 1229
Würdig, N., Porto Alegre, Brazil 467

X, Y, Z

Xu, M.-Y. Xian, P.R. China 1283

Yajima, M., Tokyo, Japan 1073
Yang, F., Beijing, P.R. China 519
Ye, D.-Q., Daqing, P.R. China 1217

Zhang, L.-J., Shenyang, P.R. China 1173
Zhao, Y.-H., Nanjing, P.R. China 235
Zhao, Q.-H., Shanghai, P.R. China 805

Participants

A

Abe, K., Tokyo, Japan
Adachi, S., Tsukuba, Japan
Adamczak, F. J., Stockholm, Sweden
Al-Furaih, Ali A. F., Riyadh, Saudi Arabia
Athersuch, J., Sunbury, England, U.K.

B

Bentley, C. J., Canberra, Australia
Berdan, J. M., Washington, D.C., U.S.A.
Bismuth, H., Tunis-Belvédère, Tunisia
Bodergat, A.-M., Villeurbanne, France
Bonaduce, G., Naples, Italy

C

Chinzei, K., Kyoto, Japan
Choe, K.-L., Seoul, Korea
Christensen, O. B., Stavanger, Norway
Cohen, A. C., Los Angeles, U.S.A.
Colin, J.-P., Bégles, France
Colizza, E., Trieste, Italy
Copeland, M. J., Ottawa, Canada
Cronin, T. M., Reston, Virginia, U.S.A.

D

De Deckker, P., Clayton, Australia
Dias-Brito, D., Riode Janeiro, Brazil
Dingle, R. V., Cape Town, South Africa

F, G

Frydl, P. M., Calgary, Canada

Gou, Y.-S., Nanjing, P.R. China
Groos-Uffenorde, H., Göttingen, F.R.G.

H

Hall, S.J., Sydney, Australia
Han, D.-X., Beijing, P.R. China
Hanai, T., Tokyo, Japan
Hao, Y.-C., Beijing, P.R. China
Hartmann, G. F., Hamburg, F.R.G.
Hatanaka, M., Tokyo, Japan
Hayami, I., Tokyo, Japan
Hayashi, K., Tokyo, Japan
Hazel, J.E., Baton Rouge, Louisiana, U.S.A.
Hiruta, S., Kushiro, Japan
Honigstein, A.C., Tel-Aviv, Israel
Hou, Y.-T., Nanjing, P.R. China

I

Ikeya, N., Shizuoka, Japan
Inoue, H., Tokyo, Japan
Ishizaki, K., Sendai, Japan
Iwasaki, Y., Kumamoto, Japan

K

Kaesler, R.L., Lawrence, Kansas, U.S.A.
Kamiya, T., Kanazawa, Japan
Keen, M.C., Glasgow, Scotland, U.K.
Keyser, D.A., Hamburg, F.R.G.
Khosla, S.C., Udaipur, India
Kitazato, H., Shizuoka, Japan
Kontorovitz, M., Monroe, Louisiana, U.S.A.
Koshikawa, K., Tokyo, Japan
Krstić, N., Beograd, Yugoslavia

L

Lee, E.-H., Seoul, Korea
Li, Y.-G., Beijing, P.R. China
Li, Y.-W., Chengdu, P.R. China
Lord, A.R., London, England, U.K.
Lundin, R.F., Tempe, Arizona, U.S.A.

M

Maddocks, R.F., Houston, Texas, U.S.A.

Malz, H., Frankfurt am Main, F.R.G.
Maybury, C.A., Aberystwyth, Wales, U.K.
Mckenzie, K.G., Wagga Wagga, Australia
Moriya, S., Tokyo, Japan
Moura, J.A., Rio de Janeiro, Brazil

N, O

Neale, J.W., Hull, England, U.K.
Nohara, T., Okinawa, Japan

Oertli, H. J., Pau, France
Oji, T., Tokyo, Japan
Okada, H., Shizuoka, Japan
Okubo, I., Okayama, Japan

P, R

Paik, K.-H., Seoul, Korea
Peypouquet, J.-P., Talence, France
Pugliese, N., Trieste, Italy

Reyment, R.A., Uppsala, Sweden
Rosenfeld, A., Jersalem, Israel

S

Sato, T., Tokyo, Japan
Schallreuter, R.E.L., Hamburg, F.R.G.
Scharf, B.W., Mainz, F.R.G.
Schmidt, N.J., Tucson, Arizona, U.S.A.
Schweitzer, P.N., Woods Hole, U.S.A.
Shi, C.-G., Nanjing, P.R. China
Siddiqui, Q.A., Halifax, Canada
Singh, P., Dehra Dun, India
Siveter, D.J., Leicester, England, U.K.
Sohn, I.G., Washington, D.C., U.S.A.
Steineck, P.L., Purchase, New York, U.S.A.

T

Tabuki, R., Okinawa, Japan
Tambareau, Y.J., Toulouse, France
Titterton, R., Gwynedd, Wales, U.K.
Tohbaru, M., Okinawa, Japan
Tsukagoshi, A., Shizuoka, Japan

U, V

Ueda, H., Shizuoka, Japan
Van Harten, D., Amsterdam, Netherlands
Van Nieuwenhuise, D.S., Tulsa, Oklahoma, U.S.A.

W

Wang, P.-X., Shanghai, P.R. China
Watson, K.A., Aberystwyth, Wales, U.K.
Weitschat, W.U., Hamburg, F.R.G.
Whatley, R.C., Aberystwyth, Wales, U.K.
Wilkinson, I.P., Keyworth, England, U.K.

X, Y

Xu, M.-Y., Xian, P.R. China

Yajiam, M., Tokyo, Japan
Yamaguchi, T., Chiba, Japan
Yang, F., Beijing, P.R. China
Ye, D.-Q., Daqing, P.R. China

Non-Attending Members

Al-Abdul-Razzaq, S.K., Kuwait, Kuwait
Blom, W., Sydney, Australia
Carbonel, P., Talence, France
Carbonnel, G., Villeurbanne, France
Danielopol, D.L., Mondsee, Austria
Decrouez, D., Geneva, Switzerland
Dewey, C.P., Mississippi, U.S.A.
Ducasse, P.O., Talence, France
Finger, K.L., La Habra, California, U.S.A.
Haskins, C.W., Gwynedd, Wales, U.K.
Ishiwada, Y., Tokyo, Japan
Jones, P.J., Canberra, Australia
Kielbowicz, A.A., Florencio Varela, Argentina

I

Addresses at the General Assembly

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Ostracoda—A Historical Perspective

John W. Neale
University of Hull, England

The Organising Committee of the Ninth International Symposium greatly honoured me by their kind invitation to give this Keynote Address. At the same time they presented me with a considerable problem. In his Keynote Lecture to the Eighth Symposium at Houston, Professor Kesling not only said most of what I wanted to say, but said it with considerable elegance and wit. In looking for a different approach I thought that it might be useful to consider our field of study in its historical context, and in so doing perhaps assist new workers entering the field by drawing attention to some of the more interesting and useful papers that can be read with profit. A necessarily brief review of this sort immediately introduces a great element of selectivity, some would say bias. Thus, at the outset, let me say that in the following remarks I shall make no reference to that large group of ostracods the Myodocopida nor to the eminent zoologists who worked on them. At the same time I am sure that colleagues working in the Palaeozoic will also feel that their special interests are under-represented. Nevertheless, I hope that at the end we shall have achieved a broad, and not too distorted, overview of where we and our subject stand as we start our more detailed deliberations.

In the current issue of 'Cypris' we are invited to contemplate a piece of Pueblo pottery dating back to about A.D. 1000–1150 in which the Mogollon people of New Mexico used what appear to be undoubted ostracods in one of their decorative designs. The figures have even been tentatively named as *Chlamydotheca* or *Megalocypris!* In 1746 Linnaeus described an ostracod but our starting point may be taken as 1753 when Mr. Henry Baker published his "Employment for the Microscope" as a supplement to his "Microscope Made Easy" of 1742. Here, 232 years ago, what appears to be a species of *Cypris* was both figured and described.

We may ponder that in that same year King George II sat on the throne of England and Sir Hans Sloane founded the British Museum. In Japan the Shogun Tokugawa Ieshige held sway, while in China the Manchu Dynasty was paramount with the Ch'ien Lung Reign of Kao Tsung. Louis XV occupied the throne of France, whilst in America a young English surveyor by name of George Washington was sent by the Governor of Virginia to Fort Le Boeuf to ask these same French to withdraw from Ohio.

Progress in the early days was slow and dominated by Taxonomy, that discipline which must precede all other work in the field of Natural History.

TAXONOMY

The start of Linnean taxonomy in our group may be taken as 1776 when the Danish worker Otto Friedrich Müller established the genus *Cypris*, to be followed by his *Cythere* in 1785. Appropriately enough in its bicentenary year, the latter is the subject of a paper to be given by Ikeya and

Malz later in this Symposium. The next significant date is 1806, ingrained in our minds from writing "Subclass Ostracoda Latreille 1806". Pierre André Latreille (1762–1833) was a Frenchman who was known to the early 19th Century as the "Prince of Entomology". Oertli (1983) tells the fascinating story of how Latreille was sentenced to deportation in 1795 after the French Revolution on account of his religious education. The discovery of a new species of beetle in his cell which was drawn to the attention of Bory de Saint-Vincent saved his life and thus kept his name perpetually before us. Another Frenchman, Anselme Gaetan Desmarest (1784–1838) has the honour of describing the first fossil ostracod, *Cypris faba,* collected from the Oligocene between Vichy and Cusset at La Balme d'Allier. He may justly be claimed as the "Father of Ostracod Micropalaeontology". Thereafter, progress in the field of both Recent and fossil taxonomy was swift. The early part of the nineteenth century was dominated by such figures as Strauss, Jurine, Roemer and Reuss, followed a little later by Cornuel and Bosquet to name but a few. In Britain it was fossil forms that first received monographic treatment, T.R.Jones' Cretaceous work of 1849 preceding Baird's Recent monograph by just one year. During the second half of the century, work on fossil ostracods continued with people like Chapman, Seguenza and Terquem, and Recent freshwater forms were well served by Moniez, Vavra and others. Work on Recent marine forms occupied a dominant position, however, and received attention from five of the best known ostracod workers. In Britain David Robertson (1806–1896), The Reverend A.M.Norman (1831–1918) and G.S.Brady (1832–1921) produced a whole series of papers and monographs which are familiar to most of us. In Norway G.O.Sars (1837–1927) working in Bergen established the categories "Myodocopa, Cladocopa, Podocopa and Platycopa" as early as 1866, while in Germany G.W.Müller is particularly remembered for his great work on the Gulf of Naples Fauna of 1894. The beginning of the twentieth century was marked by something of a pause until the late 1920's and 1930's saw a great expansion of interest as the pace of oil exploration quickened, with increasing attention paid to ostracods in America and Germany.

In the first half of this century one of the main pre-occupations was the recognition of the problem of juvenile moults and sexual dimorphism in taxonomy. By the mid-1950's the general awareness of this problem meant that it no longer dominated the thoughts of taxonomists to quite the same extent.

In the taxonomy of any group there is a primary analytical phase mainly concerned with the description of new species, followed by a phase of synthesis when the knowledge gained is collated and ordered in various ways. In ostracods the analytical phase has lasted well over 200 years and is still very much with us. We are still only at the outset of the phase of synthesis which will gather momentum in the coming years. At this stage it is useful to look more closely at taxonomy from the point of view of some of the problems involved.

In the establishment of any species there are three mandatory requirements namely 1, Illustration 2, Diagnosis and 3, Description (to some extent now becoming superfluous). To this one may add a fourth which is not mandatory but which is perhaps second only to illustration in usefulness, namely a discussion of affinities and differences. If we now look at problems which arise in taxonomy we may list them broadly under three headings.

Illustration

This has been the cause of numerous problems of interpretation. From earliest times until the present day illustration has been by means of shaded drawings and line diagrams, exclusively so until the beginning of this century. These have varied from the very good to the very bad. The "very bad", the cause of many of our problems, we need mention no further but superb examples of the shaded drawing at its best may be seen in Brady's "Challenger" Monograph of 1880 and Müller's "Gulf of Naples" Monograph of 1894 to name but two among many. This tradition is continued by a number of living workers at the present day and one may perhaps pay tribute here to the standard of line drawing set by C.W.Wagner in his 1957 work on the Pleistocene which has rarely been equalled for clarity in showing the essential internal features of the shell. The conventions employed in the shaded, three-dimensional drawings are legion and would make an interesting thesis.

Optical photography came late on the scene and only really developed in the 1930's. Its basic drawback was the problem of overcoming the inherent incompatibility between resolution and depth of focus consequent on the material whose size falls just between the availability of two different photographic techniques. The one master in this field of optical photography was Eric Triebel (1894–1971) who worked in the Senckenberg Museum in Frankfurt. His daughter regularly demonstrated to visitors the ease and simplicity of the technique but few could equal the quality of his pictures. The literature contains many examples of papers published with illustrations so poor as to be completely useless.

This inter-regnum of some forty years ended with the development of the electron scanning microscope in the late 1960's. Peter Sylvester-Bradley (1913–1978) was the first to realise its full significance and potential and as a result founded the Stereo-Atlas of Ostracod Shells. This development of three-dimensional representation by means of stereo-pair photographs has revolutionised taxonomy. The fact that the photograph is often better and shows more than the actual specimen under the light microscope has cut down the need to visit collections or borrow specimens to a large extent. It has also rendered the need for pedestrian description in establishing taxa largely superfluous. Alas authors can still be badly served by the printer who has it in his power to ruin even the most perfect of original photographs. Generally, however, illustration is no longer a problem.

Variation, Moulting and Sex

The taxonomic problems caused by these have been noted already and other problems have now assumed a greater importance.

Present Problems

At the present day problems arise in three main areas. These may be listed as 1, Communication; 2, The Taxonomic Explosion and 3, Data Handling.

Communication

Rapid dissemination of information and results has always been an important requisite in Science, and even more so with the current spate of papers appearing daily. The solution to this has been two-fold. Firstly, with great prescience Harbans Puri, helped by Gioacchino Bonaduce arranged the First International Ostracod Symposium in Naples in 1963 attended by twenty-three ostracodologists. This provided a valuable forum for the interchange of ideas and a catalyst for work in this field. Many valuable taxonomic papers have resulted and one may instance the detailed analysis of the furcal attachment and its use in the taxonomy of freshwater ostracods by Dom Rome (1893–1974) presented to the Second Symposium held in Hull in 1967. These Symposia have proved their worth and have been held at intervals ever since, so that we now find ourselves attending the Ninth.

The Naples Symposium also set up the second branch of communication in establishing an ostracod newsletter "The Ostracodologist" which Ephraim Gerry produced single handed for nearly twenty years. Now that "The Ostracodologist" has evolved into "Cypris" it is fitting to pause and remember the very great debt that we owe to Ephraim Gerry's dedication.

The Taxonomic Explosion

In many ways this is the most worrying and intractable problem for new taxa have been appearing at an accelerating rate over the last twenty years. The task of keeping up with an ever increasing and widely spread literature is daunting. There are a number of ways in which some amelioration is possible and which help in the task of synthesis and simplification.

Keys

The production of a key to genera and species is one of the standard approaches of the biologist and can be strongly recommended as a discipline to clarify the mind for palaeontologists as well. The development of a good and usable key is a surprisingly difficult exercise. Personal experience of keys suggests that they often fail at the critical moment. It is no use referring to structures found only in males if you have no males among your specimens!

The Greater Use of Subgenus and Tribe

These can make an appreciable contribution to the simplification of what is rapidly becoming an unmanageable output of new names. They have been used to great effect by a number of our most active taxonomists and it is a source of concern that the current Treatise of Invertebrate Paleontology Committee has apparently decided that the Tribe, an accepted taxonomic category, shall not be used. It is to be hoped that the Committee will have second thoughts on this and leave such matters to the taxonomic judgement of the authors concerned.

Check Lists

The development of Check Lists over the last fifteen years has provided a most useful aid in coping with the enormous increase in taxonomic output. They cover many areas including South Africa (McKenzie, 1971), India and Ceylon (McKenzie, 1972), Japan (Hanai *et al.*, 1977), Australia and Papua (De Deckker and Jones, 1978) and South East Asia (Hanai, Ikeya and Yajima, 1980). Very much more than Check Lists, but of great value as such, are the detailed faunal studies of certain regions such as those of Hartmann (1962 and others) on the Chilean Coast, and the coasts of West Africa, Australia and elsewhere.

Taxonomic Handbooks

An important source of reference, these represent a synthesis of information as known at the time of publication. Modern works started essentially in 1952 with the ongoing Ellis and Messina "Catalogue of Ostracoda", Howe's "Handbook of Ostracod Taxonomy" (1955) and Grekoff's "Guide Pratique" (1956). Since then we have had Pokorný's Grundzüge der Zoologischen Micropaläontologie (1958), the Russian (1960) and Anglo–American (1961) Treatises, Van Morkhoven's two-volume work (1962/3) and Hartmann (1963, 1968). Since then the most significant work has been the Classification of Hartmann and Puri (1974). With the growth in taxa in the last twenty years a revised Treatise is long overdue. It will, however, need to be a very different work from its predecessors. An old drawing or figure of the holotype is no longer sufficient. A good S.E.M. photograph (preferably stereoscopic) is essential, and failing the holotype, figures of a lectotype or at very least topotype material of each genus is needed coupled with a unique diagnosis. A counsel of perfection would include also a note on affinities and differences and a key.

Data Handling

This has received increasing attention over the last ten years.

Data Bases

All taxonomists maintain some sort of data base. One of the earliest, most comprehensive and best known is that established by Henry van Wagenen Howe (1896–1973) at the Louisiana State University, Baton Rouge. In the past such data bases have tended to become so burdensome, or required such a disproportionate amount of time to maintain, as to leave little or no time for research. The advent of the easily available computer has altered all that and given exciting possibilities for the interchange of data on disc and tape as well as by print out. The Cologne Index of non-marine ostracods produced by Kempf in 1980 and now being expanded to include marine ostracods is a case in point. There is no doubt that this area will continue to develop and grow during the next few decades.

Computerised Recognition of Taxa.

A taxonomist's dream, this seems unlikely to be realised even though work on computerised recognition of pollen grains is well advanced in my own University. Ostracods would seem to present too many variables in the form of growth stages, sexual dimorphism and phenotypic variation to make such a development possible. History, however, has a long record of overturning statements such as this and in future such pessimistic views may well be proved wrong to our great and lasting benefit.

Taxonomy continues to be the basic foundation of ostracod studies. It took a century before a second strand became firmly established.

BIOSTRATIGRAPHY

Work on fossil ostracods gathered pace in the first half of the nineteenth century but their use in biostratigraphy was overshadowed by other groups. It is no surprise that their first useful application was in the non-marine Mesozoic rocks. The English Purbeck and Wealden deposits contain many biostratigraphically unrewarding materials such as plant remains, insects, dinosaur, turtle and crocodile bones and non-marine Mollusca, but ostracods (especially the genus *Cypridea*) often turn up in great abundance on the bedding planes. Recognition of their biostratigraphical value was due to Edward Forbes (1815–1854) although his views were expressed in only two short papers. It was left to T. Rupert Jones in the second half of the nineteenth century to augment Forbes' work and produce the zonal system, later refined by F.W.Anderson (1905–1982) and P.C. Sylvester-Bradley (1913–1978), which now forms the standard for correlation of these non-marine deposits throughout Western Europe. In the last thirty years similar work by Krommelbein (1920–1982) and others has provided a standard for South American and West African non-marine Mesozoic rocks.

Marine biostratigraphy, as distinct from description of faunas, has been largely a twentieth century phenomenon. Techniques are standard and results have been mixed. Many local schemes exist but ostracods are very dependent on their environment and wide-ranging zonal indices still elude us. Perhaps the most interesting development in this area has been the attempt by Sissingh (1976) to correlate late Tertiary deposits from different environments in the Mediterranean and Aegean areas. With this growth of taxonomic and biostratigraphical work there came a growing awareness of ecological controls and the development of work in this field which we may look look at next.

ECOLOGY

Ecology covers a wide range of topics. The early workers were well aware of the principal controls such as salinity and temperature although their primary concern was with taxonomy and related matters. Predation by ostracods was recognised as early as 1821 when Strauss described *Cypris* feeding on carrion. Over a century later this topic caused considerable interest when Deschiens, Lamy and Lamy (1953) described *Cypridopsis hartwigi* Müller from Africa feeding on the snails which form one of the vectors in the transmission of the disease bilharziasis. Unfortunately the value of this ostracod as a potential biological control has never been proved and even so its use would probably be impracticable.

Ostracods as victims of predators are much better known. At the turn of the century Scott was investigating the numbers and taxonomy of ostracods eaten by fish for the Fisheries Board of Scotland. They are also known to be eaten by a wide variety of other organisms such as ragworms, echinoids, gastropods and amphibians. There is even a record from the Trias of India of freshwater ostracods ingested, apparently accidently, by what is thought to have been a rhynchosaur whilst munching vegetation. It was Rees (1940), however, who demonstrated a relationship between the size of ostracod population, presence of ragworms, nature of the substrate and availability of food supply on a mud flat in the Severn Estuary and so linked together a number of different factors affecting the population. The varying distribution of juveniles and adults and of the different sexes has also elicited a considerable literature and the idea of seasonal migration was introduced by Tressler and Smith (1948).

Colour in ostracods is a neglected subject. H. Munro Fox, author of the standard work on colour in animals, only took up ostracod research in the last ten years of his life after retirement. During this period he made no particular contribution on colour in ostracods. Yet some freshwater species show brilliant purple and orange markings, or are suffused with deep green or sepia hues and patterns and the subject may be well worth exploring. *Strandesia sexpunctata* from South East Asia has three bright violet, perfectly circular spots on each valve which perhaps suggests the eyes of a much larger animal and thus acts as a defence mechanism to deter would be predators. Function in these matters, however, is always difficult to determine with any certainty. A whole range of other factors is relevant to ecological studies as an acquaintance with the literature will confirm. Ecological studies, as distinct from works containing ecological comments incidental to other studies, may perhaps be said to start with Elofson's study of the ostracods of the Skagerrak (1941) in which he gives information on temperature, salinity and substrate and makes some attempt to relate the nature of the shell form to the substrate. With the intervention of the war, ecological studies were slow to develop and the next major study was that by Swain on San Antonio Bay, Texas (1955) since when a whole range of studies in varying detail has covered many parts of the world.

PALAEOECOLOGY

With the interest and value of modern ecological studies firmly established, work on fossil faunas soon followed. As the modern starting point one may single out C.W. Wagner's work on the Quaternary of the Netherlands (1957). Here, by applying information gained from living representatives of the same taxa, he was able to reconstruct the old Pleistocene environments. Many palaeoecological studies have appeared since then, often concerned with particular aspects of the environment. Deductions regarding salinity have been based on extrapolation back from modern taxa or on associations, but one aspect of salinity studies deserves further mention. Salinity and its effect on the development of nodes on the shell (almost synonymous with studies on the genus *Cyprideis*) has produced a whole literature of its own as the arguments have raged between the proponents of genotypy, phenotypy, polyploidy and the like. From many papers one may single out for reference Sandberg's work on *Cyprideis* in the Americas (1964) and Kilenyi's paper dealing with transient and balanced genetic polymorphism as an explanation of variable noding (1972). Bibliographies in these papers will provide anyone interested with plenty of further reading.

Temperature has been covered many times in Quaternary and Tertiary studies but an interesting use of Uniformitarianism can take us as far back as the Cretaceous. There are no species in common with the present and few genera either, but the present day platycopids *Cytherella* and *Cytherel-*

loidea are well represented. Sohn (1962) showed that the genus *Cytherella* has a world-wide distribution at the present day whilst *Cytherelloidea* is confined to waters where the temperature never drops below approximately 11° C. This gives a useful means of making some judgement about temperature in Cretaceous and Jurassic times when these genera occur. Admittedly one makes the assumption that temperature constraints in these genera have not changed through time but there is a certain amount of contributory evidence to suggest this when the distribution of fossil *Cytherelloidea* is plotted with reference to the equator of Cretaceous times.

A more recent application of ostracods to the elucidation of temperature based on Uniformitarian principles is seen in Hazel's investigation of Pleistocene deposits in submarine canyons off the eastern coast of North America (1968). Here, by using the present temperature ranges and distributions of Recent species represented in the faunas, he was able to show that the Pleistocene faunas were comparable with those living at latitudes approximately 5° further north than today or, in other words, that the faunas in the canyons lived at water temperatures at least 5° colder than those found in the area at present.

Predation in the fossil record is not easy to ascertain. Animals that are eaten have an unfortunate habit of leaving no trace! Gastropods, however, eat their prey by boring a hole in the shell and removing the soft parts but leaving the shell intact. In a series of papers Reyment (1963 and others) demonstrated not only the preferred locus of attack but also that in the Nigerian Palaeogene the steep-sided, cylindrical holes made by the Family Muricidae could be differentiated from the dished conical holes surrounded by a frosted area due to scraping of the radula made by gastropods belonging in the Family Naticidae.

The late 1960's and early 1970's saw the development of three interesting ideas of great value in palaeoecological studies. In 1967 and again in 1971, Pokorný examined the theme of diversity and diversity indices. In a penetrating study of the value and limitations of this method and the Walton and Simpson Indices commonly used, he took as an example a study of two sections in the Upper Cretaceous of Bohemia. This enabled him to recognise regressions and transgressions and thus to compare two very different sections, the one located in the axial zone of sedimentation, the other in the shallow water zone far removed from it. In 1969, Kilenyi, working in the Thames Estuary, drew attention to the problem of differentiating biocoenosis and thanatocoenosis together with the problem of transported material. In 1971 he returned to this topic with the reconstruction of the biocoenosis, questions of population structure and constancy, the significance of valve — carapace ratio, and post-mortem transport of valves and carapaces amongst other matters. In the same year, Oertli (1971) covered aspects of burial, rate of sedimentation, the significance of separated valves compared with carapaces, colour and degree of pyritisation and the separation of juveniles and adults by current activity. These can all be used to give important insights into the nature of the environment affecting past communities. Study of the work of these three authors mentioned above is essential for any ostracodologist aspiring to work in this field.

PALAEOGEOGRAPHY, MIGRATION, DISTRIBUTION

With the basic techniques in palaeoecology established, other considerations came to the fore, among which were questions of distribution, migration and palaeogeography. Starting in 1967, McKenzie published a number of papers which examined the migration, distribution and implications of Tertiary ostracods in the Tethyan Region. In Western Europe a somewhat different approach was adopted by Keen (1977 and others) who was able to construct salinity profiles for the Tertiary deposits of the Hampshire Basin. His recognition of assemblage environments led on to a reconstruction of the palaeogeography of that area in early Tertiary times.

Meanwhile, in the area in which we are holding this Symposium, careful examination of a sequence of samples allowed Ishizaki (1977) to establish the existence back in the Upper Pliocene of the forerunner of the Kuroshio Current which today flows northwards between Taiwan and Okinawa to Kyushu.

Some of the most stimulating work of the last two decades has come from studies of the Cretaceous System. The non-marine rocks of the northern hemisphere have raised many problems, some of which are still far from solution. Particularly difficult has been the problem of dispersal of the non-marine ostracods (preponderantly *Cypridea*) between disjunct water bodies stretching from the western United States through Western Europe to China. General opinion suggests a movement from west to east with local modifications, but mechanism, direction and rate of dispersal still await a definitive solution. Recently Hou You-Tang (1979) has published an interesting paper showing that *Cristocypridea* in China migrated south-westwards as time progressed. The extinction of *Cypridea* and the rise and fall of related genera is another intriguing problem and the suggestions and ideas put forward by Colin and Danielopol (1979) are well worth reading. In the southern hemisphere Krommelbein (1962 and others) and others have shown that a parallel series of problems exists.

The marine Cretaceous rocks of the northern hemisphere are now well known and in 1973 Donze showed northward migrations from Tethys into the Paris Basin, Germany and Britain in the early part of Lower Cretaceous times. An explanation presents no problem in this case for the body of water is continuous and the cause is generally regarded as a combination of marine transgression and the warming up of the seas at this time. On the other hand the marine rocks of the southern hemisphere provide many difficulties in explaining the distribution and dispersal of the ostracod faunas. In the 1970's attention was focussed on the problems inherent in the Australian Upper Cretaceous where Neale (1976) recognised a mixture of cosmopolitan, austral and endemic genera. Explanations were put forward in terms of wind systems and ocean currents developed by the unique palaeogeography of that time. Further work led to papers by Tambareau (1982) and Dingle (1982) and it is pleasing to see that Professor Dingle is returning to that theme in a paper to be given to the present meeting.

Palaeozoic work has received too little attention in this address but many excellent studies outside the purely taxonomic and biostratigraphical field exist. Most of these studies use faunal distributions to establish the various environments and the work of Van Amerom *et al.* (1970) on the Carboniferous and Becker (1971) on the Devonian may be quoted as examples.

THE 1960'S AND 1970'S

By 1960 interest was widening and a number of studies appeared which covered new ground. The following examples will illustrate the general range and scope. In 1960, Reyment introduced mathematical concepts into the discrimination of species in what may be called mathematical taxonomy. It is fair to say that attitudes to this development have always been equivocal and it has always remained very much a minority interest. Among taxonomists there is a deep rooted feeling that the human brain is a much more sophisticated instrument in the discrimination of differences than any mathematical manipulation, notwithstanding the charge of subjectivity which may be levelled against it. On the other hand, mathematical/statistical treatment can be a great help in palaeoecological studies.

At about this time Sokal and Sneath were developing their work on biological statistics at the University of Kansas. The application of cluster analysis techniques, amongst others, to the field of ostracod studies enabled relationships to be discerned either between species occurrences or between faunas at different stations. The results, usually in the form of a dendrogram, gave a graphic display of the groupings and closeness or otherwise of the different associations. An excellent example, close to the location of our present meeting, can be seen in the work of Ishizaki (1968) on the faunas of Uranouchi Bay on the Pacific Coast of Shikoku.

In a different field, great progress has been made by means of the detailed study of various morphological features. Careful analysis of the evolution of the adductor muscle scar pattern in platycopids and cavellinids by Gramm (1967, 1968 and others) has led to enhanced knowledge of the relationships within these groups. Other workers have since studied other groups with similarly useful results regarding their evolution and relationships. Terrestrial ostracods are another subject in which considerable progress has been made recently. The first species belonging in this small and little known group was described by Harding (1953) and a further species from New Zealand was added by Chapman (1961). Starting in the late 1960's, studies by Schornikov (1969, 1980) have added greatly to our knowledge of the anatomy and life style of these unusual ostracods. Turning now to water chemistry, Delorme (1969 and others) sampled fresh waters for ostracods and measured various physico-chemical parameters on a 10 km grid pattern right across Canada. This formed the core of a substantial data base and his publications kindled interest in the effects of water chemistry on the shell and other aspects of ostracod life. More recently Peypouquet, Carbonel and De Heinzelin (1979), by using their knowledge of the effects of water chemistry on the shell, coupled with other features such as decalcification, pyritisation, presence of calcite and gypsum, diversity, noding, reticulation and shell thickness, were able to trace the history of the lacustrine environments in the East African Rift Valley from the Pliocene onward.

One of the best known innovations of the 1960's was the careful analysis of pitting and the introduction of pit notation first seen in the work of Liebau (1969, 1977 and others). This work has been followed up by other workers and proved valuable in elucidating the development of ornamentation and relationships between taxa. Closely related, and complementary to this, is the work on shell architecture developed by Benson (1970 and others). Linked originally with his important work on abyssal ostracods of the psychrosphere, it developed into a much wider context and there must be few ostracod workers who are unaware of his publications or his well known figure of the "Mechanical *Aurila*". Finally in this section one must mention the resurgence of interest in the ultrastructure of the carapace helped by modern technology and seen in the work of Jorgensen (1970), Bate and East (1972) and Depêche (1974).

THE LAST TEN YEARS

Leaving aside the "mainstream" branches of ostracod study, the last ten years have witnessed various innovative studies of which only a very limited number can be quoted here.

In 1975 Peypouquet published the results of his study on the effects of the physico-chemical environment on the ostracod shell, and followed up this work in a series of subsequent papers (1977 and others). Amongst other things he showed that in *Krithe* and *Parakrithe* the relative size of the anterior vestibule and the ventral inner lamella is related to the O_2 concentration in the sea water. This has an important bearing on the role of the Krithidae in determining the nature of the marine environment geologically and has been applied recently in a study of the Maastrichtian-Thanetian of Kef in N.E. Tunisia (Peypouquet, 1983). In 1977 Rosenfeld and Vesper discovered that the shape of the normal pore canals in *Cyprideis* reflected the salinity of the waters in which they lived. In low salinities a high proportion of round pores was developed whilst with increasing salinity the proportion of elongate and irregular pores increased. This phenomenon was used to make salinity assessments in a number of deposits ranging as far back as the Miocene and looks a promising technique for determining the salinity in those fossil sediments which contain *Cyprideis*. The chemistry of the shell has proved another fertile field for investigation. Anne Marie Bodergat has shown how ostracods can be utilised to determine pollution (1978a) and how the chemistry of the shell can be used to obtain information on the environment in which the animal lived (1978b, 1983). Chivas, De Deckker and Shelley (1983) have also investigated the possibility of using the chemistry of the shell to determine certain characteristics of the palaeoenvironment. Another aspect of recent work has been the examination of the form and function of the soft parts in Recent taxa as seen in the work on cerebral sensory organs and mechano-receptors by Andersson (1979) and Keyser (1981) respectively. This is complemented by the detailed analysis of the limb bristles (chaetotaxy) as an aid to clarifying phylogenetic relationships initiated by Danielopol in the 1970's and seen today in studies such as those of Broodbakker and Danielopol (1982). Similarly detailed work has been carried out by Okada (1982) in his investigations of the correlation between epidermal cells and cuticular reticulation, and the structure of pores with setae by means of ultrathin sections. It is but a short step from these three Recent studies to the Cambrian ostracods with beautifully preserved appendages described by Müller (1979 and others) in some of the most interesting and elegant work on ancient ostracods ever published.

Also in the Lower Palaeozoic rocks, Adamczak (1981) introduced his concept of a Bioturbation Index to give some assessment of animal activity in mixing up the substrate. This makes use of most unpromising material, intractable rocks in which ostracods can only be examined in thin section. The proportion of valves orientated at angles of more than 45° to the horizontal in the sample is used as a measure of the bioturbation. Results obtained from the pilot study in the Silurian rocks of Gotland have been considered interesting and useful.

Experimental work in the laboratory has also had its practitioners and much more could be attempted in this field. As an example, attention may be drawn to the work of Sohn and Kornicker (1979) who were able to show that the eggs of freshwater ostracods could be subjected to low temperatures and pressures and still remain viable. This proved that they are capable of surviving transport by winds through the upper atmosphere and stratosphere although whether this is a significant means of dispersal remains uncertain. Finally in this field, Smith and Bate (1983) by the use of Ion Beam Etching techniques have been able to resolve a persistent problem connected with the ultrastructure of the shell.

Altogether these few examples serve to show that the present decade has been a stimulating one for ostracod studies but what of the future?

THE FUTURE

The future would seem to be very much a continuation of the past with work continuing under three main headings.

Continued "Servicing"

Under this heading come Symposia, Newsletters, Text-books, Treatises and Data Banks which will continue to provide the essential base for forward progress in the research field. It is certain, however, that increasing use will be made of word processors, interlinked computers and other modern aids which will greatly help the rapid dissemination of information.

Continuing "Standard" Studies

These will follow the mainstream or core branches of ostracod studies in taxonomy, biostratigraphy, palaeoecology and palaeogeography—again with increasing use and availability of modern aids and techniques such as scanning electron microscopes, freeze-dry techniques etc..

Fringe and Innovative Studies

Studies outside the categories above, often using "high tech." aids such as X-Ray Fluorescence, Microprobe, Ion Beam Etching etc., which require considerable capital funding. One of the interesting developments recently has been the hologram—the production of a three dimensional image on an almost flat surface. One wonders if we may yet see a "Hologram Atlas of Ostracod Shells"!

I hope that these few thoughts may have been of some help in placing where we stand today in historical perspective. Crystal gazing is all very well but firm facts are much better. With a large and varied Symposium Programme in front of us I am sure that in five days time we shall have a much clearer idea of what the future may hold.

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A Taxonomist's View on Classification

TETSURO HANAI
University of Tokyo, Japan

The effect of language barriers on scientific communication often seems unthinkably fatal. However, the scanning electron microscope provided us with clear three-dimensional photographs of very high magnification with unusually deep focal depth, and gave ostracod workers a trustworthy means of communication. Since the proposal for a new paleontography by the late Professor Peter C. Sylvester-Bradley, descriptions of ostracods have been rejuvenated. This has had a profound effect in surmounting communication barriers. The *Stereo-Atlas*, as noted by Sylvester-Bradley (1973: 2), is a "combination of illustration and an internationally agreed nomenclature [that] breaks every language barrier". Numerous data are now being stored in our memory at an ever increasing rate of accumulation. As Sylvester-Bradley (1973: 3) correctly pointed out, an attempt at a new way of describing ostracods, as distinct from their interpretation, has undoubtedly been successful due to the exploitation of the scanning electron microscope.

However, when we proceed to look at the description of ostracods in terms of their classification, that is, when the morphology of ostracods is exposed to scientific analysis and interpretation, we face the problem of how to analyze and interpret the empirical findings of morphology. No matter how much information photomicrographs may supply, they themselves will not solve problems of classification.

At the time of Linnaeus, classification was a means to find the plan of creation by assigning the diversity of organisms to the natural system. Therefore, it has as its purpose the summarization and systematization of all knowledge regarding organisms. However, after Darwin's theory of evolution through natural selection found wide acceptance, the purpose of classification shifted from the discovery of the plan of creation to the presentation of the evolutionary relationships among organisms.

When we look at this change in terms of methodology, a far-reaching change seems to have taken place in the field of classification, *i.e.*, a change from the traditional methods strongly influenced by inductive argument which were prevalent at the time of Linnaeus to the hypothetico-deductive method that was unconsciously employed by Darwin (Gould, 1980: 97; Mayr, 1982: 29). Darwin wrote in his autobiography (Darwin, F., 1888: 83), "I worked on true Baconian principles, and without any theory collected facts on a wholesale scale." Thus, Darwin believed that he had followed inductive reasoning, but in actuality he collected facts relevant to his hypothesis of natural selection. Paraphrasing the words of Northrop (1947: 57), the natural history stage of scientific inquiry shifted into the stage of deductively formulated theory. The method of hypothesis formation is a deductive approach in which one invents hypotheses as tentative answers to a given problem and then subjects them to empirical testing (Hempel, 1966: 17). In either methodology, classification is not a purpose but a means. It is a means for drawing generalizations in the case of the narrow inductivist concept, and it is a means for presenting the tested hypothesis in the form of a classificatory hierarchy in the case of the hypothetico-deductive method.

Hempel (1966: 12, 13) explained that "empirical facts and findings ... can be qualified as logically relevant or irrelevant only in reference to a given hypothesis, but not in reference to a given problem." He further noted that "without such hypothesis, analysis and classification [for analysis] are blind." If one wants to clarify the relationship of a given taxon based on the method of hypothesis testing, the first thing one must do is to pinpoint the problem, *i.e.*, the relationships among a given group of organisms, and then give a tentative answer to that problem, *i.e.*, the hypothesis, and, further, subject it to empirical tests. In this case, classification is a poor, or at best, optimized presentation of the hypothetical proposition in a hierarchical manner, no matter what kind of relationships one may choose to study.

On the other hand, the observations and recordings of all the facts, and their analysis and classification, done so laboriously by inductivists, no longer had a purpose when the effort to discover the plan of creation ended in failure. However, the classification system that had become highly developed by the nineteenth century remained as a general frame of reference. As explained by Mayr (1972: 94), the system provides a sound foundation for all comparative studies in biology, and serve[s] as an efficient information storage and retrieval system. Thus it is somewhat similar to an information data base in a computer system. As has been noted by Mayr (1974: 96) and quoted elsewhere by many authors, classification is thus considered to be best, when it "allow[s] the greatest number of conclusions and predictions" following the concept of the best possible classification by Mill (1874: 466, 467). Thus, the status of classification has turned out to be a product of scientific systematization.

Before going into the discussion on scientific systematization, the relationship between classification and classificatory theories will be considered. Hempel (1965: 139) noted that the construction of a classification "may be considered as a special kind of scientific concept formation" in which classificatory theories have played an important role. Indeed, the relationship between the formation of classification and the formation of underlying theory is quite similar to that of concept formation and theory formation. The classificatory procedure requires theories to provide criteria for distinguishing similarities and differences among the organisms under consideration, and the resulting classificatory schemes differ according to their classificatory theories. Therefore, the classes thus formed are considered by Hempel to be an extension of the corresponding classificatory concept.

Early biological classifications were based directly on observed morphological characteristics, and each class was grouped through a procedure of comparative anatomy. After Darwin, however, classification came to rest on a far more theoretical basis, that is, on a phylogenetic and genetic basis. We have observed, for example, a change from the concept held by Linnaeus, which was strongly influenced by Aristotle's work, to the species concepts advanced by Dobzhansky (1937: 321), Mayr (1942: 120), Simpson (1961: 153), and others, being defined in phylogenetic and/or genetic terms.

The change to the new species concept is effective not only at the species level of classification, but also influences higher categories of classification, because the secondary effects of speciation persist even after populations reach species level. In either case, morphological and other characteristics become simply the observational criteria for the assignment of individuals to a classificatory category systematized according to phylogenetic, genetic and other theories. Thus it seems to me that biological classification is not constructed to test phylogenetic and genetic theories, but is, on the contrary, constructed based on these theories.

In general, the differences between the theories underlying classification are reflected in the differences in the nomenclature of the classes. In the case of biological classification, however, binominal nomenclature, for example, has long been in use since Linnaeus in spite of the radical change in theories behind classification. This is perhaps because we have treated "objective existence in nature as 'carving nature at the joints,' " to use Hempel's phrase (1965: 147). However, a profound change seems to have occurred in the meanings implied by binomials and this is reflected in the diagnosis and description of organisms.

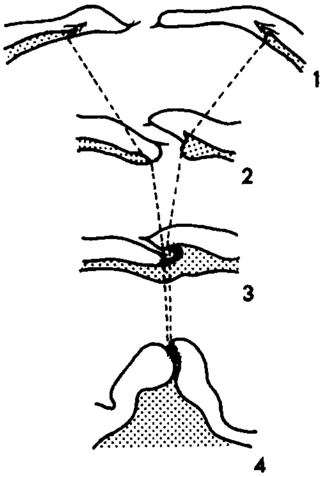
The characteristics chosen for diagnosis and description are those considered to be important for the particular theory behind a classification. The differences in classificatory theories issuing from the corresponding concepts give rise to differences in scientific vocabulary selected for description. As biological understanding of organisms advances, the shift from a predominantly descriptive to an increasingly theoretical emphasis is reflected in the replacement of the purely descriptive terms by terms of theoretical background, again as explained by Hempel (1965: 140).

To cite some examples from previous lectures presented at this ostracod symposium, Harding (1964: 1, 2), at the Neapolitan symposium emphasized the continuity of the ostracod carapace and pointed out that

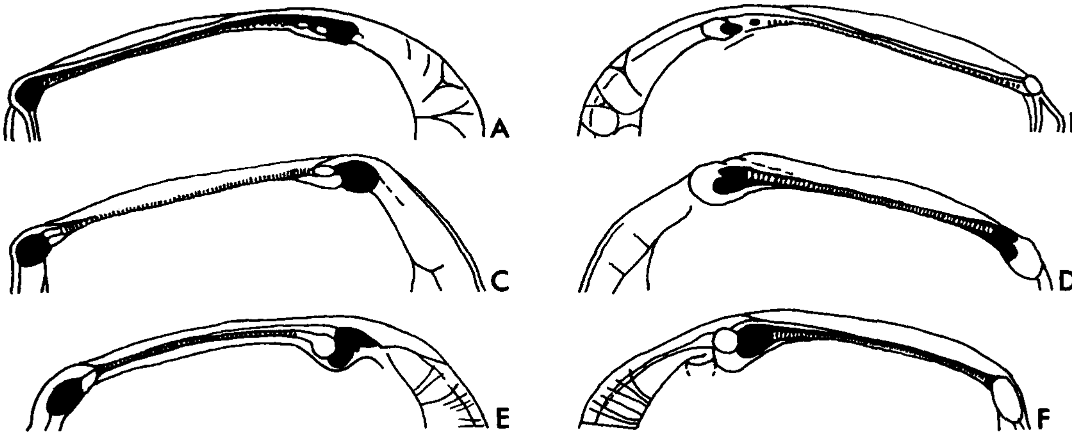
> the shell is not made up of two separately secreted entities, as is the shell of a bivalve mollusk . . . [but] the two calcified valves of an ostracod shell and the soft cuticle jointing them together are one continuous piece of cuticle . . . The cuticle forms one continuous sheet, soft in some places and hard in others according to the functional needs of the part concerned.

Thus the attached margin of the carapace is not considered to be the margin of the carapace, but to be the crease or joint along the median line of the carapace. Further, the ligament is elastic, but it does not take part in the opening force of the carapace.

At the Hull symposium, Kornicker (1969: 109) illustrated details of the calcified portion of the cuticle (Text-fig. 1). He traced the inner margin of the "duplicature" into the dorsal ligament. Thus, the structures of the free margin which is the exterior of the inner margin of the "duplicature" lost their homologous counterpart on the exterior surface of the dorsal ligament. This is perhaps because structures of the free margin of one valve converge on the anterior and posterior juncture of the attached margin and then probably continue to those of the opposite valve. Thus Kornicker's work gave strong support to Harding's idea that the ostracod shell is a calcified portion of one continuous piece of cuticle, and the ligament is a soft zone demanded by functional requirement.



TEXT-FIG. 1—Figures showing successive sections of the marginal area of the free margin (1–3) and the dorsal hinge area (4). When one traces the inner margin from the free margin towards the hinge area (broken line), the inner margin moves from the inside of the carapace to the outside of the carapace. Dotted area shows the part occupied by the animal body. Thus the hinge is divisible into exterior and interior portions with the ligament between. After Kornicker, 1969, modified.



TEXT-FIG. 2—Three types of hingement in terms of the upper and lower elements *i.e.*, exterior and interior portions. A,B. *Leptocythere pellucida* (Baird, 1850), left valve has a median groove termed the 'containant (Hanai, 1957, p. 432)' to receive the ridge of the right valve. The containant may well be an exterior element. C, D. *Pectocythere quadrangulata* Hanai, 1957, anterior and posterior tooth of the left valve is divided into upper and lower, *i.e.*, exterior and interior elements. Note that the median element of the left valve is a ridge and may well be an exterior element. E, F. *Hemicythere* sp., typical amphidont hingement for comparison.

The concept of distinguishing interior and exterior surfaces of the shell, derived from this one continuous sheet theory of the ostracod carapace, introduced a useful operational criterium to understand the arrangement and disposition of minor structures on the marginal area of the shell. The so-called "calcified portion of the inner lamella" or "duplicature" is not related to the inner lamella, but turns out to be actually an infold portion of the shell margin, and the zone of concrescence is considered to be the axial plane of the marginal folding along the free margin of the shell. Kornicker (1969:119) explained that the hinge structure may be exterior, interior or both and the concept of distinguishing interior and exterior hinge structures might prove useful for classification. The upper and lower subdivision of the hinge structure that was described without any knowledge of its biological significance by myself (1957: 473) thus has a solid theoretical basis may be called the exterior and interior elements, respectively (Text-fig. 2). Indeed, it is possible to offer a description of characters even if little or nothing is initially known about their biological function.

The single continuous sheet theory of the ostracod carapace covers wide explanatory and predictive areas. Explanation covers not only the structures from which the theory is derived, but also indirect phenomena of a different nature. Examples may include the dominantly intact whole carapace occurrences of the oldest group of ostracods, Bradorina. In general, the arrangement of normal pores over the ostracod carapace surface is concentric with one center.

To give an example, four types of normal pores are distinguishable on the carapace of *Cythere omotenipponica* (Text-fig. 3). The first type (Pl. 1, fig. 1) is distributed in the marginal area along the free margin. Seta is stout in its lower half, tapers rapidly and is easily twisted in its upper half, and terminates somewhat like a tube. The pore of this type of setae has irregular decoration around its opening. The second type (Pl. 1, fig. 2) is also distributed along the free margin, but is more or

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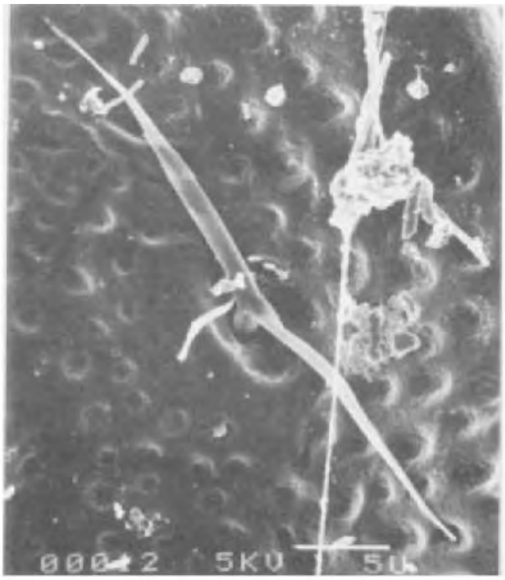
PLATE 1—Various kinds of trichoid sensillia which open on the outer surface of the ostracod carapace.
Figs. 1-5. *Cythere omotenipponica* Hanai, 1959.
Fig. 6. *Keijella bisanensis* (Okubo, 1972).
[Single and double scale bars indicate 5 microns and 0.5 microns respectively.]

1



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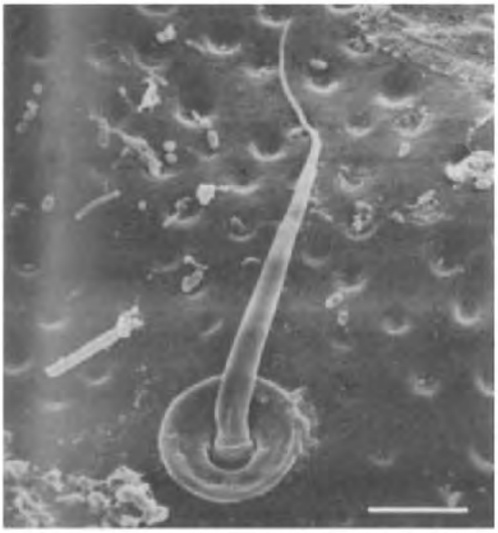

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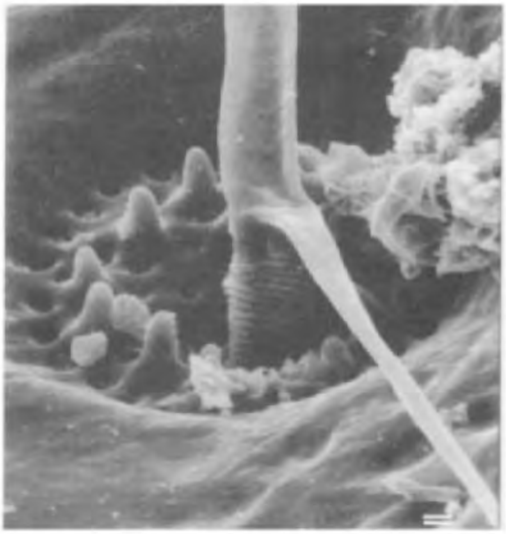

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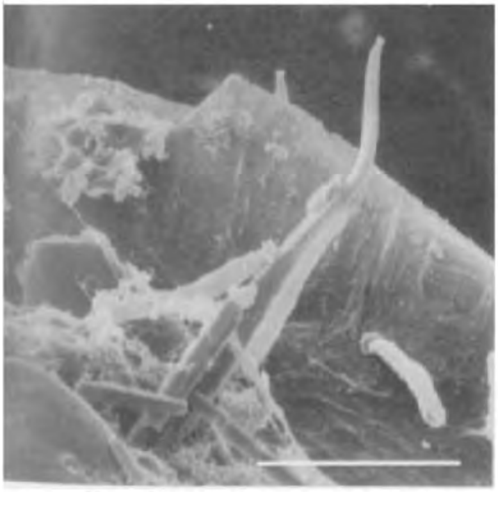

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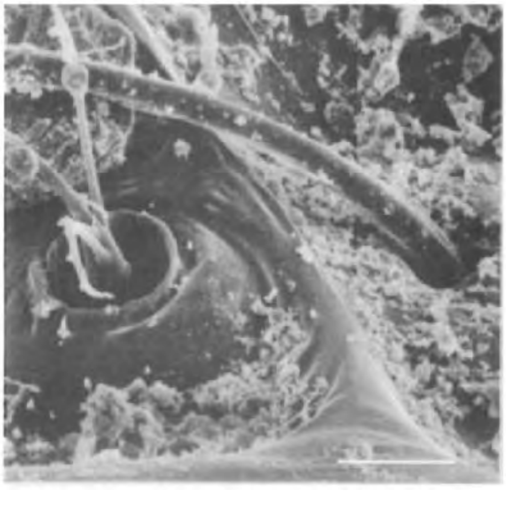

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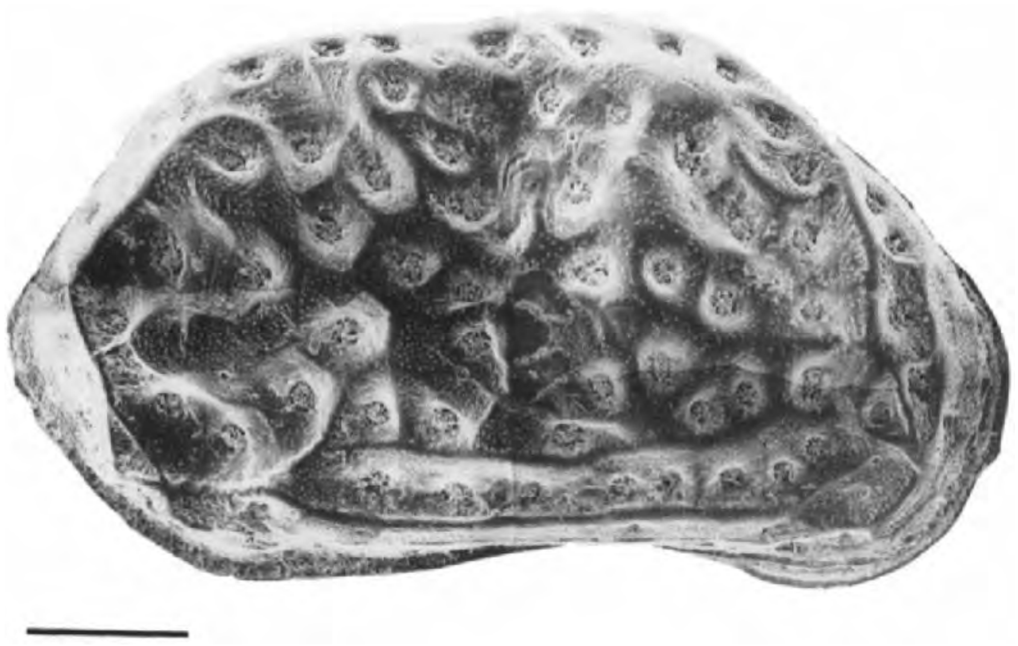
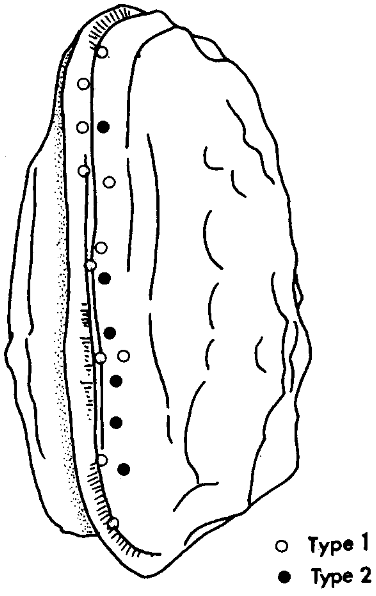


Text-Fig. 3—*Cythere omotenipponica* Hanai, 1959, lateral view. [scale bar indicates 100 microns.]



Text-Fig. 4—Distribution of trichoid sensillia along the ventral margin of *Cythere omotenipponica* Hanai, 1959. An example of type 1 is shown in Plate 1, fig. 1 and type 2 in Plate 1, fig. 2.

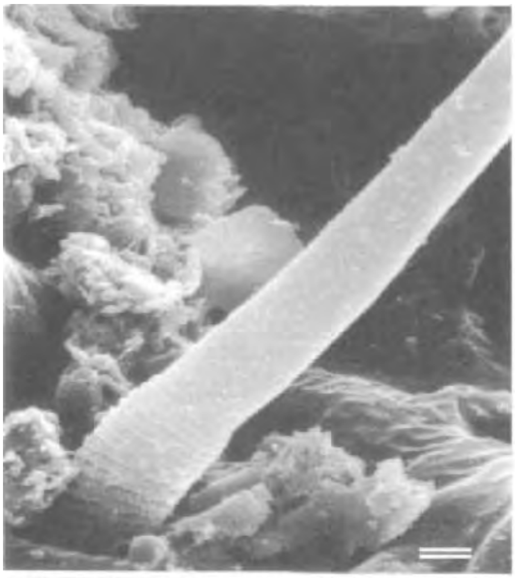
less inside the area of the zone of the first type (Text–fig. 4). Setae of this type bifurcate near their base, and have branches of similar size that extend widely apart parallel to the free margin. The branched setae taper gradually to a sharp point. Pores of this type are small and simple with no decoration. The third and fourth setal types are distributed widely in the central and dorsal area, except along the hinge margin, and correspond to the two types of setae or two types of pore canals that coexist on one carapace and have been described elsewhere. Type three (Pl. 1, fig. 3) is a long stout seta that tapers gradually and terminates with a pointed end. The associated pore has a wide and clearly rimmed lip. Pore canals of the fourth type correspond to sieve type pore canals. The fourth type of seta seems to include two forms. One is a stout seta without branches, and the other (Pl. 1, fig. 4) is a stout seta with one slender branch near its base. The setal pore of the former seems to occupy on margin of the sieve plate, whereas that of the latter emerges from the central area of the sieve. The nature of the stout seta of both forms seems similar to the first type of seta. Further, a homologous relationship of the structural elements of so-called normal pore canals and radial pore canals was predictable considering the concept of the marginal infold. This relationship was proved by Okada (1982: 254). Thus, the diversity of pore canal structures that has been encountered in relation to the position on the carapace are concordant with the continuous nature of the ostracod carapace across the hinge margin.

Description of setae and pore canals has for the most part been purely morphological. I recall a period just after the invention of the scanning electron microscope when many new terms were proposed to describe the minute details of the ostracod carapace without understanding anything of their biological significance. However, since these pores are sensillium, theorization to systematize these morphological characteristics as receptors may be desirable for utilization in a theory that impacts on the establishment of a biological classification. Since ostracods are marine crustacea, the most essential information may concern their physical environment *e.g.* nature of substratum, water movement, chemical nature of the water, and water temperature.

The presence of mechanoreceptive sensillia with two types of sensory setae (Pl. 1, fig. 6) has been known since the 1894 monograph by G.W. Müller. One is thick and long, and is interpreted as a receptor for direct touch by a solid object. The other is fine and short, and is sensitive to more delicate elements such as the movement of the surrounding water. This has been well established by Hartmann (1966: 113–117), Keyser (1983: 649–658), and Okada (1983: 640–648).

The presence of chemoreceptive sensillia has been doubted. However, Sandberg (1970: 120) illustrated the sensory seta of a sieve pore of "*Aurila*" *conradi floridana.* The seta is dendritic with a stout upright stem that terminates like a tube. *Cythere omotenipponica* also have setae (Pl. 1, fig. 5) that terminate somewhat like the trunk of an elephant, if, of course, we disregard size. Finally, in a current study Kamiya has found in *Loxoconcha japonica* an arm-like structure on the tip of the seta (Pl. 2, fig. 1, base; Pl. 2, fig. 2, tip). The general behavior of ostracods in response to the chemical nature of sea water, the dendrites with ciliary structure inside of the seta, together with the tube-like nature of the seta, make the presence of chemoreceptive sensillia on the carapace highly likely.

At the Saalfelden symposium, Rosenfeld and Vesper (1976) showed the relationship between the form of the sieve pore and the salt concentration in water. At the Houston symposium, the secretion or excretion of a certain hydrophobic substance was suggested as the function of sieve pores by Keyser (1983: 654). Yet, Müller's old hypothesis that the sieve pores may be a light sensory organ, as is suggested by the distribution of underlying pigment cells in *Loxoconcha stellifera*, still needs to be reckoned with, but at this time in relation to the possibility of their being a thermoreceptor. In *Loxoconcha japonica*, there are structures shaped like a bundle of test tubes, which open distally to form a sieve plate thrusting through the shell layer and inserting their blind proximal ends fairly deeply into the tormogen cell (Pl. 2, fig. 4). The proximal tips of the test-tube-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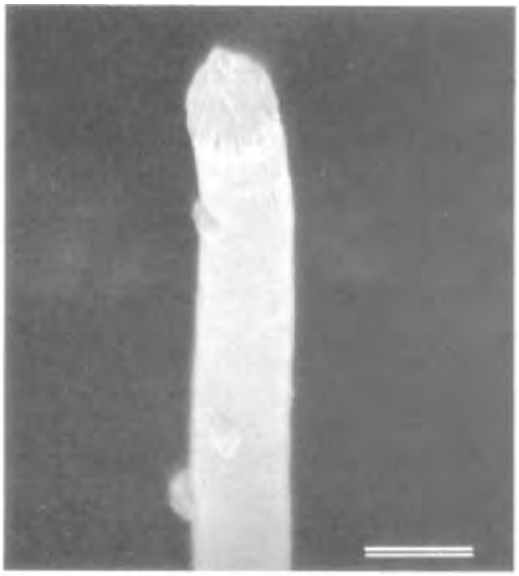
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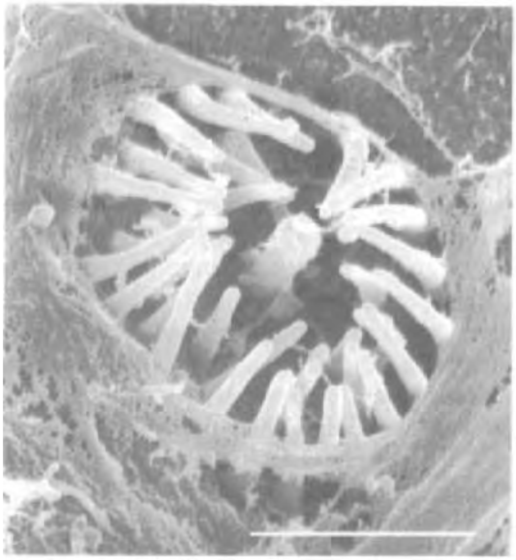
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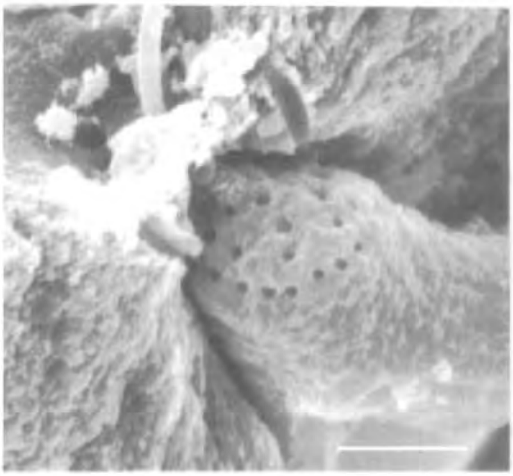
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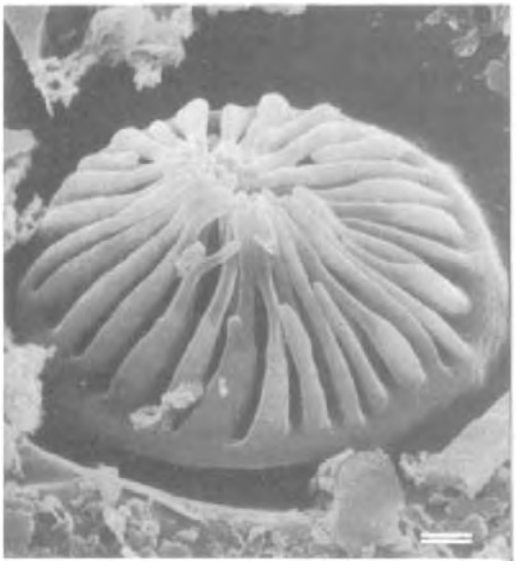
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like structures converge upon an area surrounding the core of the dendrites (Pl. 2, fig. 3). In 1982, my colleagues and I described a peculiar shaped pore (Pl. 2, figs. 5 and 6). We called this type of pore "Ben-type pore," because the general shape of the cap remined us of the device used to prevent the back flow of dirt in the hole of a Japanese-style water closet (*Benjo* in Japanese) in the Shinkansen bullet trains. It has been suggested that the purely morphological term "Ben-type pore" replaces the theoretical term "exocrine pore." However, such change of terminology requires great circumspection. Are there any other species that have exocrine pores or something similar to them? Why does the exocrine pore, which is supposed to have high inside pressure, need a cap with this peculiar structure which at a glance looks useful for protection against the back flow of dirt? These questions require explanation. The presence of a thermoreceptive cell associated with other receptors may be even still more undeniable in relation to the sieve pores. Water temperature is quite likely to be a vital environmental factor, especially for ostracods living in shallow water environments such as tide pools. Yet, in general terms, theorization of sensillia on the ostracod carapace and, hence, the simplification of vocabulary seems only to be a matter of time.

Hempel (1966: 94) notes that "scientific systematization requires the establishment of diverse connections, by laws or theoretical principles, between different aspects of the empirical world, which are characterized by scientific concepts." The examples given above are extremely minor in terms of the classification of the ostracods, yet they will have direct or often indirect but definite effects on the classification, because what we try to classify is not the very nature of ostracods, but the ostracods that one comprehends, and the theorization exemplified above has no doubt advanced the comprehension of ostracods. If one applies Hempel's view on the interrelationships between the scientific concepts and theoretical principles to the classification, then the more theoretical principles converge directly and indirectly upon the classification thus formed, and the stronger will be its systematizing role. Of course, simplicity in the sense of economy will be an important feature of the classification, when one deals with the same amount of information. Argument between classifications of different information content seems to me of little substance. It seems to me that many major and minor theoretical principles converge directly and indirectly upon the classification of the ostracods and operational criteria for classification have been modified. In this way the classification of ostracods has been advanced with growing knowledge on ostracods ever since *Monoclus* of Linnaeous.

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PLATE 2—Outside (Figs. 1, 2) and inside (Fig. 3) views of minute structures of the trichoid sensillia including tormogen cell (Fig. 4), and other types of pore openings on the ostracod carapace (Figs. 5, 6).

Figs. 1–4. *Loxoconcha japonica* Ishizaki, 1968.

Figs. 5,6. *Keijella bisanensis* (Okubo, 1975).

[Single and double scale bars indicate 5 microns and 0.5 microns respectively.]

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II

Taxonomy

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A Recent Dutch Microorganism (A. J. Keij), with the Description of *Jankeijcythere* New Genus (Crustacea, Ostracoda)

KENNETH G. MCKENZIE
Riverina-Murray Institute of Higher Education, Wagga Wagga, Australia

ABSTRACT

The major contributions of A.J. Keij to ostracod studies in the Recent of the Indowestpacific and in the Tertiary of Europe are outlined briefly. *Jankeijcythere* new genus (Podocopida, Cytheracea, Cytheridae) is described from the Indowestpacific with the type species *J. koenigswaldi* (Keij, 1954). Its distribution is given and some other species are listed. Ecological associations also are recorded.

INTRODUCTION

A.J. Keij, who retired early this year, holds a widely acknowledged and deserved place among the pioneers of modern ostracod studies. His major contributions have lain in the description of numerous taxa from the Indowestpacific; and also in the revision of classical work on the Eocene–Oligocene of Belgium and the Miocene of Aquitaine, France (Bosquet, 1852).

Keij was born on the 7th April 1927 and passed some years of his early life in Indonesia. In a letter to H.J. Oertli (dated December 1954) he refers to spending almost 3 years during the Second World War as an uninvited guest at an uncomfortable hospice in Java. He was to return to southeast Asia in 1957 as a fully professional oilfield micropalaeontologist.

Keij's doctoral thesis on the Eocene and Oligocene Ostracoda of Belgium (Keij, 1957) was part of a team effort by the Palaeontological Department of the Mineralogical Geological Institute of the State University of Utrecht, Netherlands. The project was supervised by Dr. (later Prof.) C.W. Drooger, and Keij's study was complemented by papers on the Eocene and Oligocene Foraminifera by Kaasschieter and Batjes respectively. While working on his thesis, Keij combined with these colleagues to record the Aquitanian–Burdigalian microfauna of southeastern France (Keij, in Drooger, Kaasschieter and Keij, 1955). This publication followed a gap of nearly 100 years in the study of Aquitaine Ostracoda (J. Moyes, letter dated July 1985).

The thesis was completed in late 1955 with Keij passing the examinations *cum laude.* By this time he was already married and a family man with 2 children. The next 18 months were spent working for the Bataafsche Petroleum Maatschappij (Royal Dutch/Shell Group), first at The Hague and then at Scheveningen, Netherlands, studying in particular the microfauna of the Liassic strata of the Avallon-Semur district in the eastern Paris Basin. Already his stratigraphical experience was considerable (Liassic–Recent) his expertise with Foraminifera as well as Ostracoda proven (Keij, in van Andel and Postma, 1954a), and he had published his first papers on Indowestpacific ostracods (Keij, 1953, 1954b). The outstanding Eocene–Oligocene monograph (Keij, 1957) appeared shortly before his transfer to Seria, Brunei.

At Seria, Keij worked for the Brunei Shell Petroleum Company Ltd., a Royal Dutch/Shell subsidiary. In spite of professional and family responsibilities (by mid-1959 there were 4 children), he kept in correspondence with ostracodologist colleagues, notably van den Bold and Oertli, and produced important papers on Indonesian *Cytherelloidea* and *Paijenborchella.*

In 1965, after 8 years in Brunei, A.J. Keij was posted to Nigeria (1965/1966) then returned to the Netherlands where he has spent the remainder of an active professional life and the address listed in his subsequent publications has remained 30 Klarinetstraat, Rijswijk (Z.H.).

TERTIARY OF EUROPE

Keij's famous monograph on the Eocene and Oligocene ostracods of Belgium had a profound impact on the study of Tertiary Ostracoda. It appeared the year after publication of H.J. Oertli's thesis on the Alpine Tertiary, another major and ground-breaking study (Oertli, 1956), yet Oertli himself was selflessly generous in praise writing:

> "Dear friend,
> Yesterday, I got a thick parcel, mailed by some A.J. Key. This person wants to make concurrence to G.W. Mueller 1894!?—Indeed, your wonderful monograph is the most complete published since the Neapel Ostracoda. And very well illustrated, the drawings are really outstanding. My compliments for these "fruits of hard work"!" (letter dated 2nd August 1957).

Although the impact for most ostracodologists was sudden, Oertli but also Triebel were already familiar with Keij's commitment to painstaking and detailed comparison between the materials disposed to him by the Drooger team, the Bosquet collections and exchange specimens. The result of much correspondence with Oertli was a joint paper (Oertli and Keij, 1955) the brevity of which prevents full appreciation of the close attention to detail, comparative specimens and experimentation with photography that engendered it.

The 1957 monograph is accepted universally as a major contribution to stratigraphy as well as ostracodology. The point is evident when we consider that the Belgian sections studied by Klie included the type localities for the Ypresian, Ledian and Wemmelian (= Bartonian) Stages of the Eocene; as well as the Tongrian and Rupelian Stages of the Oligocene. Remembering that Keij had already dealt with the type Aquitanian-Burdigalian (Miocene) sections from Aquitaine (Keij *op. cit.*, 1955) and that Table 6 of the 1957 monograph listed Bosquet's Miocene and Pliocene species—the latter including study of the Antwerp Crag—, it must have seemed to many an European Tertiary micropalaeontologist that Keij's stratigraphic authority was complete. As ostracod specialists, however, we are most grateful for his excellent taxonomy and, as Oertli recognised immediately, the outstanding illustrations-around 600 of them! The taxonomic details are that Keij referred to 62 genera of which 4 were new (a new subgenus, *Goerlichia*, was a junior synonym of *Neocyprideis* Apostolescu, 1957), and 168 species of which 42 species and 2 subspecies were new. In the following year (Keij, 1958) descriptions of a further two new Eocene genera appeared. In spite of much intensive effort, including training sessions with the old master, Erich Triebel, at Frankfurt, Keij never achieved very good photographic results, but his drawings are remarkably faithful to the taxa they represent. Just as G.W. Mueller set a standard for ostracod biologists in the Naples monograph, A.J. Keij set a standard in the Belgian monograph that any ostracod stratigrapher-palaeontologist would naturally aspire to emulate.

RECENT OF THE INDOWESTPACIFIC

Keij had important predecessors to his work on Indowestpacific Ostracoda. The Young Tertiary of Indonesia had been the thesis project of his countryman J. Th. Kingma (1948); and N. de B. Hornibrook (who also retires this year—as Director of the New Zealand Geological Survey) had provided another sound taxonomic basis via his monograph on the Tertiary and Recent marine Ostracoda of New Zealand (Hornibrook, 1952).

The originality of Keij's contribution to Indowestpacific studies can be gauged from reference to his first two papers (Keij 1953, 1954b). They include illustrations of the following characteristic regional genera: *Keijcyoidea* Malz, 1981 (Pl. 1, fig. 1, Keij, 1953), *Triebelina* Bold, 1946 (Pl. 1, figs. 4, 5, Keij, 1953), *Neomonoceratina* Kingma, 1948 (Pl. 1, fig. 11, Keij, 1953), *Rhombobythere* Schornikov, 1982 (Pl. 2, figs. 1, 2, Keij, 1953), *Hanaiceratina* McKenzie, 1974 (Pl. 2, figs. 4, 5, Keij, 1953), *Paijenborchella* Kingma, 1948 (Pl. 2, figs. 6, 7, Keij, 1953), *Bishopina* Bonaduce, Masoli and Pugliese, 1976 (Pl. 1, fig. 2, Keij, 1954); *Keijia* Teeter, 1975 (Pl. 1, fig. 3, Keij, 1954); *Morkhovenia* Teeter, 1975 (Pl. 1, fig. 4, Keij, 1954; *Phlyctenophora* Brady, 1880 (Pl. 1, fig. 6, Keij, 1954), *Hemicytheridea* Kingma, 1948 (Pl. 1, figs. 7–9, Keij, 1954); *Alocopocythere* Siddiqui, 1971 (Pl. 2, figs. 3–6, Keij, 1954); *Atjehella* Kingma, 1948 (Pl. 2, figs. 9, 10, Keij, 1954); *Gambiella* Witte, 1985 (Pl. 3, fig. 1, Keij, 1954); *Javanella* Kingma, 1948 (Pl. 3, fig. 9, Keij, 1954); and, finally, *Jankeijcythere* McKenzie, herein (Pl. 3, figs. 14–18, Keij, 1954). Keij's clear illustrations provide still useful data on its habitus for each genus cited.

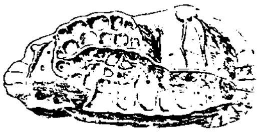
In subsequent papers he was to embellish considerably this excellent beginning with descriptions of the following new genera and subgenera; *Eopaijenborchella* (Keij, 1966); *Ornatoleberis* (Keij, 1975); and *Pterobairdia* (McKenzie and Keij, 1977). But the main contribution of the papers from this final period lies in the uniformly meticulous text, clear drawings and excellent SEM micrographs. For the latter, Keij consistently acknowledges his debt to H.J. Oertli who organised photography on the Elf/Aquitaine SEM at Pau, France. Thanks to these papers we have a good understanding of Indowestpacific species of *Triebelina* Bold, 1946 (Keij, 1974); *Saida* Hornibrook, 1952 (Keij, 1975); *Loxoconchella* Triebel, 1954 (Keij, 1978); *Baltraella* Pokorný, 1968 (Keij, 1979a); *Atjehella* Kingma, 1948 (Keij, 1979b); and the type species of Kingma's new Neogene Indonesian genera (Kingma, 1948) namely *Tanella*, *Hemicytheridea*, *Neomonoceratina* and *Paijenborchella* (Keij, 1979c).

OTHER CONTRIBUTIONS

Keij sustained his interest in other microfossils with several papers on calcareous *problematica* (Keij, 1969a, b, 1970); and he produced superbly illustrated papers on the striking bairdiid genus *Havanardia* Pokorný, 1968, describing 3 new species from the West African shelf (Keij, 1973), and on this genus and *Triebelina* (Keij, 1976).

SYSTEMATICS

Suborder PODOCOPINA Sars, 1866
Family CYTHERIDAE Baird, 1850
Subfamily PERISSOCYTHERIDEINAE van den Bold, 1963
Genus JANKEIJCYTHERE n.g.
(Plate 1)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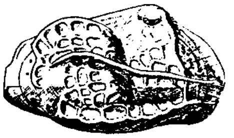
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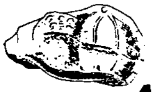
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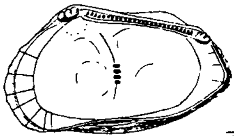
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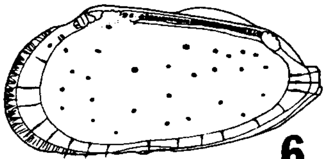
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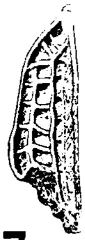
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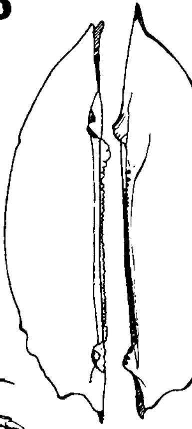
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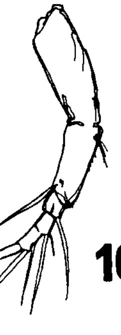
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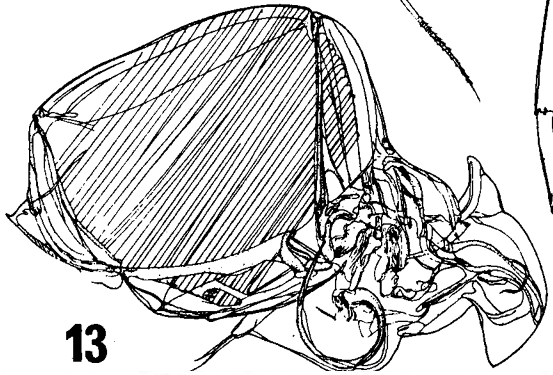
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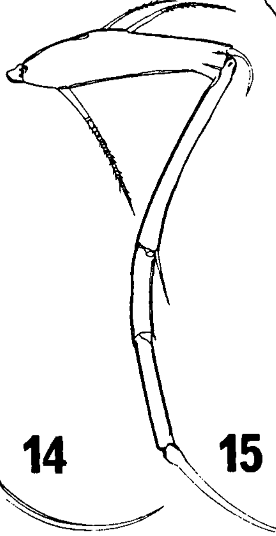
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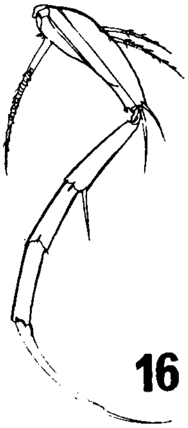
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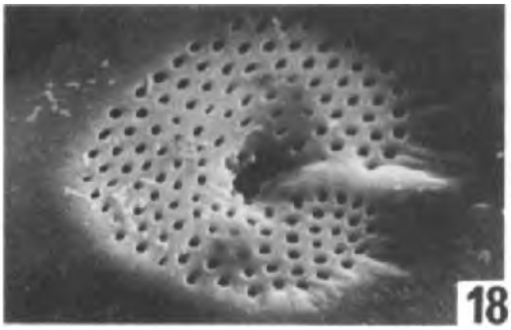
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Type species.—Jankeijcythere koenigswaldi (Keij, 1954)

Derivation of name.—For Dr. A.J. Keij, ostracode specialist.

Stratigraphic range.—Pliocene-Recent.

Geographical distribution (for the genus).—Mauritius; Malagasy(?); Indonesia; Philippines; Australia.

Remarks and Diagnosis.—As noted by McKenzie and Sudijono (1981) the species on which this new genus is based seems distinct from *Neomonoceratina* s.s. where Keij (1954) originally placed it; such distinctions were also remarked on by Keij in the original species description (Keij, 1954, p. 361) and amplified by Hartmann (1978, pp. 76–77, Figs. 75–84, Pl. 3, figs. 1–8).

Jankeijcythere is a perissocytherideine genus of the Cytheridae which is distinguished by a medium sized carapace with a well marked dorso-medial sulcus. The hinge is an antimerodont type comprising broad, crenulate terminal teeth in the RV, separated by a crenulate median furrow in which the anteriormost pits are deeper than the rest, and a more complex accommodating LV consisting of a small anterior tooth followed by a deep socket then by a crenulate median ridge in which the anteriormost elements are relatively prominent (especially the second) and ending in a deep terminal socket with a small post-like tooth at the bottom of its posterior corner. The surface is distinguished by a flexuous but narrow medial sagittal rib, with arcuate dorsal ridges on each compartment formed by the dorso-medial sulcus, a straight anterodorsal ridge and a ventral ridge. Other ornament consists of shallow reticules or minor transverse riblets; and the eye tubercle is prominent. The normal pore canals are sieve-type and large. Internally, the inner lamella is moderately broad and (as is usual in cytherids) it is traversed by a few straight marginal pore canals. There is no vestibule. The valve margins extend well beyond a distinct outer list, especially anteriorly. The central muscle scar complex comprises 4 small adductors plus a frontal scar. Sex dimorphism is distinct with females relatively shorter and higher than males.

The antennule is 6-segmented with the terminal segment longer than segments 3–5 combined. The antennal flagellum is 3-segmented, the last segment particularly long; as a whole the flagellum extends well beyond the terminal claws of the antenna. The mandibular epipod bears 2 long and 1 short Strahlen (ray-like setae). The maxillular epipod seems to lack any distinctly downwards-pointing Strahlen—a characteristic of Cytheridae as noted by Hartmann and Puri (1974, p. 25). The three walking legs increase in size from P1 to P3. Their bristle formulas are, respectively, 221/211/111 on the protopodite. The female body ends in a hairy lobe with a thorn-like terminal spine. The male hemipenis is large with a very prominent basal capsule and a complex headpiece; the copulatory tube is short and curved.

Comparisons.—Jankeijcythere can be removed from Paijenborchellinae Deroo, 1960 where it is usually placed on the grounds of its larger (0.6–0.7mm) size and different hingement (paijenborchellines have a schizodont type of hinge). Among perissocythereideines it seems closest to *Sulcostocythere* Benson and Maddocks, 1964 which has a similar size and hinge type to *Jankeijcythere.* But the shell ornament of *Sulcostocythere* is very distinct comprising an anchor-shaped ridge system of which the anterodorsal element (the hook of the anchor) does not occur in *Jankeijcythere.* The 'T'

PLATE 1—*Jankeijcythere koenigswaldi* (Keij, 1954).

Fig. 1. External lateral view, adult male RV. Fig. 2. External lateral view, adult female RV (holotype). Fig. 3. External lateral view, A-1 instar RV. Fig. 4. External lateral view, A-2 instar RV. Fig. 5. Internal lateral view, adult female RV (holotype). Fig. 6. Internal lateral view, adult male RV. Fig. 7. External ventral view, adult female RV (holotype). Fig. 8. External dorsal view, adult female RV (holotype). Fig. 9. Dorsal view, adult male. Fig. 10. Male antennule. Fig. 11. Male antenna. Fig. 12. Posterior female body. Fig. 13. Male hemipenis. Fig. 14. Male P3. Fig. 15. Male P2. Fig. 16. Male Pl. Fig. 17. External lateral view, female RV. Fig. 18. Sieve type normal pore, female RV. Magnifications: 1–5, 7 and 8 = ×53; 17 = ×91; 18 = × 1.9 k. 1–5, 7 and 8, after Keij (1954); 6, 9–16, after Hartmann (1978). Figs. 17, 18 are SEM micrographs of a specimen from Sahul Shelf.

of the anchor is curved both dorsally and ventrally, forming ridges, of which the posterodorsal ridge is more prominent than in *Jankeijcythere* while the posteroventral ridge does not occur in the new genus. A ventral ridge and the dorso-median sulcus are common to both taxa. Apart from its different ridge pattern *Sulcostocythere* is virtually smooth over most of its lateral surface except for a few indistinct transverse posterodorsal riblets (Benson and Maddocks, 1964, fig. 9, Pl. 3, figs. 1–10).

Once there are sufficient soft part descriptions available for comparison, *Sulcostocythere* and *Jankeijcythere* may well form a separate tribe within Perissocytherideinae.

When compared with the soft parts of *Paijenborchella* illustrated by Hanai (1970), those of *Jankeijcythere* seem quite different. For *Paijenborchella*, Hanai (*op. cit.*) illustrates a 5-segmented antennule with a terminal segment that is about as long as the penultimate segment. The antennal flagellum in *Paijenborchella* while 3-segmented is nowhere near as long as in *Jankeijcythere.* Hanai (*op. cit.*) only illustrates 2 long (but unequal) Strahlen on the mandibular epipod of *Paijenborchella*, perhaps a third, short, Strahl was obscured on his preparation. The maxillule seems rather similar in both taxa. The 3 walking legs have a different bristle formula, viz. 221/211/211 in *Paijenborchella*; and the male hemipenis has a larger coiled tube but a less complex headpiece in *Paijenborchella* than in *Jankeijcythere* (Hanai, 1970, Text-figs. 10–13).

Description.—Jankeijcythere koenigswaldi was sufficiently described and illustrated by Keij (1954) as amplified by Hartmann (1978); the former paper includes length/height measurements for a population of 70 detached valves (Keij, 1954, Fig. 1).

Location of types.—The primary types for *J. koenigswaldi* are in the collection of the Mineralogical Geological Institute of the State University of Utrecht; hypotypes are kept at the Zoological Museum and Institute, Hamburg (Hartmann, 1978, 1981), at the Geological Research and Development Centre, Bandung (McKenzie and Sudijono, 1981), and at the Geological and Mining Museum, Sydney (McKenzie and Pickett, 1984).

Distribution.—In Australia, *J. koenigswaldi* is known to occur along the northwest coast from Sahul Shelf and Derby to Carnarvon, Western Australia (Hartmann, 1978, McKenzie in preparation); around Lismore, New South Wales, where it is recorded as a Pleistocene fossil (McKenzie and Pickett, 1984); and near Gladstone, Queensland (Hartmann, 1981).

Apart from the several Australian localities, *J. koenigswaldi* occurs in Indonesia as a Pleistocene fossil at Sangiran, Java (McKenzie and Sudijono, 1981); and the type locality is Manila Bay, Philippines (Keij, 1954). It was not found in any of the SOPAC cruise samples available to the author from Fiji, Samoa, Tonga, Ontong-Java and Kula Gulf; nor does it occur in the author's collections from Saipan and Onotoa (McKenzie, 1986).

Other species.—There is at least one other definite species of *Jankeijcythere*, namely *J. bispinosa* (Brady, 1868) described originally from Mauritius. It differs from *J. koenigswaldi* in that, instead of shallow reticules, its surface is ornamented by minor transverse riblets. Types are kept in the Brady Collection, Hancock Museum, Newcastle-on-Tyne, England.

Maddocks (1966) assigned to *Sulcostocythere* two taxa from Nosy Bé, Malagasy, Species SA and SB, which clearly have a shallow reticulate ornament, at least in part. This would appear to remove them from *Sulcostocythere* s.s. and support their transfer to *Jankeijcythere* but the illustrations are not complete enough to justify this. Types are deposited in the Museum of Invertebrate Paleontology, University of Kansas.

Ecological associations.—The type species is known to be associated with shallow water sands and muds, sometimes carrying considerable shelly and organic detritus (Hartmann, 1978, 1981), including substrates with a volcanic provenance (Keij, 1954). Often, it occurs in the upper eulittoral among mangroves. The recorded water temperature range is 24.5–27.5° C.; dissolved O_2 between 8.4–10.09 ml/l; the salinity tolerance probably ranges from brackish (Keij, 1954) to slightly hypersaline (38.4‰); and the recorded pH from 7–7.5 (Hartmann, 1978, 1981). Keij (1954) records the faunal and microfaunal association as including numerous foraminifers—notably *Ammonia beccarii* (Linnaeus) and *Elphidium crispum* (Linnaeus)—other ostracods, many molluscs, abundant ambulacral ossicles of ophiuroids, some sponge spicules, anchors of holothurians, bryozoans, otoliths and fish teeth.

Brady (1868a) describes the Mauritius substrate simply as mud. He provided greater detail of the same location later (Brady, 1868b p. 82) noting that it was principally a carbonate mud, associated with abundant detritus of shells and corals, many fragments of the latter covered in green algae and with some local iron encrustation (possibly a type of beach rock); with terrestrial clay, quartz and black (volcanic) sand amounting to less than 10% of the substrate.

Maddocks (1966) gives the habitats of her Nosy Bé taxa, Species SA and SB, as intertidal mud among mangroves on estuarine banks and amongst intertidal quartz sand, with occasional specimens found in washings of algae, dead coral fragments, carbonate sands and sandy carbonate muds. The temperature range at Nosy Bé is about 24–28 °C, the tidal fluctuation rather large (4.44m maximum) with an average of 2.22m.

Summarising, *Jankeijcythere* may be regarded as a characteristic shallow water, intertidal, subtropical-tropical Indowestpacific ostracod genus, associated with carbonate muddy and sandy substrates characterised by abundant coralline and shelly detritus, and with affinities also for mangroves and volcanic sands/muds.

ACKNOWLEDGEMENTS

A.J. Keij (letters to H.J. Oertli dated July/August 1955) classified himself as a Recent Dutch microorganism, and as a Dutch variant of *Homo ostracodensis* characterised by eye tubercle present, with double lens! While deferring to his self-deprecating humour, I am sure that all colleagues who have corresponded with him scientifically would add an appreciation of his attention to detail and exactness which is the unfailing hallmark of his publications.

H.J. Oertli very kindly made available copies of his considerable correspondence with Keij when they were both doctoral students until they joined the petroleum industry (Oertli at Chambourcy, near Paris, Keij at The Hague), and of occasional subsequent letters to 1960. J. Moyes commented on the particular value for Aquitaine geologists of Keij's three main papers on the Tertiary of Europe. W.A. van den Bold donated the material from Seria, Brunei sent to him by Keij. G. Hartmann generously allowed reproduction of his soft parts drawings of *J. koenigswaldi* (Hartmann 1978, Figs. 75–84) for Plate 1.

Finally, I thank T. Hanai and the Organising Committee for the opportunity to present this tribute at the Shizuoka Symposium.

APPENDIX

Rijswijk, July 8

"Dear Ken,

I got your letter a few days ago. To prepare a list of my articles dealing with Indo-Pacific ostracods is easy, but I have no slide showing my frontal configuration. My youngest son tried to remedy this yesterday but I am not sure that the results will reach you in time.

My first encounter with ostracods was when I was grabled by Koos Kingma, who was then busy with his thesis on Indonesian ostracods, and declared his personal slave in between attending lectures and practical exercises. I had to pick, arrange species, etc. That was in 1948. Then, a long time, nothing. In 1953 I chose ostracods as my favourite group, contrary to the others who all went after the foraminifera. I taught myself the then existing systematics, using van den Bold's and Kingma's collections and Triebel's 'Zur Morphologie und Oekologie der fossilen Ostracoden', etc.

My thesis on Tertiary Belgian ostracodes was published in 1957; the same year I was transferred by Shell to Seria in Brunei (then British Borneo), where I stayed till 1965. During that period I fiddled around with *Distichoplax,* arenaceous foraminifera, etc., but also with South China Sea *Cytherelloidea* (1964) and *Paijenborchella* (1966). Illustrations were made during evening hours in the air-conditioned bedroom. One drawing per night (good old time)! The next assignment was Nigeria (1965/66) and then back to Holland.

Till '73 I played with problematical bryozoans (*Bicornifera, Encicellaria, Dicasignetella*) and questionable tintinnids (*Skylonia, Voorthuyseniella*). I drifted back to ostracods when searching Recent West African material (all homework, after office hours). I found *Havanardia* there. From then on it was ostracods again. During my period of Dutch publications I was generously assisted by Henri Oertli, who offered to produce electron micrographs of my species and did so very well (please mention this) . . . . . . A list of my few contributions to southeast Asian ostracods will be appended. Wish you all the best at the Congress.

Signed J.K."

Note: Keij's appended list of publications forms part of the bibliography of this paper.

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The North American Genus *Climacoidea* Puri, 1956, and the Tribe Campylocytherini (Neogene and Quaternary)

JOSEPH E. HAZEL AND THOMAS M. CRONIN
Louisiana State University, Baton Rouge, U.S.A. and
U.S. Geological Survey, Reston, U.S.A.

ABSTRACT

The genera *Reticulocythereis* Puri, 1960, and *Climacoidea* Puri, 1956, which occur in Pliocene to Holocene marine deposits of the Atlantic and Gulf Coastal Plain, have been examined and found to possess a vertical row of four adductor muscle scars and two frontal scars, a carapace that is subovate in lateral view and widest behind the middle, and an amphidont hinge having a conical anterior tooth in the right valve. These and other characteristics indicate placement in the North American ostracode tribe Campylocytherini. *Climacoidea* and *Reticulocythereis* differ from one another and from the campylocytherine genus *Proteoconcha* Plusquellec and Sandberg, 1969, only in details of carapace ornament. We propose that *Proteoconcha* and *Reticulocythereis* be relegated to subgenera of the genus *Climacoidea.* As do other genera of the tribe, species of *Climacoidea* inhabit inner sublittoral to brackish environments in mild-temperate to subtropical waters.

Two new species *C.* (*Reticulocythereis*) *foresteri,* and *C.* (*Reticulocythereis*) *reticulata* are diagnosed.

INTRODUCTION

The ostracode tribe Campylocytherini (Campylocytherinae; Trachyleberidae) is an endemic North American taxon whose species are common in Neogene and Quaternary marine deposits of the Atlantic and Gulf Coastal Plain physiographic province. Living species of this tribe inhabit inner sublittoral to brackish-water environments. None of its species are found north of Cape Cod, Massachusetts, which is the northern limit of the mild-temperate climatic zone; the known southern limits are the subtropical-tropical transition areas of the north coast of Puerto Rico and the north coast of the Yucatan Peninsula of Mexico and Central America. The campylocytherine genera are quite valuable in both paleoclimatological and paleobathymetrical studies along the Atlantic and Gulf coasts. The purpose of this paper is to clarify taxonomic relationships among the known campylocytherine genera vs. *Proteoconcha* Plusquellec and Sandberg, 1969, and two other proposed genera, *Reticulocythereis* Puri, 1960, and *Climacoidea* Puri, 1956, which upon examination also were found to belong to the Campylocytherini. *Climacoidea, Reticulocythereis,* and *Proteoconcha* possess similar muscle-scar patterns, hinges, shapes and marginal-pore patterns, and we relegate these genera to the status of subgenera of the genus *Climacoidea.* They are distinguished from one another primarily on the basis of surface ornament.

Previous Studies of *Reticulocythereis* and *Climacoidea*

Climacoidea was originally described by Puri (1956) from the Caloosahatchee Formation (upper Pliocene and lower Pleistocene) of southern Florida; *C. plueurata* Puri, 1956, is the type species by monotypy. Puri did not assign *Climacoidea* to any family, stating only that it differed from the genus *Hemicythere* in hinge and ornament. The muscle-scar pattern was described as "obscure." Howe and others (1961) placed *Climacoidea* in "family uncertain."

Swain (1955) described the species *Paracytheretta multicarinata* from San Antonio Bay, Texas, and later Puri (1958) assigned Swain's species to another cytherettine genus, *Protocytheretta*. Subsequently, Puri (1960) erected the genus *Reticulocythereis* for the morphologically similar species *R. floridana*. He characterized *Reticulocythereis* as being bean-shaped, oblong-ovate, and having a lateral surface with a reticulum, the ridges of which radiate from the center. He also stated that the hinge in the right valve has a bilobed anterior tooth and a trilobed posterior tooth. Neither Swain (1955) nor Puri (1960) described or illustrated the muscle-scar patterns of the two species.

King and Kornicker (1970), in an ecological study of ostracodes from Texas bays and lagoons, assigned *Paracytheretta multicarinata* to *Reticulocythereis* rather than to the Cytherettinae because the inner lamella is neither wide nor sinuous as it is in typical cytherettines and because *Reticulocythereis* possesses an eyespot. King and Kornicker also noted that *R. multicarinata* possesses a distinct alate extension, a feature we believe to have taxonomic significance at the subgeneric level.

Keyser (1975a) described *Reticulocythereis purii* from mangrove swamps of southwest Florida. Keyser (1975b, 1977, 1978) reported on specimens of *Reticulocythereis* from southwest Florida, which he assigned to *R. floridana* Puri, 1960. He commented on the similarities between *R. floridana* and *R. multicarinata* Swain, 1955, and called for detailed study of variation in surface ornament to determine the relationship between taxa.

Morphology of *Climacoidea*

Our morphological investigations, coupled with the work of Plusquellec and Sandberg (1969), show that *Climacoidea* Puri, 1956, *Reticulocythereis* Puri, 1960, and *Proteoconcha* Plusquellec and Sandberg, 1969, should be considered subgenera within the genus *Climacoidea* Puri, 1956, and the tribe Campylocytherini Puri, 1960. *Climacoidea* (*Proteoconcha*) possesses a smooth to variably pitted surface (in some species), *C.* (*Reticulocythereis*) has a regular surface reticulation and a posteroventral alar projection, and *C.* (*Climacoidea*) is characterized by extremely strong development of raised, curved carinae. *Climacoidea* differs from the other two campylocytherine genera *Campylocythere* Edwards, 1944, and *Acuticythereis* Edwards, 1944, in carapace shape, hinge, normal and radial pores, and details of the muscle scars.

We assign the following species to the three subgenera of *Climacoidea*:

- *C.* (*Reticulocythereis*)
  - *Reticulocythereis floridana* Puri, 1960
  - *Paracyheretta multicarinata* Swain, 1955
  - *C.* (*Reticulocythereis*) *foresteri* n. sp.
  - *C.* (*Reticulocythereis*) *reticulata* n. sp.
- *C.* (*Climacoidea*)
  - *Climacoidea plueurata* Puri, 1956
- *C.* (*Proteoconcha*)
  - *Basslerites giganticus* Edwards, 1944
  - *Acuticythereis multipunctata* Edwards, 1944
  - *Acuticythereis nelsonensis* Grossman, 1967 (= *Proteoconcha protea* Plusquellec and Sandberg, 1969)

Acuticythereis tuberculata Puri, 1960
Campylocythere concinnoidea Swain, 1955
Reticulocythereis purii Keyser, 1975 (?= *Acuticythereis tuberculata* Puri, 1960)
Cythere redbayensis Puri, 1954
Proteoconcha mimica Plusquellec and Sandberg, 1969
Proteoconcha edwardsi Plusquellec and Sandberg, 1969
Proteoconcha jamesensis Hazel, 1983
Proteoconcha costa Krutak, 1978

Females of *Climacoidea* (*Reticulocythereis*) are subovate in lateral view, whereas males are more elongate (Plates 1 and 3). In dorsal view, both sexes are widest behind the middle; females are wider than males. In contrast to species of *C.* (*Proteoconcha*) and *C.* (*Climacoidea*), species of *C.* (*Reticulocythereis*) are consistently ornamented by regular reticulation including longitudinal ridges in the dorsal half. A variably developed posteroventral alate projection, which consists of a subcircular flat region from which projects a small ala (Pl. 1, fig. 3; Pl. 3, figs. 2–6), this alar is also characteristic of the subgenus *C.* (*Reticulocythereis*). The widest part of the carapace is in region. Although several species of *C.* (*Proteoconcha*) sometimes have pitted surfaces (*C.* (*P.*) *nelsonensis*; *C.* (*P.*) *multipunctata*), this ornament is quite variable within a single population, and areas of the carapace are often smooth.

Males and females of *C.* (*Climacoidea*) are subovate to subquadrate in lateral view; males are not as high as females (Pl. 1, figs. 1, 4). The subquadrate shape results from the characteristically strong development of curved longitudinal carinae that overlap the valve margin. Some raised carinae parallel the valve margin; the most peripheral carinae project beyond the valve margin posteroventrally and posterodorsally. Between carinae, the surface is variably reticulate. The extreme development of the carinae is the major diagnostic feature that distinguishes *C.* (*Climacoidea*) from the other subgenera.

Climacoidea (*Proteoconcha*) was described and illustrated by Plusquellec and Sandberg (1969). Most species of this subgenus have a smooth valve surface; a few species have weak pitting. *Proteoconcha costa* Krutak has minute longitudinal riblets which parallel the valve margins and minute papillae as secondary ornament (Krutak, 1978). This subgenus lacks the strong reticulum and alate projection of *C.* (*Reticulocythereis*) and the raised carinae of *C.* (*Climacoidea*).

Plusquellec and Sandberg (1969) found that among the three campylocytherine genera that they studied, *Acuticythereis* has the most normal pore canals, *Campylocythere* has slightly fewer, and *Proteoconcha* has the least. We have found that *Climacoidea* (*Climacoidea*) and *C.* (*Reticulocythereis*) are similar to *C.* (*Proteoconcha*) in having relatively few normal pores, about 80 to 100.

The marginal areas of the three *Climacoidea* subgenera are very similar to one another, but differ significantly from those of *Campylocythere* and *Acuticythereis*. A shallow anterior vestibule, limited to the central and anteroventral parts of the inner lamella, is present in all three, in contrast to the very wide anterior vestibules in *Campylocythere* and *Acuticythereis*. In *Climacoidea*, anterior radial and false radial pore canals number about 15–25, are irregularly spaced, and vary in length. Conversely, *Acuticythereis* and *Campylocythere* have many more radial and false pore canals that are shorter and more regularly spaced (see Plusquellec and Sandberg, 1969, for details).

The close affinity of *Climacoidea* subgenera is well illustrated in the similarity in hinges (Pl. 5, this paper; Plusquellec and Sandberg, 1969). All possess an amphidont hinge, having a conical anterior tooth in the right valve sloping rapidly into a deep postjacent socket. The posterior tooth in the right valve of *C.* (*Reticulocythereis*) is more elongate than those in *C.* (*Climacoidea*) and *C.* (*Proteoconcha*). The median groove is crenulate in the vertical plane in all three subgenera. Although Puri (1956) described the anterior right valve tooth of *Climacoidea* as bilobed and the posterior tooth as trilobed, no specimens in our collections possess these features. The hinge of *Climacoidea* differs significantly from those of *Acuticythereis* and *Campylocythere*, which both have elongate anterior hinge elements and a much shallower, narrower groove in the right valve (see Plate 5, this paper; Plusquellec and Sandberg, 1969).

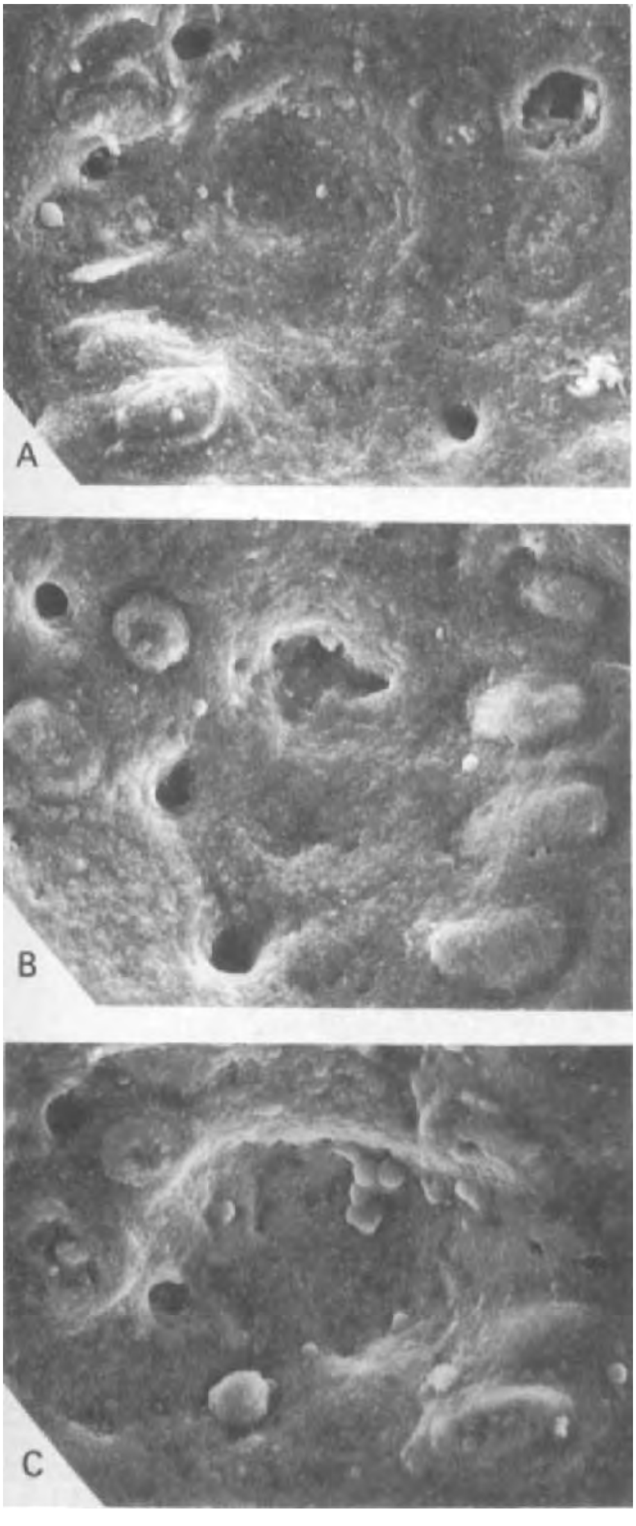
All three *Climacoidea* subgenera as well as *Acuticythereis* and *Campylocythere* have the same basic muscle-scar pattern, consisting of a near vertical row of four oval to slightly elongate adductor scars, and two frontal scars anterior to the adductors (Text-fig. 1). The dorsal frontal scar is round, the ventral is larger, elongated, and slightly incised in the middle. Plusquellec and Sandberg (1969) provided a detailed discussion of campylocytherine dorsal and mandibular muscle scars, which are generally very similar in *Acuticythereis*, *Campylocythere*, and *Climacoidea*. Dickau and Puri (1976) studied the soft parts of *Acuticythereis laevissima* Edwards, 1944, and found a five-jointed first antennae and chitinous supports in the knees of this species.

Note on *Campylocythereis* Omatsola, 1971

Omatsola (1971) proposed the genus *Campylocythereis* for Holocene species from the Niger Delta area of the West African coast and placed it in the Campylocytherinae because of its carapace shape, the stated similarity of the dorsal muscle scars to those of *Campylocythere* (both having divided dorsal muscle scars), and its compound normal pores. However, the value of dorsal muscle scars in classification is as yet untested. *Campylocythereis* does have a carapace shape similar to that seen in the Campylocytherini, particularly some *C.* (*Proteoconcha*). However, the frontal and adductor muscle scars, which are of known taxonomic value (Hazel, 1967; this paper), are unlike those of known Campylocytherini. Similarly, normal pores are considered by some authors to be important taxonomic characters for supergeneric categories, yet those of *Campylocythereis* are quite different from those of the campylocytherines. All campylocytherini have what Puri (1974) refers to as Type D normal pore configuration, described as sieve plates having a subcentral small pore and separate single pores that have a sensory hair (in living material). We are not sure where in Puri's classification of pore types those described by Omatsola for *Campylocythereis* can be classified, but they are not similar to those seen on our specimens of Campylocytherini, nor on those illustrated by Puri (1974). Moreover, *Campylocythereis* has a dorsal adductor scar that points towards the anterodorsal region, a much elongated and anteroventrally pointing dorsomedian scar, and two ventral adductors that "are in close contact with each other but sometimes show continuity" (Omatsola, 1971, p. 108). The frontal scars of *Campylocythereis* consist of one J-, U-, or heart-shaped scar, or a double or triple frontal scar (Omatsola, 1971). These muscle-scar patterns are quite distinct from the typical campylocythereine pattern, which, as mentioned above, consists of a near-vertical row of four undivided adductors and a double frontal scar (see our Text-fig. 1; Plusquellec and Sandberg, 1969). *Campylocythereis* has muscle scars that are very similar to genera of the largely Southern Hemisphere subfamily Rocaleberidinae Bertels, 1969. Compare, for example, the illustrations given by Omatsola (1971) with those given by Bertels (1969) for *Wichmanella* and *Neoveenia*. We believe *Campylocythereis* to be more closely related to the rocaleberidines than to the campylocytherines. Omatsola (1971), of course, did not have benefit of the normal pore data given in Puri (1974), nor had he seen Bertel's (1969) work.

Note on "*Acuticythereis*" *cocoaensis* Krutak, 1961

The range of the tribe Campylocytherini has been extended by some authors back to the Eocene because of the inclusion in the taxon of the late Eocene species *Acuticythereis cocoaensis* Krutak, 1961. This species, we believe, is referable to the Campylocytherinae but not to the campylocytherini. The presence of a dorsal muscle platform (see Krutak, 1961, Pl. 93, fig. 11) and the shape of the valves suggests closer affinity with Leguminocythereidini such as *Triginglymus* than with genera of the Campylocytherini. We therefore exclude it from the Campylocytherini.

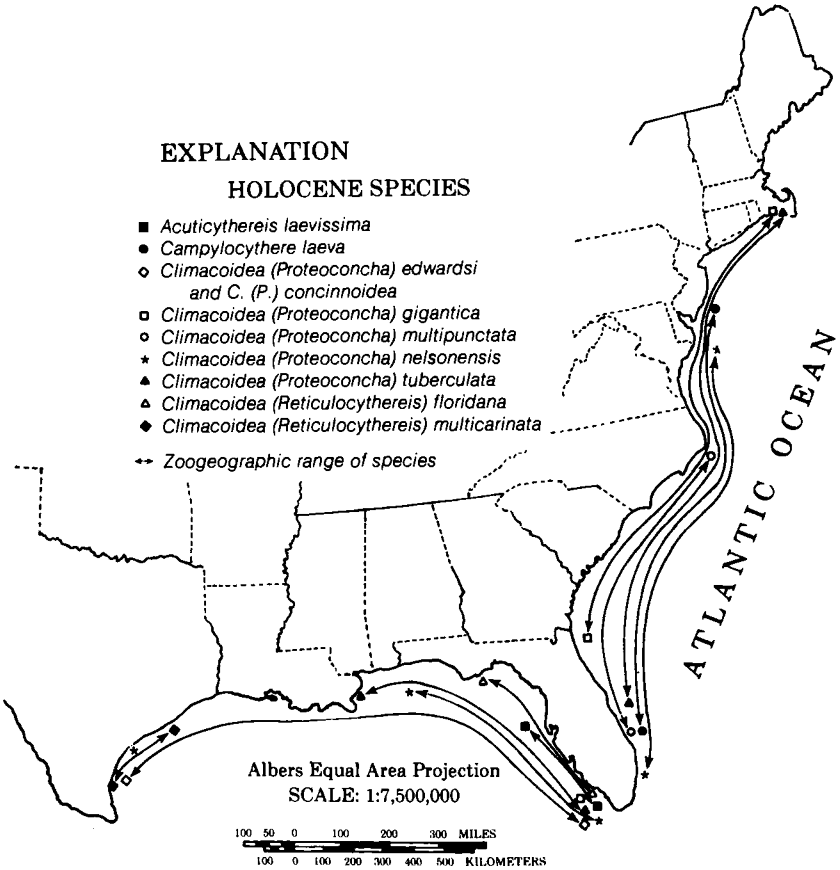


TEXT-FIG. 1—Campylocytherine muscle scars. A. *Climacoidea* (*Climacoidea*) *plueurata* Puri, 1956, muscle scars of male left valve, USNM 254586, × 925; B. *Climacoidea* (*Reticulocythereis*) *reticulata* n. sp., muscle scars of female right valve, USNM 254578, × 1000; C. *Climacoidea* (*Reticulocythereis*) *floridana* Puri, 1960, muscle scars of female right valve, USNM 254582, 5, × 900.

STRATIGRAPHIC DISTRIBUTION

The tribe Campylocytherini evolved during the latest early Miocene or earliest middle Miocene; the Miocene species *C.* (*Proteoconcha*) *redbayensis* (Puri, 1954), first appeared in the Chipola Formation of Florida. By the early Pliocene, at least eight species had evolved within the genera *Campylocythere*, *Acuticythereis*, and *Climacoidea* (*Proteoconcha*). The subgenus *C.* (*Reticulocythereis*) first appeared in Florida and Delaware during the Pleistocene. *C.* (*Climacoidea*) has been found in upper Pliocene deposits at Sarasota, Florida, and in Pleistocene deposits from elsewhere in southern Florida.

The stratigraphic distributions of species of *Acuticythereis*, *Campylocythere*, and *Climacoidea* (*Proteoconcha*) in some Atlantic and Gulf Coastal Plain deposits were given by Plusquellec and

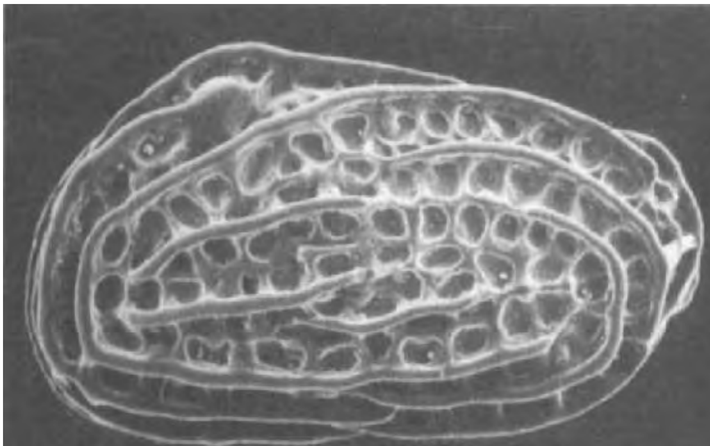


TEXT-FIG. 2—Holocene distribution of campylocytherines.

PLATE 1—Figs. 1, 4. *Climacoidea* (*Climacoidea*) *plueurata* Puri, 1956. 1. female left valve, lateral view USNM 254563, 5, ×135; 4. male carapace, dorsal view, USNM 254564, 5, ×140.

Figs. 2, 5. *Climacoidea* (*Reticulocythereis*) *reticulata* n. sp., Holotype, female left valve, lateral view, USNM 254572, 4, ×155; 5. male carapace, dorsal view, USNM 254573, 2, ×155.

Fig. 3. *Climacoidea* (*Reticulocythereis*) *foresteri* n. sp., Holotype, female left valve, lateral view, USNM 254583, 10, ×120.



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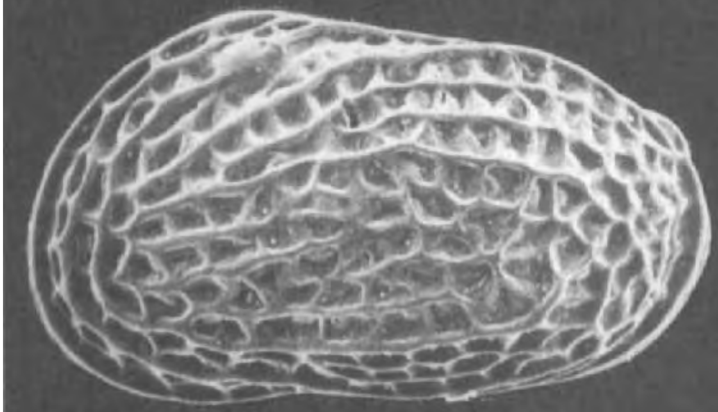

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Sandberg (1969); see also Hazel (1983). *Climacoidea* (*Climacoidea*) *plueurata* is known only as a fossil from upper Pliocene and Pleistocene deposits of Florida. *C.* (*Reticulocythereis*) *floridana* is the only species of the subgenus that has a known fossil record. It has been found in the Pleistocene of southern Florida, in upper Pleistocene deposits on the St. Mary's River on the Florida-Georgia border (Cronin, 1979), and in the Pleistocene of Delaware on the Delmarva Peninsula.

GEOGRAPHIC DISTRIBUTION AND HABITAT

Text-figure 2 summarizes the generalized Holocene zoogeographic distribution of campylocythereine species in the northern Gulf of Mexico and on the Atlantic Coast on the basis of our collections and published occurrence data. *C.* (*Reticulocythereis*) *foresteri* n. sp. is known only from waters of the Yucatan Peninsula, whereas *Acuticythereis laevissima* is known from the Gulf of Mexico off Florida and the north coast of Puerto Rico.

In terms of climate, the region between about Cape Cod, Massachusetts, and Cape Hatteras, North Carolina, is a mild-temperate climatic zone and constitutes the Virginian faunal province (Hazel, 1970). The region from Cape Hatteras to southern Florida contains assemblages of the Carolinian faunal province and has a subtropical climate. The northern Gulf of Mexico is also a subtropical climatic zone, although the ostracode assemblages from the Gulf are quite distinct from those of the southeastern Atlantic Coast (Cronin, 1979). Southern Florida and the northern coasts of the Greater Antilles are a transitional zone between the subtropics and tropics.

The campylocytherine zoogeographical data show several salient trends. *Campylocythere* is restricted to Atlantic Coast mild-temperate and subtropical regions; *Acuticythereis* is an inhabitant of subtropical (off western Florida) to subtropical-tropical transitional (off Puerto Rico) areas. All extant species of *Climacoidea* (*Proteoconcha*) inhabit inner sublittoral areas of the Atlantic and Gulf Continental shelf, except *C.* (*P.*) *edwardsi*, *C.* (*P.*) *costa* and *C.* (*P.*) *concinnoidea*, which are restricted to the Gulf of Mexico. The subgenus *Climacoidea* (*Proteoconcha*) is predominantly a subtropical taxon; *C.* (*P.*) *tuberculata*, *C.* (*P.*) *gigantica*, and *C.* (*P.*) *nelsonensis*, however, range into the mild-temperate Virginian faunal province. *Climacoidea* (*Reticulocythereis*) is today restricted to the Gulf of Mexico; its occurrence in Pleistocene deposits near the Florida-Georgia border and in Delaware suggests a faunal interchange during Pleistocene time (Cronin, 1979).

Campylocythere and *Acuticythereis* inhabit primarily inner continental shelf environments at depths less than about 40 m and in normal marine salinity (about 35–36 ppt (parts per thousand)). Most species of *C.* (*Proteoconcha*) also inhabit the inner continental shelf, although *C.* (*P.*) *nelsonensis*, *C.* (*P.*) *costa* and *C.* (*P.*) *concinnoidea* are most common in polyhaline environments having salinities of about 20–30 ppt (Grossman, 1967; Swain, 1955).

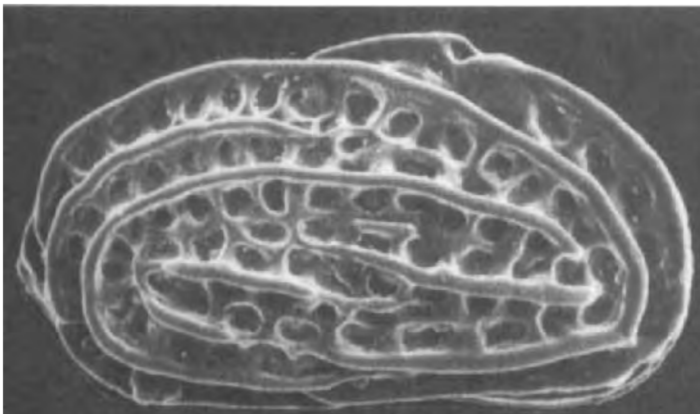
Although known only as a fossil, *Climacoidea* (*Climacoidea*) *plueurata* was considered characteristic of salinities greater than 30 ppt and depths less than 10 m by Puri and Vanstrum (1971).

In general, *C.* (*Reticulocythereis*) inhabits a wide range of nearshore marine environments. *C.* (*R.*) *multicarinata* is common in Texas bays and lagoons in water 0 to 1.5 m deep, having salinities of 11.3 to 50.0 ppt and temperatures 10.8° to 33.0°C (King and Kornicker, 1970). Our specimens of *C.* (*R.*) *foresteri* came from a shallow brackish lagoon on the coast of Yucatan. Puri (1960, p.

PLATE 2—Figs. 1, 4. *Climacoidea* (*Climacoidea*) *plueurata* Puri, 1956. 1. female right valve, lateral view, USNM 254565, 5, ×140; 4. female carapace, dorsal view, USNM 254566, 6, ×140.

Fig. 2. *Climacoidea* (*Reticulocythereis*) *reticulata* n. sp., female right valve, lateral view, USNM 254574, 4, ×155.

Figs. 3, 5. *Climacoidea* (*Reticulocythereis*) *floridana* Puri, 1960. 3. female carapace, right-lateral view, USNM 254579, 4, ×120; 5. female carapace, dorsal view, USNM 254575, 5, ×120.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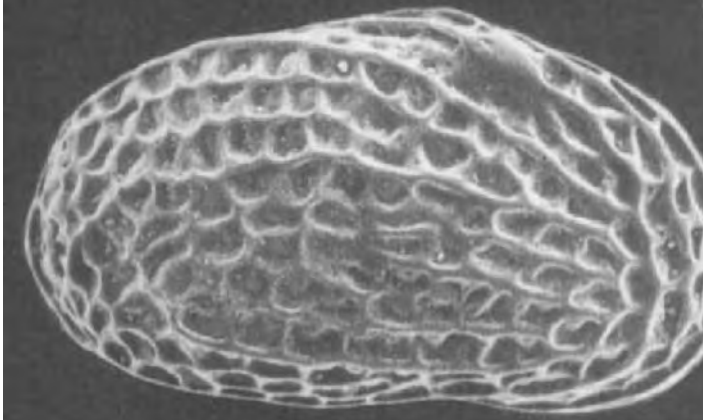
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108) described *C.* (*R.*) *floridana* from "shore sand near public beach," and Keyser (1975a, 1978) found this species on sandy substrata in mangrove swamps off southwestern Florida, in waters of 11 to 34 ppt salinity.

SYSTEMATIC PALEONTOLOGY

All measurements are in microns; L = length, H = height, W = width. All illustrated specimens have been deposited in the collections of the Department of Paleobiology, Smithsonian Institution, U. S. Museum of Natural History (USNM).

Subclass OSTRACODA Latreille, 1802
Order PODOCOPIDA Sars, 1865
Suborder PODOCOPINA Sars, 1865
Superfamily CYTHERACEA Baird, 1850
Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1968
Subfamily CAMPYLOCYTHERINAE Puri, 1960
Tribe CAMPYLOCYTHERINI Puri, 1960
Genus CLIMACOIDEA Puri, 1956

Type species.—*Climacoidea plueurata* Puri, 1960

Diagnosis.—Distinguished from other campylocytherine genera by its low number of normal pores, its lower number, uneven distribution, and relatively long length of radial and false radial pore canals, its small shallow anterior vestibule, its subovate to subquadrate shape, and its steep anterior conical tooth and deep round postjacent socket in right valve.

Remarks.—We include three subgenera in the genus *Climacoidea* Puri, 1956: *C.* (*Reticulocythereis*) Puri, 1960, characterized by its regular reticulation and posteroventral alate projection, *C.* (*Climacoidea*) Puri, 1956, characterized by its extremely well developed curved carinae, and *C.* (*Proteoconcha*) Plusquellec and Sandberg, 1969, characterized by its smooth to variably pitted valves.

Stratigraphic Range.—Lower?, middle Miocene to Holocene.

Subgenus CLIMACOIDEA (CLIMACOIDEA) Puri, 1956

Diagnosis.—Characterized by extremely well developed curved carinae, which parallel and in places overlap the valve margin. Carapace variably reticulated between carinae.

Remarks.—At present, *C.* (*Climacoidea*) *plueurata* Puri, 1956, is the only species known in this subgenus.

Stratigraphic Range.—Upper Pliocene to Pleistocene.

CLIMACOIDEA (CLIMACOIDEA) PLUEURATA Puri, 1956

(Pl. 1, figs. 1, 4; Pl. 2, figs. 1, 4; Pl. 3, fig. 1; Pl. 4, figs. 3, 4; Pl. 5, figs. 1, 2; Text = fig. 1 A)

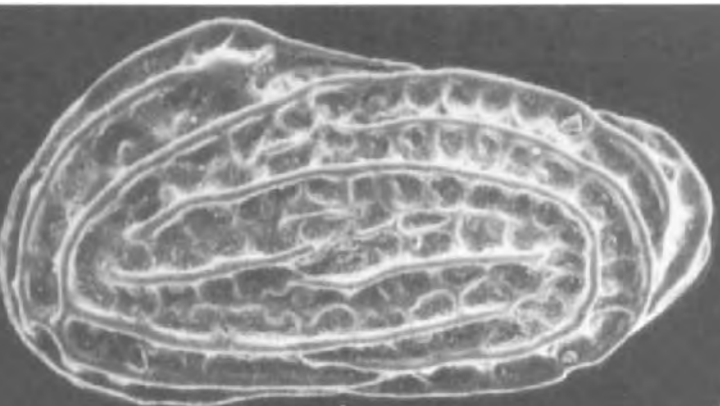
Climacoidea plueurata PURI, 1956, p. 275, 276, Pl. 36, figs. 5–12.
Climacoidea pleurata (sic) Puri. PURI AND VANSTRUM, 1971, p. 440, fig. 4.

PLATE 3—Fig. 1. *Climacoidea* (*Climacoidea*) *plueurata* Puri, 1956, male left valve, lateral view, USNM 254567, 4, ×150.

Fig. 2. *Climacoidea* (*Reticulocythereis*) *reticulata* n. sp., male left valve, lateral view, USNM 254576, 2, ×175.

Figs. 3, 5. *Climacoidea* (*Reticulocythereis*) *foresteri* n. sp. 3. male left valve, lateral view, USNM 254584, 10, ×120; 5. female carapace, dorsal view, USNM 254585, 10, ×110.

Figs. 4, 6. *Climacoidea* (*Reticulocythereis*) *floridana* Puri, 1960. 4. male carapace, left-lateral view, USNM 254580, 6, ×130; 6. male carapace, dorsal view, USNM 254580, 6, ×135.



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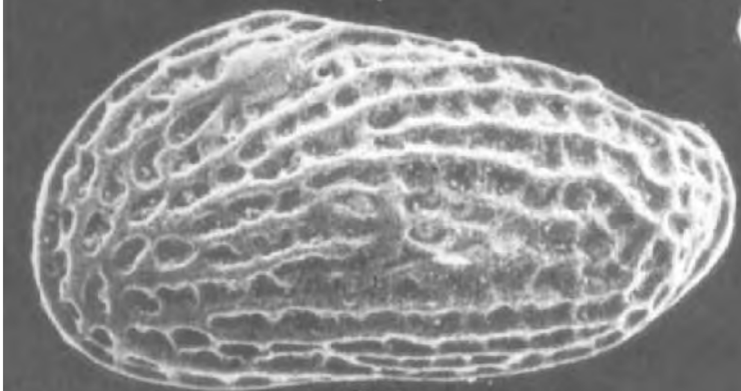

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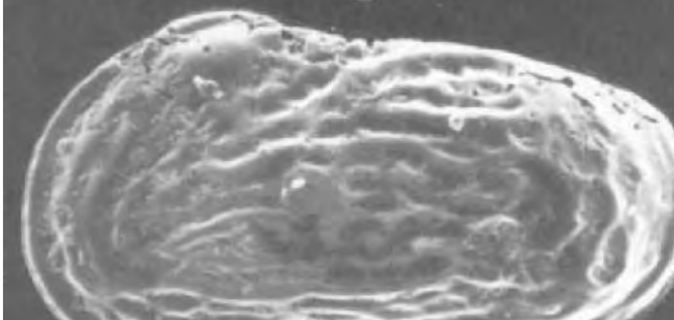

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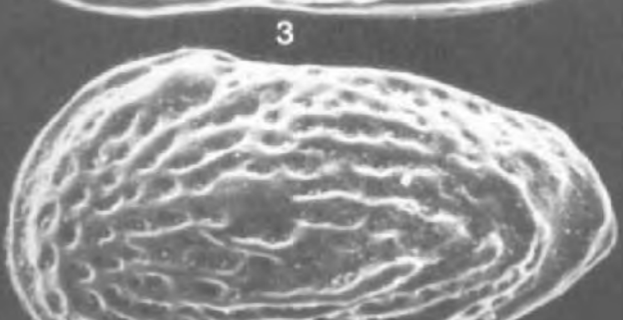

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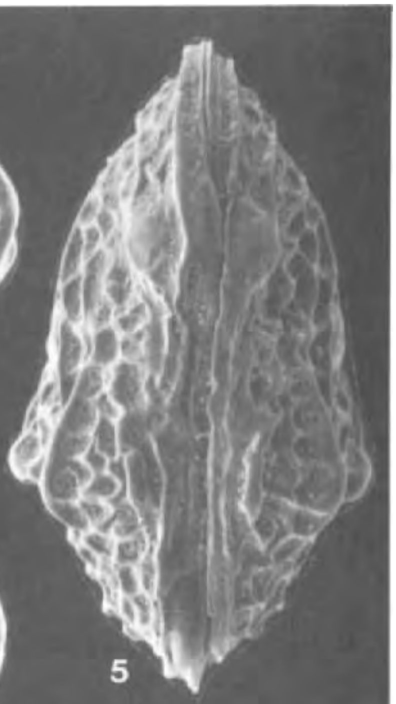

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Remarks.—The development of intercarinae reticulation varies in this species, but the regions between carinae are never smooth.

Stratigraphic Range.—Upper Pliocene to Pleistocene.

Occurrence.—Localities 1, 2, 3, 4, 5, 6A, 7, 8, 9, 11.

Dimensions.—USNM 254563, female left valve, L = 620, H = 370; USNM 254564, male carapace, L = 605, H = 340, W = 320; USNM 254565, female right valve, L = 600, H = 325; USNM 254566, female carapace, L = 630, H = 375; USNM 254567, male left valve, L = 605, H = 335; USNM 254568, male left valve, L = 590, H = 335; USNM 254569, female right valve, L = 630, H = 345; USNM 254570, male right valve, L = 625, H = 320; USNM 254586, male left valve, L = 585, H = 350.

Subgenus CLIMACOIDEA (PROTEOCONCHA) Plusquellec and Sandberg, 1969

Type Species.—*Proteoconcha proteus* Plusquellec and Sandberg, 1969 (= *Acuticythereis nelsonensis* Grossman, 1967)

Diagnosis.—Characterized by smooth to variably pitted surface; pitting of some species varies among and within single populations.

Remarks.—*C.* (*Proteoconcha*) *nelsonensis* Grossman, 1967, and *C.* (*P.*) *multipunctata* (Edwards, 1944) have pitted valves; other species are smooth. Species of *C.* (*Proteoconcha*) can be distinguished from one another primarily on the basis of carapace shape and the number and arrangement of anterior radial and false radial pore canals (Plusquellec and Sandberg, 1969).

Stratigraphic Range.—Lower?, middle Miocene to Holocene.

Subgenus CLIMACOIDEA (RETICULOCYTHEREIS) Puri, 1960

Type Species.—*Reticulocythereis floridana* Puri, 1960

Diagnosis.—Characterized by regular subquadrate to polygonal reticulation over entire carapace, arranged longitudinally dorsally; it possesses a variably developed posteroventral alate projection.

Remarks.—Species of *C.* (*Reticulocythereis*) are distinguished from one another on the basis of carapace size and shape, development of the posteroventral alate projection and details of reticulum.

Stratigraphic Range.—Pleistocene to Holocene.

CLIMACOIDEA (RETICULOCYTHEREIS) FLORIDANA Puri, 1960

(Pl. 2, figs. 3, 5; Pl. 3, figs. 4, 6; Pl. 4, figs. 5, 6; Pl. 5, figs. 5, 6; Text-fig. 1C)

?New genus 1, n. sp. 1, PURI AND HULINGS, 1957, fig. 11, Clastic Province No. 12.

Reticulocythereis floridana PURI, 1960, p. 126, Pl. 1, figs. 3, 4; Text-fig. 25; PURI, 1974, Pl. 5, fig. 9; ?Pl. 3, fig. 1; KEYSER, 1977, p. 69, Pl. 3, figs. 8–13; KEYSER, 1978, p. 214, fig. 4, No. 24; CRONIN, 1979, p. 148, Pl. 17, fig. 2.

?Protocytheretta multicarinata (Swain, 1955). BENDA AND PURI, 1962, p. 339, Pl. 3, figs. 11, 12.

Diagnosis.—Characterized by moderate size, a carapace that tapers posteriorly more than other

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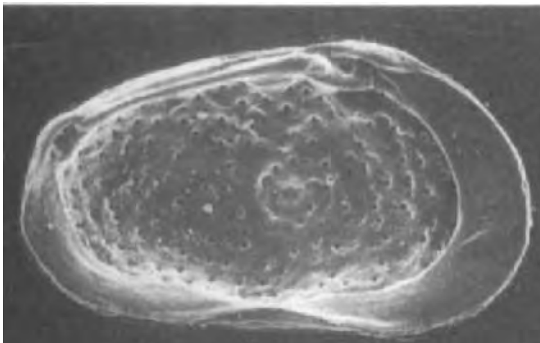
PLATE 4—Figs. 1, 2. *Climacoidea* (*Reticulocythereis*) *reticulata* n. sp. 1. female left valve, internal view, USNM 254577, 4, ×102; 2. female right valve, internal view, USNM 254578, 2, ×112.

Figs. 3, 4. *Climacoidea* (*Climacoidea*) *plueurata* Puri, 1956. 3. male left valve, internal view, USNM 254568, 4, ×98; 4. female right valve, internal view, USNM 254569, 2, ×112.

Figs. 5, 6. *Climacoidea* (*Reticulocythereis*) *floridana* Puri, 1960. 5. female left valve, internal view, USNM 254581, 4, ×102; 6. female right valve, internal view, USNM 254582, 4, ×116.

Figs. 7, 8. *Climacoidea* (*Reticulocythereis*) *foresteri* n. sp. 7. male left valve, interior view, USNM 254584, 10, ×90; 8. male right valve, interior view, USNM 254571, 10, ×100.



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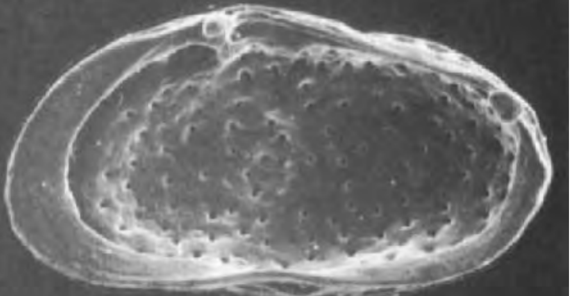

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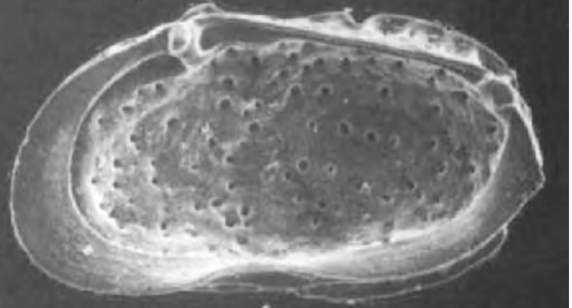

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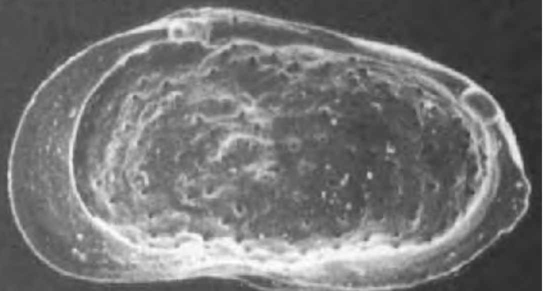

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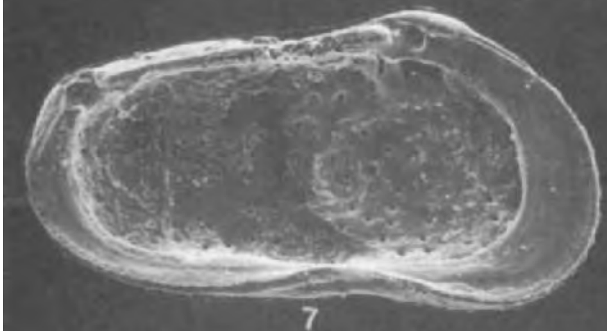

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C. (*Reticulocythereis*) species, moderate development of alate projection, and the lack of alignment of fossae of the reticulum in anterior region.

Remarks.—*C.* (*Reticulocythereis*) *floridana* lacks the strong longitudinal ribs of *C.* (*R.*) *multicarinata* Swain, 1955, and is bigger and more quadrate than that species. Garbett and Maddocks (1979) placed *C.* (*Reticulocythereis*) *floridana* in synonymy with *C.* (*R.*) *multicarinata*, attributing the size difference to environmental factors. In light of the morphologic variation in surface ornament within this subgenus, it is possible that western and eastern Gulf and Atlantic populations are conspecific. However, the majority of published illustrations of *C.* (*R.*) *multicarinata* and all Holocene specimens in our collections from Texas bays show a morphotype with strong development of the two posterodorsal and ventral ridges, small carapace size and distinct subhorizontal alignment of fossae. Eastern Gulf and Florida specimens have more even development of horizontal and vertical ridges forming poorly aligned fossae and have slightly larger carapaces. No Florida samples examined show the strong ridges and well developed ala which typify those in the western Gulf.

We have examined Holocene and Pleistocene specimens from Corpus Christi Bay which have extremely thick shells and two posterodorsal ribs so strongly developed they overlap the dorsal margin and form the dorsal outline in lateral view. The posteroventral rib forms a very strong ala. We are not sure if these specimens are conspecific with *C.* (*R.*) *multicarinata*, but they seem to represent an extreme morphology in this genus. *C.* (*Reticulocythereis*) *floridana* is smaller and has smaller alae than *C.* (*R.*) *foresteri* n. sp.; it is longer than *C.* (*R.*) *reticulata* n. sp. and lacks the subparallel rows of fossae in the anterior region of that species.

In some cases, single specimens of *C.* (*Reticulocythereis*) cannot be assigned to a particular species. It is advisable to examine large sample sizes and to obtain specimens in which the surface ornament is not worn. Further study of material from the Central Gulf is advisable to confirm the relationships of Gulf species and morphotypes.

Stratigraphic Range.—Pleistocene to Holocene.

Occurrence.—Localities 4, 5, 6B, 6C, 9, 10.

Dimensions.—USNM 254575, female carapace, L = 700, H = 410, W = 380; USNM 254579, female carapace, L = 680, H = 390, W = 410; USNM 254580, male carapace, L = 615, H = 320; USNM 254581, female left valve, L = 670, H = 350; USNM 254582, female right valve, L = 590, H = 315.

CLIMACOIDEA (RETICULOCYTHEREIS) RETICULATA n. sp.

(Pl. 1, figs. 2, 5; Pl. 2, fig. 2; Pl. 3, fig. 2; Pl. 4, figs. 1, 2; Pl. 5, figs. 3, 4; Text-fig. 1B)

Diagnosis.—Characterized by small size, longitudinally aligned subparallel rows of fossae, very weakly developed alate projection consisting only of a curved posteroventral rib bordering a circular group of pits (see Pl. 1, fig. 2).

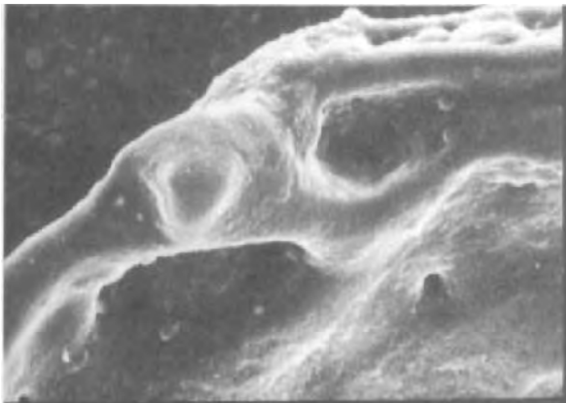
Remarks.—This species lacks the well-developed alae and longitudinal ridges of other *C.* (*Reticulocythereis*) species. It may have evolved from the subgenus *C.* (*Proteoconcha*), specifically *C.* (*P.*) *multicarinata* (Edwards, 1944).

Holotype.—Female left valve (USNM 254572) from Bermont Formation (DuBar, 1974, locality 2).

PLATE 5—Figs. 1, 2. *Climacoidea* (*Climacoidea*) *plueurata* Puri, 1956. 1. male right valve, anterior hinge element, USNM 254570, 4, ×500; 2. same specimen, posterior hinge element, ×500.

Figs. 3, 4. *Climacoidea* (*Reticulocythereis*) *reticulata* n. sp. 3. female right valve, anterior hinge element, USNM 254578, 2, ×500; 4. same specimen, posterior hinge element, ×500.

Figs. 5, 6. *Climacoidea* (*Reticulocythereis*) *floridana* Puri, 1960. 5. female right valve, anterior hinge element, USNM 254582, 4, ×600; 6. same specimen, posterior hinge element, ×600.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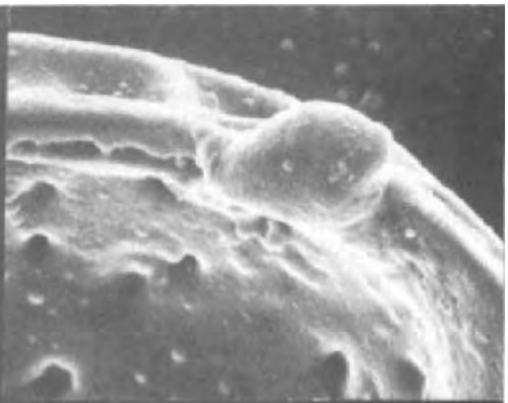
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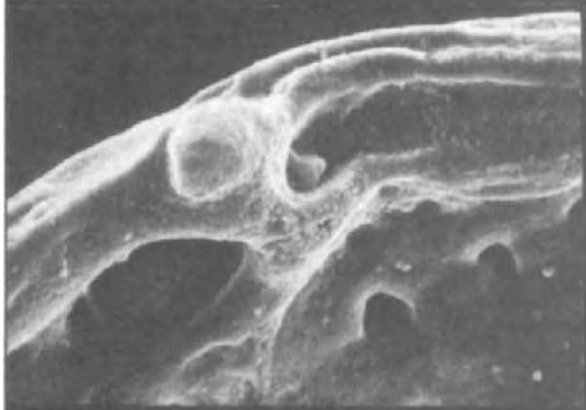
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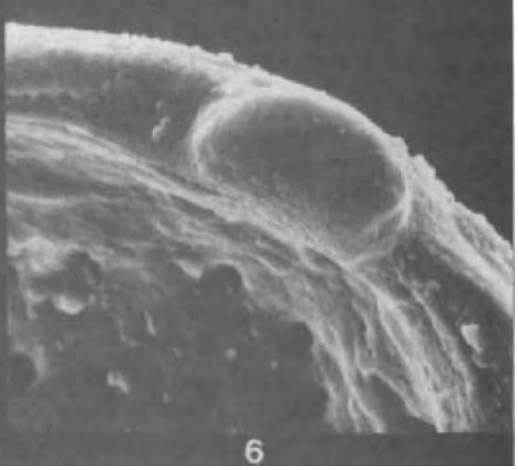
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Etymology.—For the reticulate surface.

Stratigraphic Range.—Pleistocene.

Occurrence.—Localities 2, 4, 6C, 7, 9.

Dimensions.—Holotype; USNM 254572, female left valve, L = 570, H = 330, Paratypes: USNM 254573, male carapace, L = 570, H = 340; USNM 254574, female right valve, L = 595, H = 330; USNM 254576, male left valve, L = 525, H = 280; USNM 254577, female left valve, L = 590, H = 350; USNM 254578, female right valve, L = 550, H = 300.

CLIMACOIDEA (RETICULOCYTHEREIS) FORESTERI n. sp.

(Pl. 1, fig. 3; Pl. 3, figs. 3, 5; Pl. 4, figs. 7, 8)

Diagnosis.—Characterized by its large size, subquadrate shape; with subparallel dorsal and ventral margins in both sexes, "L"-shaped posteroventral ala, and strong development of longitudinal ribs in dorsocentral region (Pl. 1, fig. 3; Pl. 3, fig. 5).

Remarks.—The large size, distinctive shape and well-developed surface ornament distinguish this species from other species of *C.* (*Reticulocythereis*). In particular, *C.* (*R.*) *foresteri* does not taper posteriorly, but has a bluntly rounded posterior outline, even in males. Males are longer and higher than males of *C.* (*R.*) *multicarinata* (compare Pl. 3, fig. 3 with Garbett and Maddocks, 1979, Pl. 14, fig. 2). *C.* (*R.*) *foresteri* also differs slightly from *C.* (*R.*) *multicarinata* in the surface ornament in which the fossae are more concentrically arranged anteriorly, paralleling the margin in the former species.

Holotype.—Female left valve (USNM 254583) from waters off Yucatan, locality 12.

Etymology.—After Richard M. Forester, U.S. Geological Survey, who provided the material.

Stratigraphic Range.—Holocene.

Occurrence.—Locality 12.

Dimensions.—Holotype: USNM 254583, female left valve, L = 725, H = 420; Paratypes: USNM 254584, male left valve, L = 715, H = 390; USNM 254585, female carapace, L = 780, H = 450, W = 480; USNM 254586, male left valve, L = 585, H = 350; USNM 254571, male right valve, L = 680, H = 325.

ACKNOWLEDGEMENTS

We are grateful to R.F. Maddocks, University of Houston, E.M. Brouwers and L.W. Ward of the U.S. Geological Survey for their helpful reviews. R.M. Forester, U.S.G.S., kindly provided specimens from Yucatan, James Demarest, University of Delaware, supplied samples from the Pleistocene of Delaware, and G.M. Shideler, U.S.G.S., obtained specimens from Corpus Christi Bay.

COLLECTIONS

Fossil material for this study came from outcrops (localities 1–5) and from subsurface test-well samples (localities 6–10). The location, lithostratigraphic unit, lithology and depth interval for test-well samples were taken from Parker *et al.* (1955) and are given below.

The Holocene samples of *C.* (*R.*) *foresteri*, provided by R.M. Forester, U.S. Geological Survey, came from waters off the Yucatan Peninsula (locality 12). Holocene samples of *Climacoidea* (*Proteoconcha*) and *Campylocythere* from the Atlantic Continental Shelf came from U.S. Geological Survey bottom grab samples collected by a joint USGS-Woods Hole Oceanographic Institution program to study the marine geology of the Atlantic continental margin (Emery, 1966). Detailed locality data have been given in Hathaway (1966). Specific locality data for samples used in the present study to determine campylocytherine zoogeography will be provided by the authors upon request.

Pliocene and Pleistocene

1. "Miami Canal Pump Station," Pump No. 8 at Broward-Palm Beach County, Florida, line. From matrix removed from *Malea* sp., Thomas Hughes Collection. Caloosahatchee Formation (lower Pleistocene). East spoilbank 2 km S. of county line. (USGS Cenozoic locality 24723).
2. Harney Pond Canal, Glades County, Florida; N. of Structure 71, Caloosahatchee Formation (lower Pleistocene). (USGS Cenozoic locality 22281).
3. "Tropical River Groves", Charlotte County, Florida; pit about 1.0 km N. of Florida S-74, about 8 km E. of intersection with Florida 31, Telegraph Swamp NW quadrangle. Bermont Formation (middle Pleistocene) of DuBar (1974). (USGS Cenozoic locality 23677).
4. LaBelle, Hendry County, Florida; Sears quadrangle, about 100 m S. of Florida 80, about 4 km W. of intersection with Florida 29. Bermont Formation (middle Pleistocene) of DuBar (1974). (USGS Cenozoic locality 23670).
5. Sussex County, Delaware; Selbyville quadrangle, Dirickson Creek ditch, about 1.5 km E. of Roxana; 1.3 km N. of Johnson; lat. 35° 29.75′ N., long. 75° 7.75′ W. (Collected by James Demarest, Univ. Delaware). Omar Formation (upper Pleistocene).

Test Wells

6. GS-1: SE. 1/4 SE. 1/4 sec. 29, T. 48 S., R. 39 E. On Florida Highway 25, 9.7 km N. of Florida Highway 84, Broward County. Land surface altitude 2.6 m above sea level (ASL). Shelly quartz sand. Pleistocene Fort Thompson Formation (upper Pleistocene) *sensu* Parket and others (1955).
   Depth: (m) A. 3.8–4.3; B. 4.3–4.9; C. 11.1–12.2; D. 13.4–15.8
7. GS-11: T. 47 S., R. 40 E. S. side of Hillsboro Canal, 17.7 km W. of Florida Highway 7, Palm Beach County. Land surface altitude 3.7 m ASL. Sandy, shelly limestone. Fort Thomson Formation (upper Pleistocene).
   Depth: (m) 11.7–12.4
8. GS-13: Sec. 30, T. 50 S., R. 38 E. NE. side of Miami Canal, 0.4 km NW. of South New River Canal, Broward County, Florida. Land surface altitude 3.5 m ASL. Sandy, shelly limestone. Fort Thompson Formation (upper Pleistocene).
   Depth: (m) 14.8–14.9.
9. G-182: NW 1/4 NW 1/4 sec. 19, T. 53 S., R. 41 E. Morningside Drive and Curtiss Parkway, Miami Springs, Dade County, Florida. Land surface altitude 1.8 m ASL. Calcareous sandstone, sandy, shelly limestone. Fort Thompson Formation (upper Pleistocene).
   Depth: (m) 26.8–28.7.
10. G-189: NW 1/4 SW 1/4 sec. 15, T. 54 S., R. 41 E. SW 27th Avenue and Dixie Highway, Miami, Dade County, Florida. Land surface altitude 3.5 m ASL. Fossiliferous calcareous sandstone. Fort Thompson Formation (upper Pleistocene).
    Depth: (m) 26.8–28.7.
11. Borrow Pit. NW 1/4 sec. 13, T. 36 S., R. 18 E. 0.5 m north of east end of 17th Street in Sarasota, Sarasota County, Florida. Very fossiliferous shelly sands. Pinecrest facies (upper Pliocene) of the Tamiami Formation as used by DuBar (1974).

Holocene

12. Coast of Isla Cancun, northern Yucatan Peninsula, Mexico, from lagoon about 0.5 m in depth.

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Morphological Affinities in Ostracoda, Misleading and Revealing

HEINZ MALZ
Forschungsinstitut Senckenberg, Frankfurt am Main, F.R. Germany

ABSTRACT

In many cases the outline of an ostracod carapace is a first criterion for its generic determination. However, more characteristics are needed for qualified generic assignment, as shape may turn out to be a very misleading feature. For example, were it not for the bairdiid muscle scars, *Pterobairdia* could easily be mistaken for a *Cytheropteron*. Similarly a *Bairdia*-shaped ostracod may not necessarily bear any relationship to *Bairdia* or to any of its allied genera. Therefore *Bairdiacythere* is introduced as a new subgeneric taxon of *Schuleridea* and grouped within Cytheridae, Cytherideinae, Schulerideini. The new taxon which by its name alludes to the genera *Bairdia* and *Cythere* is characterized by its bairdiid shape, but proves cytherid by its muscle scars.

Schuleridea (*Bairdiacythere*) is closely related to a group of Bathonian ostracods which is included in *Schuleridea* (*Eoschuleridea*) that precedes the Upper Jurassic to Cretaceous *Schuleridea* (*Schuleridea*). Beside the phylogenetic development of *Schuleridea* (*Eoschuleridea*) to *Schuleridea* (*Schuleridea*) a local, perhaps an endemic, development simultaneously produced *Schuleridea* (*Bairdiacythere*) as an ecologically favoured offshoot of *Schuleridea* (*Eoschuleridea*). Rather than raising *Schuleridea* (*Eoschuleridea*) to generic rank in order to point out its close relationship with *Bairdiacythere* as a subgenus of it, the subgeneric status for both *Schuleridea* (*Eoschuleridea*) and *Schuleridea* (*Bairdiacythere*) is favoured. This taxonomical valuation is paralleled by the Neogene *Schuleridea* (*Amphischuleridea*) which comes closer to *Schuleridea* (*Aequacytheridea*) rather than to *Schuleridea* (*Schuleridea*).

INTRODUCTION

The Old Cement Works quarry at Kirtlington in Oxfordshire has proved to be a locality extremely rich in Upper Bathonian ostracod faunas, both in species and specimens. In the inventory of ostracod species listed by Ware and Whatley (1980) from that locality a total of 92 speces is contained, 59 of which are determined to the specific level leaving the rest to cf. and aff. determinations or to open nomenclature. By their description of a farther 12 species, Ware and Whatley increased the number of taxa to more than 70 known species from Kirtlington Quarry, mainly marine, but some also indicative for freshwater.

Among the numerous species there is a very remarkable from which is reminiscent of a bairdiid in its outline and shape. However, its muscle scars prove it to be a cytherid. Since the species occurs in great numbers, it cannot be overlooked in the various samples from the Kirtlington Forest Marble. However, since the species has not been mentioned in the literature before, it must have been misidentified (determined perhaps as *Bairdia hilda*), or left under open nomenclature (? which).

As regards the internal features of the new *Bairdia*-like cytherid, its close relationship to species grouped within *Schuleridea* (*Eoschuleridea*) Bate, 1967 can be ascertained. However, from differences in outline and hinge structure a separate status is proposed, namely *Schuleridea* (*Bairdiacythere*) subg. nov. By the introduction of a new subgeneric unit the "aspects of the Subfamily Schulerideinae" (Neale, 1982: 181) become even more complex. On the other hand, this complexity proves in fact a skilled and useful solution in taxonomy which is really "as much an art as a science".

SYSTEMATIC PART

Family CYTHERIDAE Baird, 1850
Subfamily CYTHERIDEINAE Sars, 1925
Tribe SCHULERIDEINI Mandelstam, 1959

Remarks.—With reference to Neale (1982: 180) "the Schulerideinae is a practical grouping of convenience". In correspondance with that valuation the two equivalent tribes Schulerideini and Apatocytherini Gründel, 1976 likewise and sufficiently validate Neale's conception of Schulerideinae. This devaluation of Schulerideinae to infrasubfamilia rank stands, it is true, against the opposite version approached by Bate (1967) and followed by Kollmann (1971) who raised Schulerideinae to familia rank. However, since "there has been a veritable explosion of ostracod genera in the last two decades" (Neale, 1982: 185), shifting to higher categories neither includes better possibilities for the determination and classification of genera nor does it render any help for a better understanding of ostracod phylogeny. On the contrary, since shifting to higher categories does not keep in step with the number of available features in an ostracod carapace, generic determination becomes more and more obscure by less and less features. Thus, for very practical reasons the determination of an ostracod as belonging to the family Cytheridae gives as much in formation as its determination as a cytheracean or as a cytherocopine. This pragmatic point of view is approached also by the "zoological systematics" presented by Hartmann (1975: 724) who recognizes Schulerideini within Cytherideinae of the family Cytheridae.

Genus SCHULERIDEA Swartz and Swain, 1946

Type species.—*Schuleridea acuminata* Swartz and Swain, 1946.

Subgenus SCHULERIDEA (BAIRDIACYTHERE) subg. nov.

Type species.—*Schuleridea* (*Bairdiacythere*) *bairdiaformis* sp. nov.

Name.—With reference to the *Bairdia*-like outline and the cytherid relationship.

Diagnosis.—A subgenus of *Schuleridea* without an eye swelling, but with a faintly marked ocular sinus below the anterior part of hinge in the RV. Carapace sub-ovate in side view with a concave (*Bairdia*-like) posterodorsal break behind which the posterior end is pointed, more so in the smaller

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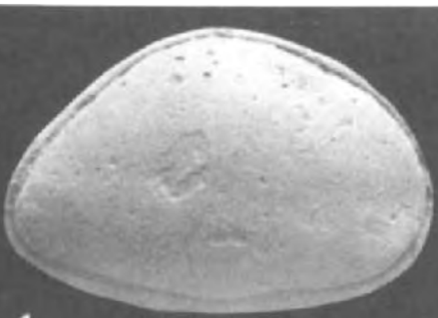
PLATE 1—All specimens are from the Upper Bathonian Forest Marble of the Old Cement Works quarry at Kirtlington, Oxfordshire (Mz 72/1967). Measurements (in brackets) refer to length of specimens in µm. LV = left valve, RV = right valve, C = carapace. Magnification ×84, unless stated otherwise.

Figs. 1–2. *Schuleridea (Eoschuleridea) bathonica* Bate, 1967. 1. Female C (710), right lateral.—Xe 12933; 2. Female LV (730), internal lateral.—Xe 12933.

Figs. 3–5. *Schuleridea (Eoschuleridea) trigonalis* (Jones, 1884). 3. Female C (730), right lateral.—Xe 12936; 4. Female LV (720), internal lateral.—Xe 12936; 5. Female C (680), dorsal.—Xe 12937.

Figs. 6–9. *Schuleridea (Bairdiacythere) bairdiaformis* sp. nov. 6. Female C (740), right lateral.—Xe 12920; 7. Male C (740), dorsal.—Xe 12921; 8. Female LV (740), a) internal lateral, b) hinge, ×165.—Xe 12922; 9. Female C (700), ventral.—Xe 12923.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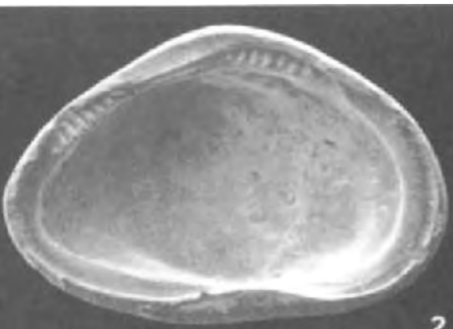
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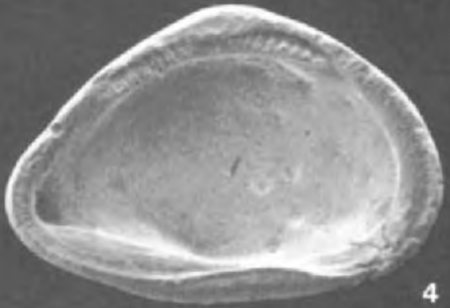
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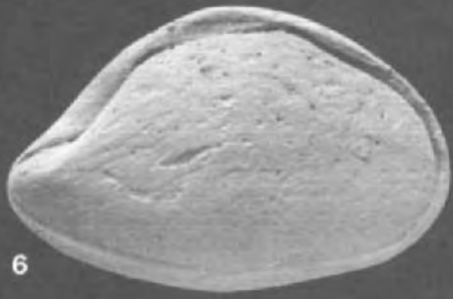
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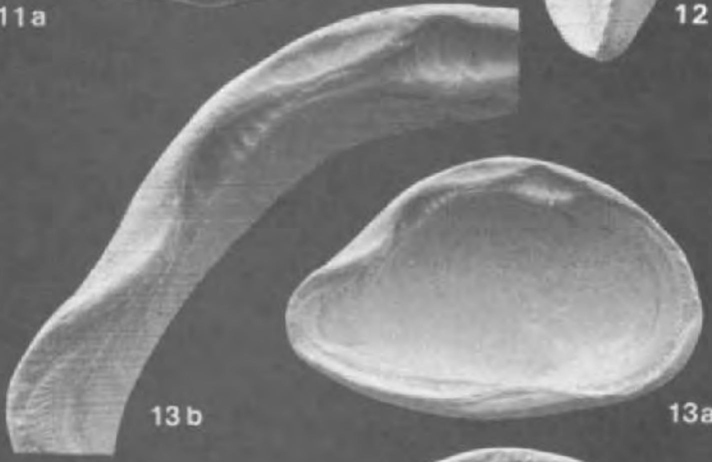
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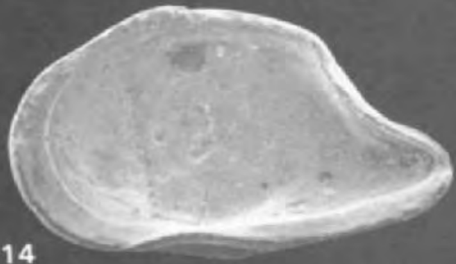
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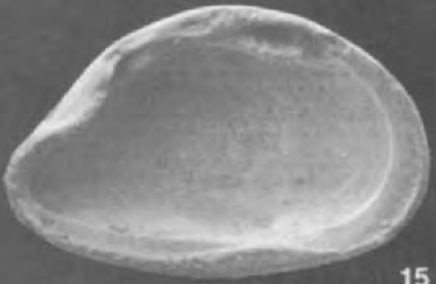
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RV than in the overlapping LV. Tripartite hinge short, restricted to mid-third of valve length, of the paleomerodont type and with an accommodation groove above the central part in the LV. Duplicature moderately broad, with about 25 radial pore canals anteriorly and 9 posteriorly. Muscle scars correspond to the cytherid type with four adductors, one frontal and two separate mandibular scars.

Description.—As for the type species.

Relationship.—The subgenus is closely related to *Schuleridea* (*Eoschuleridea*) Bate, 1967 with which it has in common the cytherid type of muscle scars and the development of the marginal zone, but differs from it in the *Bairdia*-like shape and the short compressed hinge of the paleomerodont type. Within the Schulerideini similar indentations of the outline occur in *Pseudocytheridea* Schneider, 1949 and in *Schuleridea* (*Amphischuleridea*) Kollmann, 1971. However, in both taxa (or is it only one ?) the carapace is incurved posteroventrally.

Stratigraphic range.—Middle Jurassic (Upper Bathonian).

Distribution.—Known from the Oxfordshire area only.—Although many Bathonian localities are known to me by their ostracod faunas I did not come across any form similar to the species described below. Therefore I suppose that the species developed as a very local element proving adaption to endemism.

Biotope.—The biotope in which the species occurs is dominated by marine ostracods, yet some indicators for freshwater are present, for instance *Theriosynoecum kirtlingtonense* Bate, 1965 and *Limnocythere ceratina* Ware and Whatley, 1980. The mixture of ostracods from different habitats has been subject to various explanations (referred to by Ware and Whatley, 1980). These explanations range from reworked freshwater deposits in a marine environment via autochthonous brackish water layers to an interfingering of freshwater and marine sediments in the tidal area of a river system. From the rich material at my disposal I gathered some information which may turn out useful for an explanation: The preservation of the marine species varies widely and ranges from very well to poorly preserved specimens, whereas that of the freshwater species is quite excellent. Couldn't this mixture point to a freshwater pool filled by reworked marine sediments?

SCHULERIDEA (BAIRDIACYTHERE) BAIRDIAFORMIS sp. nov.

(Pl. 1, figs. 6–9; Pl. 2, figs. 10–17)

Name.—With reference to the *Bairdia*-like outline.

Holotype.—Male carapace, Pl. 2, fig. 17; SMF Xe 12919.

Type locality and horizon.—Old Cement Works quarry at Kirtlington, Oxfordshire, England. Upper Bathonian, Forest Marble.

Paratypes.—More than 150 carapaces and valves: SMF Xe 12920–12932.

Diagnosis.—As for the monotypic subgenus.

Measurements (dimensions in μm).—The size of the adult specimens covers a wide range, from length 630/height 420 to length 780/height 500. Presumably the smaller specimens (length 630–740) represent females, whereas the larger specimens (length 690–780) represent males. As there is a large

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PLATE 2—All specimens are from the Upper Bathonian Forest Marble of the Old Cement Works quarry at Kirtlington, Oxfordshire (Mz 72/1967). Measurements (in brackets) refer to length of specimens in μm. LV = left valve, RV = right valve, C = carapace. Magnification ×83, unless stated otherwise.

Figs. 10–17. *Schuleridea (Bairdiacythere) bairdiaformis* sp. nov. 10. Female C (720), dorsal (slightly tilted to show overlap).—Xe 12924; 11. Male RV (750), a) internal lateral, b) hinge, ×165, c) muscle scars, ×165 (4 adductors, 1 frontal, and 2 mandibulars).—Xe 12922; 12. Male RV (750), dorsal.—Xe 12924; 13. Male LV (690), a) internal lateral, b) hinge, ×165.—Xe 12920; 14. Male RV (740), internal lateral.—Xe 12921; 15. Female LV (700), internal lateral.—Xe 12923; 16. Female C (740), right lateral.—Xe 12925; 17. Male C (780), holotype, right lateral.—Xe 12919.

overlap in size, sexual dimorphism remains somewhat uncertain. Therefore, specimens that are more pointed posteriorly (Pl. 2, figs. 13, 17) are regarded as males, the less pointed specimens (Pl. 2, figs. 15, 16) are taken to represent the females.—In some juvenile specimens (length$\leqq$560) a very narrow duplicature is present and the *Bairdia*-like posterodorsal break is but faintly developed.

Description.—Carapace sub-ovate in side view with a *Bairdia*-like concave break in the posterodorsal part, below which the posterior end is more pointed in the RV than in the LV. Larger LV highly arched mid-dorsally overlapping the smaller RV along the entire margin, especially in the posterodorsal break. Greatest length below mid-point, greatest height at about mid-length. Carapace oval in dorsal view with greatest width median. Surface smooth, finely punctate by widely spaced openings of lateral pore canals. Hinge short, restricted to mid-third of dorsal margin, tripartite and of the paleomerodont type. In the LV the anterior part of the hinge is developed as a deep, oval, loculate trough which is framed proximally by a torose lip. Medially there is a short, shallow, narrow furrow connecting the terminal hinge parts. The posterior part consists of a deeply incised, oval, loculate socket without any proximal frame. Above the median hinge part a distinct accommodation groove is visible, even in lateral right side views of closed carapaces. Inner margin and line of concrescence coincide; duplicature moderately broad anteriorly, rather narrow posteriorly. Radial pore canals densely spaced, slightly curved, about 25 anteriorly and 9 posteriorly, bent to openings on the sub-peripheral lateral exterior, but not terminating marginally. As a result of overlap, the terminal ends of the LV are rims projecting over the RV; proximal to the rounded rim the smaller RV rests against a subperipheral zone marked by fine striae in the LV; Pl.1, fig. 8a, Pl. 2, figs. 13a,b, 15. The vertical row of 4 adductor scars is slightly curved behind a prominent oval frontal scar. Two mandibular scars are positioned anteroventrally and ventrally.

Relationship.—*Schuleridea* (*Bairdiacythere*) *bairdiaformis* sp. nov. is closely related to a group of species assigned to *Schuleridea* (*Eoschuleridea*) occurring in the same samples from the Kirtlington quarry (Pl. 1, figs. 1–5), but differs from all the others by its bairdioid shape, its compressed hinge, and the torose lip supporting the anterior socket.

Occurrence.—So far the species has been found in several samples from the type locality.

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Recent Ornate Bairdiid Ostracoda: Origin and Distribution

HEINZ MALZ AND ALAN LORD
Forschungsinstitut Senckenberg, Frankfurt am Main, F.R. Germany and
University College London, England

ABSTRACT

Taxonomic interpretations of Recent ornate bairdiids are reviewed and monophyletic and polyphyletic origins for these forms discussed in the light of new material and new distributional data.

Triebelina sertata Triebel, here considered to include *T. rectangulata* Hu and *T. lata* Hu as junior synonyms, is recorded from Pleistocene deposits in Taiwan and from (Sub-)Recent bottom samples from the Taiwan Strait. The species is widely distributed in circum-tropical regions and its occurrence in the Mediterranean is regarded as a relict from the Tethyan history of the region. – A new large *Triebelina* species (*T. jellineki* sp. nov.) is described from the Phillipines, where it is associated with *T. amicitiae* Keij. – New records of *T. raripila* (G.W. Müller) indicate that it is an endemic Mediterranean species. – The type species of *Havanardia* (*H. havanensis* Pokorný) is recorded by new material with associated adults and juveniles from Cozumel Island, off Mexico.

In addition, new records of *Glyptobairdia coronata* (Brady) and *Pterobairdia maddocksae* McKenzie and Keij are presented. *G. coronata* is restricted to the Caribbean. *P. maddocksae*, from off W. Sumatra, has certainly suffered transport from shallow to deeper waters.

FOREWORD

Bairdiid ostracods are so widely distributed in the fossil record that no symposium on Ostracoda should lack some discussion of these forms. Indeed, (m)any opinion(s) on bairdiid taxonomy continue(s) to raise more questions and problems than can be solved at that time. New finds add new facts! Ever since the first Recent ornate bairdiid, *Bairdia coronata* Brady was described in 1870 much new evidence has come to light, but the brief review below of problems and controversies shows that the subject is far from exhausted.

HISTORICAL REVIEW

Discussion concerning Recent ornate bairdiids started soon after the two genera *Triebelina* Van den Bold and *Glyptobairdia* Stephenson were first described in 1946. Within a short time three different views of these genera were advanced. Triebel (1948) regarded *Glyptobairdia* as a junior synonym of *Triebelina*, a position followed by Key (1954), Van Morkhoven (1958, 1963), and the contributing authors of the two synoptic volumes, the Osnovy (1960) and Treatise (1961). A second view was put forward by Pokorný (1958: 227), who erroneously considered *Triebelina* a *nomen nudum* and therefore took *Glyptobairdia* as the valid generic name. Indeed, the validity of *Triebelina* was still regarded as questionable by Hartmann (1975: 698) but this view is no longer widely shared. A third version envisaged the co-existence of *Triebelina* and a re-established *Glyptobairdia* (initiated by Kollmann, 1960: 91; see also McKenzie and Keij, 1977 for further references). This interpretation is supported by zoological evidence (Maddocks, 1969), and palaeontological conclusions (Keij, 1974, 1976).

The *Triebelina/Glyptobairdia* complex of Recent ornate bairdiids was enlarged by the description of two alate to winged forms based also on Recent type species, viz. *Havanardia* Pokorný, 1968 and *Pterobairdia* McKenzie and Keij, 1977.

Opinion is further divided when ancestors are sought for these Recent ornate and winged bairdiids and both monophyletic and polyphyletic origins have been proposed:

1. The Subfamily Triebelininae Kollmann, 1963 represents a phylogenetic development from Permian to Recent, and the use by Bolz (1971) of the subgenus *Triebelina* (*Triebelina*) for Triassic species even means a lineal descent to Recent forms.
2. Van den Bold (1974: 32) considered ornate bairdiids to have developed polyphyletically. If one assumes that *Triebelina* originated from different paranesidean ancestors then the same presumption must be transferable and must logically apply also to the development of a single *Triebelina* species in different regions. From this argument migration is not needed to explain the distribution of a species, which is relevant to the anomalous distribution of *Triebelina sertata* (Pl.3, figs. 4–5) in the Eastern Mediterranean (see below, and discussion by Keij, 1974: 357). The same interpretation also affects our view of most of the ornate Triassic bairdiid taxa and the other scattered occurrences of these ostracods through the Mesozoic, e.g. *Ptychobairdia limbata* Sheppard, 1981 from the French Bathonian and *Alatanesidea pokornyi* Colin and Lauverjat, 1978 from the Upper Cretaceous of Portugal.

These Mesozoic taxa have been described quite recently, which demonstrates how any resolution of the differing interpretations of the origin(s) of Recent ornate bairdiids depends upon the discovery of new information. This paper attempts to contribute to the process by describing a new species of *Triebelina* (*T. jellineki*) and reviewing existing and new distribution data for *T. sertata* Triebel, *Havanardia havanensis* Pokorný, and *Pterobairdia maddocksae* McKenzie and Keij.

SYSTEMATIC PART

Family BAIRDIIDAE Sars, 1888

Genus TRIEBELINA Van den Bold, 1946

PLATE 1—LV = left valve, RV = right valve, C = carapace. If not stated otherwise, magnification about ×80. Measurements (in brackets) = length of specimens in μm.

Figs. 1–7. *Triebelina sertata* Triebel, 1948. Upper part of Maanshan Formation, Pleistocene; road-cut near Tianshih, S. Taiwan (figs. 1–2 = sample no. 7832; fig. 3 = sample no. 7831). 1. RV (550), a) internal lateral, b) muscle scars, ×270.—Xe 12899; 2. RV (550), external lateral.—Xe 12899; 3. LV (590), external lateral.—Xe 12898. (Sub-)Recent; beach at Hotel Palestine, Alexandria, Egypt; 4. RV (570), external lateral.—Xe 12893; 5. LV (620), external lateral.—Xe 12894. (Sub-)Recent; beach at Hurghada, Red Sea; 6. LV (580), external lateral.—Xe 12897. (Sub-)Recent; Honolulu, off reefs at 100 m waterdepth; 7. LV (570), external lateral.—Xe 12892.

Figs. 8–10. *Triebelina jellineki* sp. nov. (Sub-)Recent; Philippine Islands, Coral patches at northern beach of San Fernando (figs. 8, 9) and beach at Paradise of Juan, San Fernando (fig. 10). 8. C (juvenile; 820), external lateral.—Xe 12888; 9. RV (1030), external lateral, ×64.—Xe 12887; 10. LV (1130), holotype, external lateral, ×64.—Xe 12890.

Fig. 11. *Triebelina amicitiae* Keij, 1974. (Sub-)Recent; Philippine Islands, Coral patches at northern beach of San Fernando. C (900), right lateral.—Xe 12886.

Fig. 12. *Triebelina raripila* (G.W. Müller, 1894). (Sub-)Recent; beach at Hotel Palestine, Alexandria, Egypt. LV (660), external lateral.—Xe 12896.


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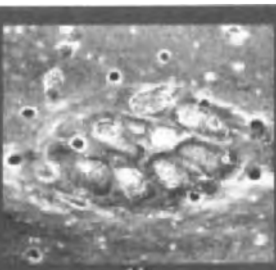
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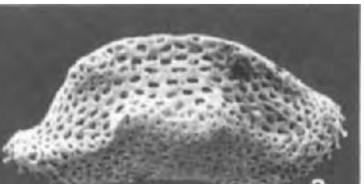
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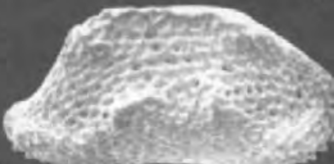
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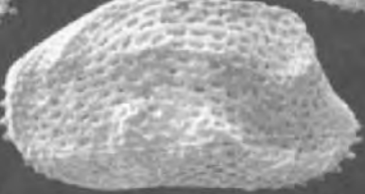
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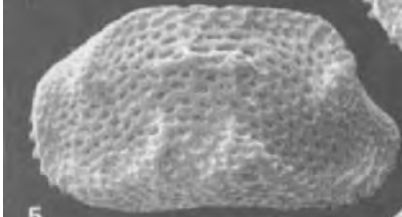
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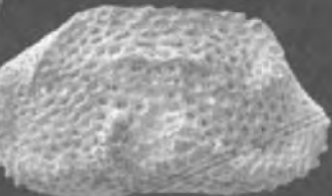
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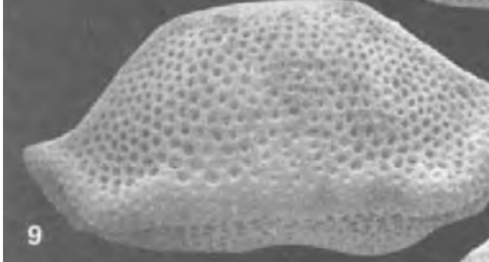
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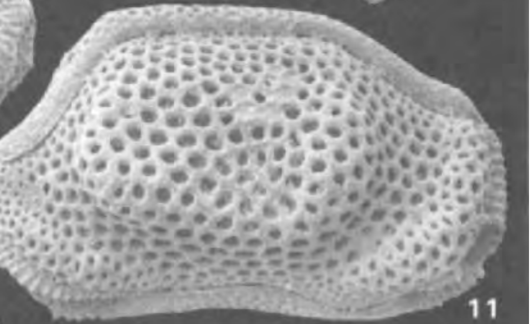
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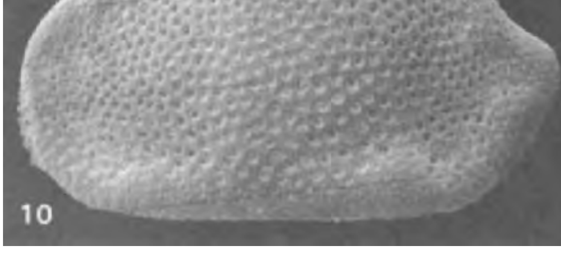
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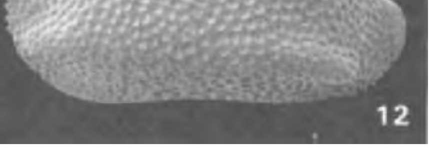
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Type species.—Triebelina indopacifica Van den Bold, 1946.

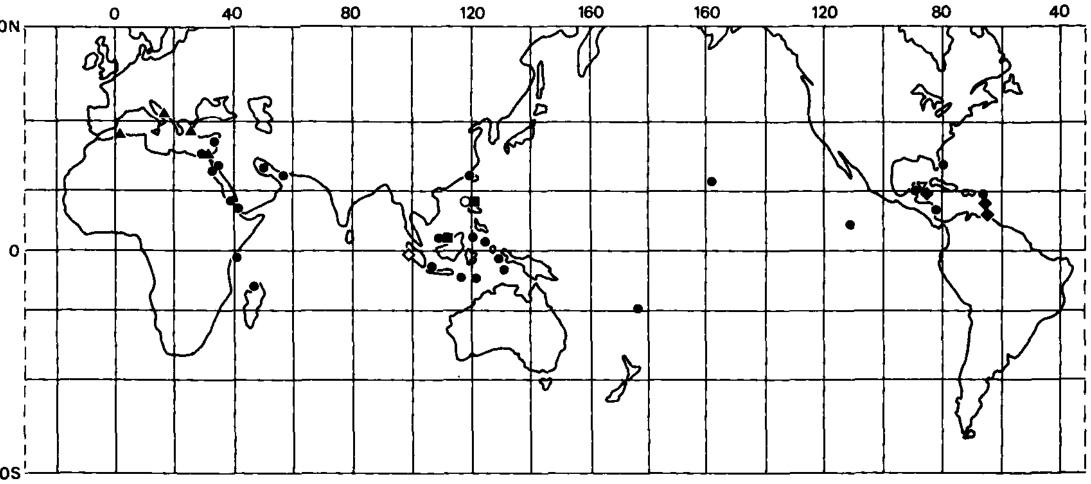
TRIEBELINA SERTATA Triebel, 1948
(Pl. 1, figs. 1–7)

Triebelina sertata Triebel. TEETER, 1975, p. 422, Text-fig. 31 [figures a single specimen found in shallow water coral sand]; HANAI *et al.*, 1980, p. 118 [summarising earlier references and distributional data from Southeast Asia]; BONADUCE *et al.*, 1980, p. 144, Pl. 1, fig. 13; HARTMANN, 1984, p. 125, Pl. 4, figs. 6, 7.

Triebelina rectangulata HU, 1980, p. 84, Pl. 2, figs. 12, 18, 22, Text-fig. 3 [3 specimens which from their lengths and very narrow duplicatures are juveniles of the A-1 stage].

Triebelina lata HU, 1984, p. 72, Pl. 9, figs. 1, 4, Text-fig. 3.

Material.—Sub-Recent and Recent specimens (all without soft parts) from off Honolulu at 100 m waterdepth (leg. J. Resig); from Taiwan Strait, station numbers 6-C, 5-A, H-7, N-1 of Huang (1983); from Kilifi beach, Kenya (coll. Th. Jellinek; see also "Remarks"); from Hurghada beach, Red Sea (coll. H. Malz); from Alexandria beach, Eastern Mediterranean (coll. H. Malz);



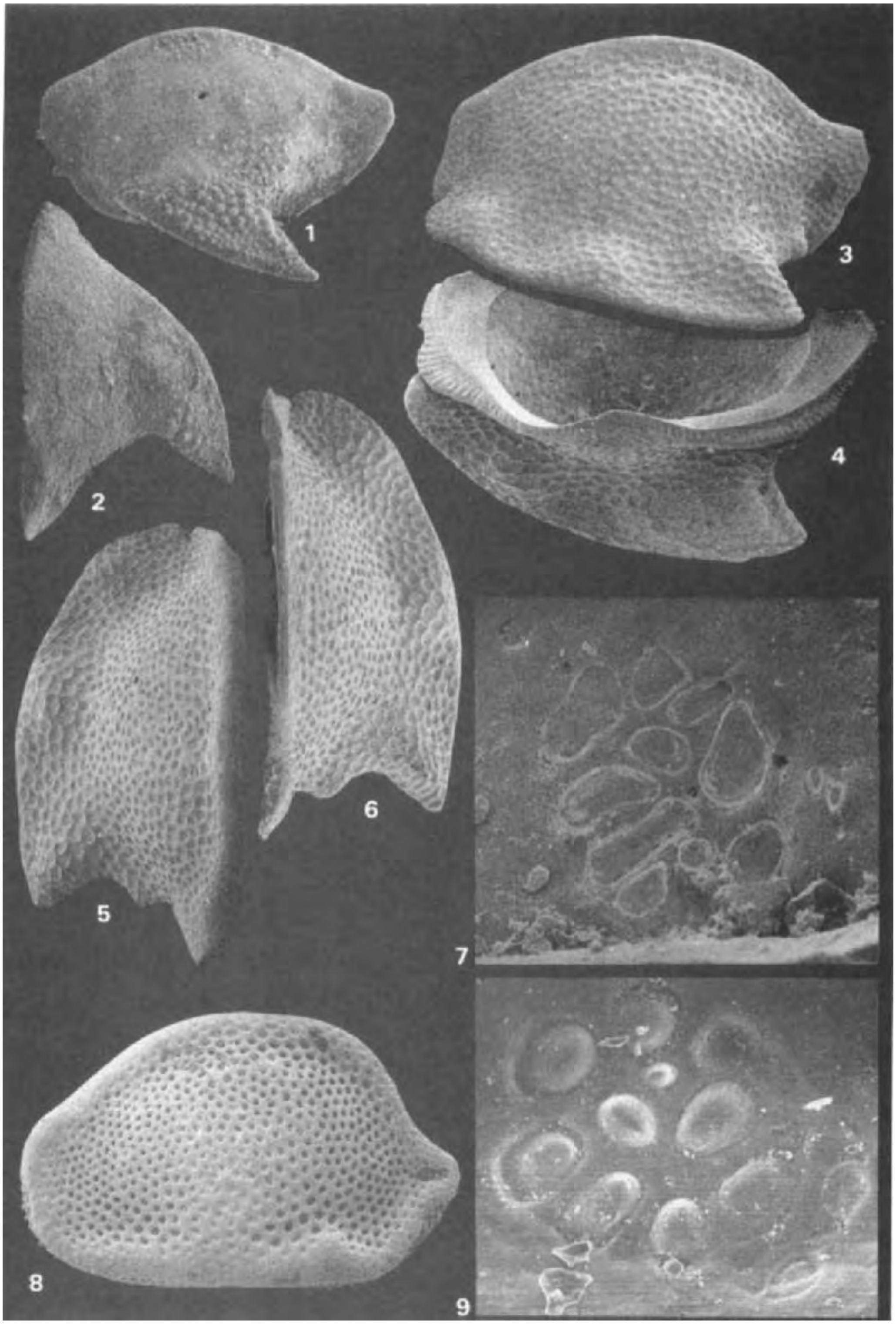
TEXT-FIG. 1—Distribution of Recent ornate bairdiid species discussed in this paper (based on Keij, 1974, Text-fig. 1). 1. *Triebelina jellineki* sp. nov.—2. *Triebelina sertata* Triebel.—3. *Triebelina amicitiae* Keij.—4. *Triebelina raripila* (G.W. Müller).—5. *Havanardia havanensis* Pokorný.—6. *Glyptobairdia coronata* (Brady).—7. *Pterobairdia maddocksae* McKenzie and Keij.

PLATE 2—LV = left valve, RV = right valve. If not stated otherwise, magnification about ×80. Measurements (in brackets) = length of specimens in μm.

Figs. 1–2. *Pterobairdia maddocksae* McKenzie and Keij, 1977. (Sub-)Recent; off W. Coast of Sumatra, near Padang, at 1°51′S/99°36′E, waterdepth 683 fathoms (Siboga Expedition). [A LV from the same locality was figured by Van den Bold, 1974, Pl. 1, fig. 12]. 1. LV (670), external lateral.—Xe 12874; 2. RV (640), dorsal.—Xe 12874.

Figs. 3–7. *Havanardia havanensis* Pokorný, 1968. (Sub-)Recent; Mexico, Cozumel Island, base of Palancar Reef at 30 m waterdepth (figs. 3–5,7) and of Paraiso Reef at 15 m waterdepth (fig. 6). 3. LV (850), external lateral.—Xe 12881; 4. RV (900), internal lateral, but inclined dorsally to show full alar extension. Muscle scars in lower half of valve partly hidden by ventral edge.—Xe 12881; 5. LV (830), dorsal.—Xe 12882; 6. RV (860), dorsal.—Xe 12880; 7. LV (fragment), muscle scars slightly retouched, ×400.—Xe 12881.

Figs. 8–9. *Triebelina jellineki* sp. nov. (Sub-)Recent; Philippine Islands, Coral patches at northern beach of San Fernando. 8. LV (1050), external lateral, ×64.—Xe 12888; 9. LV (fragment, < 1050), muscle scars, ×320.—Xe 12888.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from Palancar reef at 30 m waterdepth, Mexico (coll. Th. Jellinek), from off Tortola, Virgin Islands (leg. A. Lord). Pleistocene specimens from the upper part of the Maanshan Formation and the Szekou Formation of S Taiwan, sample numbers 7831–7833, 7836, 7837 of Cheng (1981).

Distribution.—These new distributional data can be added to the species occurrence map given by Keij (1974: Text-fig. 1); see Text-fig. 1 here. Within the wide circum-tropical distribution of the species its occurrence in the Eastern Mediterranean is rather exceptional. As the species is known fossil since the late Miocene (Keij, 1976: Text-fig. 1) it could prove to be a relict from the Tethyan history of the Mediterranean, where it developed separately as a "lineal descendant of a once-continuous population" (McKenzie, 1973: 480).—In contrast to the wide distribution of *T. sertata* is the restricted occurrence of *T. raripila* (Pl. 1, fig. 12), which is listed among "endemic-Mediterranean species" by Yassini (1979: 374). In our sample from Alexandria beach, Eastern Mediterranean both *T. sertata* and *T. raripila* occur.

Remarks.—Three samples collected at Kilifi, Kenya (from beach and at 2 m and 26 m waterdepth respectively), were extremely rich in specimens of *T. sertata*. More than 50 specimens, adults and juveniles, were measured giving the size range (in μm.): males and females, 570–630, and for various growth stages, A-1≦520, A-2≦470, A-3≦430, and A-4≦400. The faunal assemblages of these samples are characterised by many species of *Neonesidea, Paranesidea* and *Bairdoppilata*, each with large numbers of specimens. Furthermore, rare specimens of *T. bradyi* Triebel, 1948 and a new species of *Havanardia* occur. As there is only one adult RV (among several juveniles and fragments of adults) the description of the new species is postponed. Nonetheless, the occurrence of Recent *Havanardia* on the East African shelf is of some interest, as the genus has been so far recorded only from the Caribbean (Pokorný, 1968; Keij, 1976) and from off West Africa (Keij, 1973).

Annotation.—The above mentioned *Triebelina bradyi* Triebel, 1948 also stands as the valid specific replacement name for "*Triebelina truncata* (Brady, 1980)", for which McKenzie (1986: Pl. 1, fig. 12) determined a lectotype recently.

TRIEBELINA JELLINEKI sp. nov.

(Pl. 1, figs. 8–10; Pl. 2, figs. 8–9)

Name.—In recognition of Thomas Jellinek (Oberursel) for his valuable sampling activities.

Holotype.—Left valve, Pl. 1, fig. 10; SMF Xe 12890.

Paratypes.—12 valves and carapaces including juvenile specimens; SMF Xe 12887–12889.

Type locality.—Beach sand at Paradise of Juan, near San Fernando, about 30 km S. of Vigan, Philippine Islands (coll. Th. Jellinek).

Diagnosis.—Large *Triebelina* with very robust carapace, rounded sub-hexagonal in side view, with peripheral dorso- and ventrolateral carinae in LV and sub-peripheral ventrolateral carina angled to both ends in RV. Surface ornamented by rotund, densely set fossae.

Dimensions (length in μm.).—For lack of soft parts sexual dimorphism was not recognized, but

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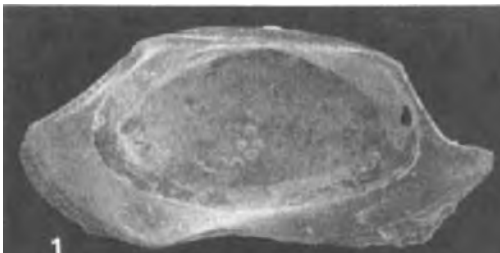
PLATE 3—LV = left valve, RV = right valve, C = carapace. If not stated otherwise, magnification about ×80. Measurements (in brackets) = length of specimens in μm.

Figs. 1–3. *Glyptobairdia coronata* (Brady, 1870). (Sub-)Recent; Mexico, Cozumel Island, base of Paraiso Reef at 15 m waterdepth. 1. RV (770), internal lateral, with "bairdoppilate structure" at anterodorsal slope.—Xe 12876. Recent; St. Barts, Lesser Antilles, bottom sample at 12 m waterdepth, S. Publico, near Gustavia. [Specimens from the same locality were figured by van Morkhoven, 1958, Pl. 46, figs. 2–6]; 2. LV (770), internal lateral.—Xe 12875; 3. C (780), right lateral (muscle scars are indicated just below short median rib).—Xe 12875.

Figs. 4–6. *Havanardia havanensis* Pokorný, 1968. (Sub-)Recent; Mexico, Cozumel Island, base of Paraiso Reef at 15 m waterdepth (figs. 4,6) and of Palancar Reef at 30 m waterdepth (fig. 5); 4. LV (860), external lateral.—Xe 12879; 5. LV (juvenile A-1; 720), external lateral (showing weakly reticulate surface ornament and smooth alar region).—Xe 12881; 6. RV (840), a) external lateral, b) and c) details of sculptured surface composed of rotund fossae with papillate sola and surrounded by muri with widely distributed openings of simple lateral pore canals, ×400, resp. ×1,600.—Xe 12879.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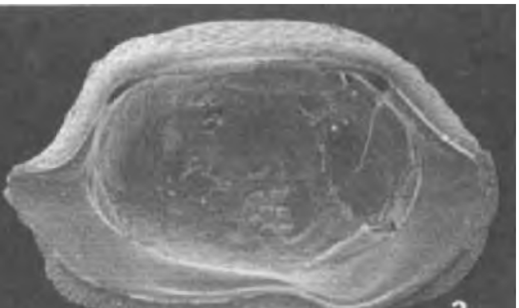
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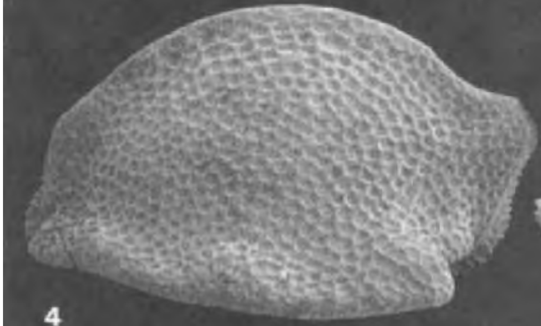
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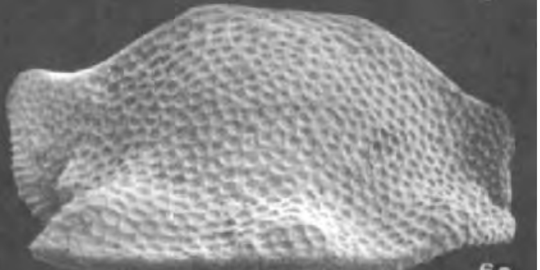
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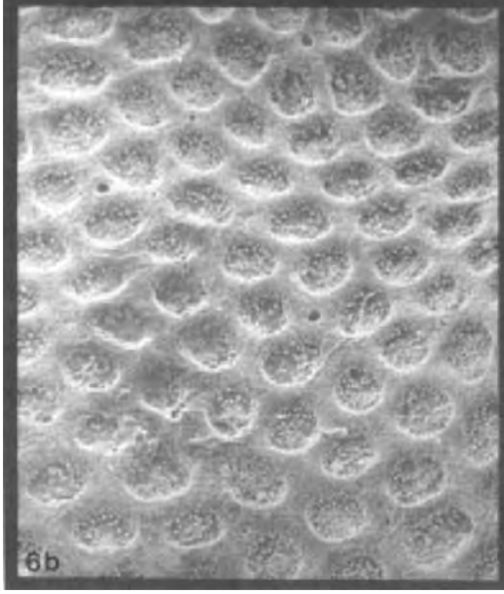
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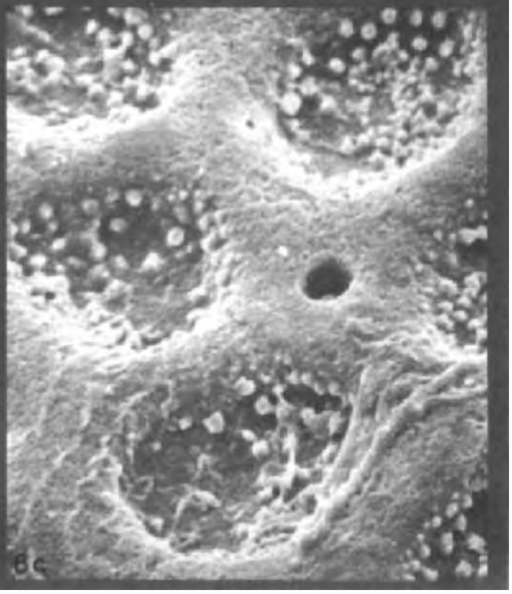
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presumably lies within the size range of the adult specimens, 1030–1130. Juvenile specimens of three different growth stages are present measuring 820, 750, and 600.

Relationships.—This species is closely related to the group of rather large-sized *Triebelina* species, especially to *T. amicitiae* Keij, 1974 occurring in the same material (Pl. 1, fig. 11). *T. jellineki* can easily be distinguished from *T. amicitiae* by its peripheral dorso- and ventrolateral carinae bent to both ends in the RV. *T. jellineki* is similar in lateral outline to the Lower Miocene *Havanardia indica* Khosla, 1978 from W. India which, however, differs in its more inflated outline in dorsal view.

Distribution.—In addition to the type locality, the species was found on Recent coral patches at the northern part of San Fernando beach, Philippine Islands. The association in which *T. jellineki* occurs is dominated by numerous specimens of *Paranesidea* sp. This species closely resembles *P. fracticorallicola* Maddocks, 1969 (originally described from Madagascar, but also recorded from the Gulf of Aqaba by Bonaduce *et al.*, 1980 and from Heron Island, Australia by Hartmann, 1981), but may be distinguished from it by its higher arched dorsum. *T. amicitiae* (Pl. 1, fig. 11), a species which is known so far from three localities below 400 m waterdepth in the South China Sea (Keij, 1974: 351) also occurs in the same sample. Although in the Philippines sample the species is documented by the figured carapace and some fragments only, it proves "that the animal lives in shallow reef environment", as has been assumed earlier by Keij (1974: 352).

TRIEBELINA AMICITIAE Keij, 1974
(Pl. 1, fig. 11)

Triebelina amicitiae KEIJ, 1974, p. 351, Pl. 1, figs. 1–6.

Material.—(Sub-)Recent material from beach sand at Paradise of Juan, near San Fernando, Philippine Islands.

Remarks.—On the Philippine Islands the species occurs with *T. jellineki* sp. nov.—A further record of *T. amicitiae* is given by McKenzie and Pickett (1984: Text-fig. 3 F, Table 1) in late Pleistocene deposits from Evans Head, New South Wales, Australia. The determination, however, can not be confirmed as the figured specimen lacks the characteristic posterodorsal vertical ridge in the LV. Therefore the record of the species is not plotted in Text-fig. 1.

TRIEBELINA RARIPILA (G.W. Müller, 1894)
(Pl. 1, fig. 12)

Triebelina raripila (G.W. Müller). KEIJ, 1976, p. 42 [summarising earlier records of the species in the Mediterranean and from the Upper Miocene of Turkey]; BONADUCE *et al.*, 1976, p. 23, Pl. 6, figs. 11, 12 [refer to earlier records of the species along the Tunisian Coast and record rare occurrences along the Apulia Coast].

Bairdia raripila G.W. Müller. YASSINI, 1979, p. 374, Pl. 1, fig. 6 [records the species from the Algerian Coast].

Material.—(Sub-)Recent specimens from Alexandria beach; Egypt.

Distribution.—Recent occurrences of the species are widely distributed in the Mediterranean: Limski Kanal (Uffenorde, 1972), Turkey (Doruk, 1974), Alexandria (this paper) and Algeria (Yassini, 1971). Fossil record from Upper Miocene of Turkey (Doruk, 1974); the species appears to be a direct descendant of *T. boldi* Key, 1955 of Aquitanian—Burdigalian age from France.

Remarks.—Occurs with *T. sertata* in Alexandria.

Genus GLYPTOBAIRDIA Stephenson, 1946

Type species.—*Glyptobairdia bermudezi* Stephenson. 1946 (= syn.: *Bairdia coronata* Brady, 1870).

GLYPTOBAIRDIA CORONATA (Brady, 1870)
(Pl. 3, figs. 1–3)

Glyptobairdia coronata (Brady). Van den Bold, 1974, p. 33 [summarising earlier references and distributional data]; Keij, 1976, p. 37, table 1 [stratigraphical range].
Triebelina coronata (Brady). Puri, 1974, p. 142, Pl. 6, figs. 3a,b.
Bairdoppilata (*Glyptobairdia*) *coronata* (Brady). Teeter, 1975, p. 421, Text-figs. 3h, 4f [figures specimens occurring rarely on carbonate-platform biofacies], table 1 [distributional data]; Palacios-Fest *et al.*, 1983, table 1, Pl. 1, fig. 5 [recording occurrence from the Gulf of Mexico to the Caribbean Province, and figuring one RV from W. off Mujeres Island].

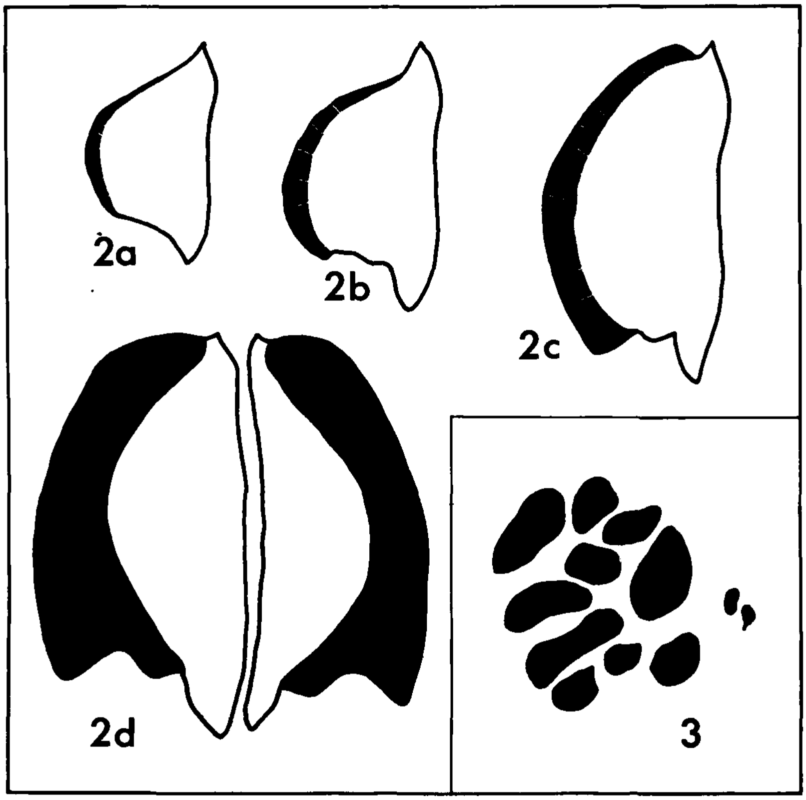
Material.—(Sub-)Recent and Recent specimens (partly with bristles and soft parts) from off St. Barts at 12m waterdepth, Lesser Antilles (leg. Van Morkhoven); from off Tobago, West Indies (leg. A. Lord); from Palancar reef at 30m and Paraiso reef at 15m waterdepth, Mexico (coll. Th. Jellinek).

Distribution.—Unknown outside the Caribbean region, to which it is obviously restricted.

Genus Havanardia Pokorný, 1968

Type species.—*Havanardia havanensis* Pokorný, 1968.

Remarks.—The type species of the alate bairdiid genus *Havanardia* Pokorný, *H. havanensis* was based originally on two right valves found in the "sand filling of a big *Strombus* shell, collected at a depth of approximately 20 meters at Rincon de Guanabo, Cuba" (Pokorný, 1968). Since then four more Recent species have been described from both sides of the Atlantic, three of which were



Text-figs. 2, 3.—*Havanardia havanensis* Pokorný, 1968. (Sub-)Recent from Palancar reef, Cozumel Island, Mexico, at 30 m waterdepth.—2. Dorsal view of various growth stages showing the increase of the fused part of the alae in juvenile left valve (2a–c) from A-3 to A-1 stage and in adult left and right valve (2d). Since the juvenile specimens are not ornamented in the alate region, pore canals can be seen in the fused alate part (in transmitted light), but not so in the entirely ornamented adult specimens; ×80.—3. Adductor (10) and mandibular (2) muscle-scar pattern of left valve (interior view); ×400.

recorded from off West Africa, *i.e.* from the inner shelf of Sierra Leone, Ghana, and western Nigeria (Keij, 1973), and the fourth one was found in a seabottom sample at a waterdepth of 24 m about 30 km offshore NE Trinidad (Keij, 1976). A further record of the genus, from early Pliocene deposits of Jamaica, is given by Keij (1976) and for Lower Miocene specimens from Midway atoll drill holes by Holden (1976) and from Gujarat, India (Khosla. 1978).—Further Recent finds of the type species were made by Palacios-Fest and Gío-Argáez (1979) in reef environments off Mujeres Island, Mexico. Sports activities of Dipl. Geol. Th. Jellinek at Palancar and Paraiso reefs, Cozumel Island, Mexico, yielded rich ostracod faunas from 15–30 metres depth, among which *H. havanensis* was also determined. Although soft parts were not preserved, the specimens showed no sign of water transport, as the species' associations contain various juvenile stages and adults together. It can be concluded therefore that the reefal slope is the natural habitat of the species.

HAVANARDIA HAVANENSIS Pokorný, 1968
(Pl. 2, figs. 3–7, Pl. 3, figs. 4–6; Text-figs. 2–3)

Havanardia havanensis POKORNÝ, 1968, p. 61, Pl. 1, figs. 1–2, Text-figs. 1–3 [2 RV from off Habana, Cuba]; PALACIOS-FEST and GÍO-ARGÁEZ, 1979, p. 25, Text-figs. 3a-d [recording 55 specimens from three stations off Mujeres Island, Mexico and illustrating four valves in different views]; PALACIOS-FEST *et al.*, 1983, table 1, Pl. 1, fig. 6 [referring to the occurrence in a transitional zone between the faunal provinces of the Gulf of Mexico and the Caribbean, and refiguring one LV (= 1979, Text-fig. 3b) from a station W. of Mujeres Island].

Material.—10 RV, 3 LV, 15 juvenile specimens and some fragments from bottom sample at Palancar reef at 30 m waterdepth, Cozumel Island, Mexico (coll. Th. Jellinek); 1 LV, 2 RV from bottom sample at Paraiso reef at 15 m waterdepth, Cozumel Island, Mexico (coll. Th. Jellinek).

Dimensions (length in mm).—The size of the specimens that prove adult by their fully developed duplicature ranges from 0.80 to 0.93 including presumably males and females. The size of juvenile specimens points to various growth stages, e.g. A-1 ≦0.74, A-2≦0.67, A–3≦0.60, and ?A–5≦0.48 (see also Text-fig. 2).

Remarks.—In the recently obtained material from off Cozumel Island the excellently preserved specimens clearly show that the fused part of the alar protrusion becomes wider with every growth stage (Text-fig. 2). In juvenile specimens the alae are smooth (Pl. 3, fig. 5), whereas in adult specimens the alae are ornamented (Pl. 2, figs. 3–5).

Distribution.—The species appears to be restricted to the Caribbean region. The faunal association in which the species occurs in the two samples from off Cozumel Island is dominated by a great number of bairdiids (*Paranesidea* sp. and *Neonesidea* sp.), whereas less frequent species are referred to *Caudites, Radimella, Orionina, Protocytheretta, Paracytheridea, Loxoconcha,* and *Xestoleberis. Glyptobairdia coronata* (Pl. 3, fig. 1), *Triebelina sertata,* and *Havanardia sohni* occur but rarely to very rarely.

Genus PTEROBAIRDIA McKenzie and Keij, 1977

Type species.—Pterobairdia maddocksae McKenzie and Keij, 1977

PTEROBAIRDIA MADDOCKSAE McKenzie and Keij 1977
Pl. 2, figs. 1–2

Bairdiidae, nov. gen., n. sp. VAN DEN BOLD, 1974, p. 32, Pl. 1, fig. 12 [locality as for the herein figured specimens, e.g. Pl. 2, figs. 1–2].

Alate species of *Bairdia* from the Recent of Australia. BENSON, 1974, p. 56, Pl. 1, fig. 11.

Pterobairdia maddocksae MCKENZIE and KEIJ, 1977, p. 370, Pl. 1, figs. 1–3, Text-figs. 3, 4.

Material.—1 LV, 1 RV from off W. coast of Sumatra, near Padang, at about 1,250 m waterdepth.

Remarks.—The type material from Onotoa, as well as that from the Flores Sea (McKenzie and Keij, 1977: Pl. 1, figs. 1–3), shows dense pitting of the valve surface, whereas the Sumatran specimens look rather smooth except for the pustulose ala. Certainly these specimens suffered from transport, as was concluded by McKenzie and Keij (1977: 369, "downslope transport from the shallow reefs is obvious").—A second recently described species, *Pt. briggsae* McKenzie, 1986 from two localities in the SW Pacific, *i.e.* at 34 m waterdepth at Ontong-Java lagoon and at 405 m waterdepth in the Kula Gulf (both localities W. of Solomon Islands), differs in several shell ornamentation features, in the width of the carapace, and in the amount of overlap.

ACKNOWLEDGEMENTS

We are indebted to Dipl.-Geol. Thomas Jellinek for the fruits of his diving activities in various parts of the world. Additional Caribbean material was collected during the CICAR Project (Co-operative Investigation of the Caribbean and Adjacent Regions), which was supported by the Natural Environment Research Council. Travelling expenses (ARL) provided by British Petroleum are gratefully acknowledged.

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DISCUSSION

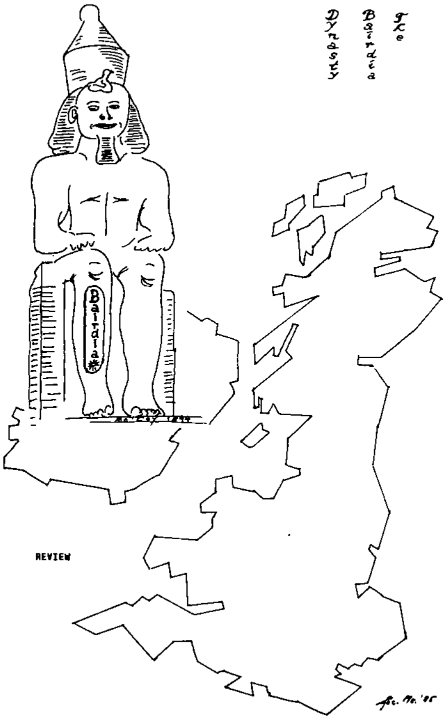
Maddocks: I have soft parts of a species of *Havanardia* in cave faunas of Bermuda, which will be published in *Stygologia* later this year. It is not a very alate species, and the soft parts are not very distinctive. There is also a species that is morphologically intermediate between *Havanardia* and *Neonesidea,* which will be classified in a new genus *Aponesidea.*

McKenzie: Would Dr. Hazel like to comment on the status of his and Holden's Eocene *Havanardia* from Tonga? The opinion would be useful in view of the authors' new record of *Havanardia* from the Indo-Pacific, because the Hazel/Holden taxon could be considered as a possible progenitor for the *Havanardia* group.

Whatley: For information Rosemary Titterton and I have a new species of *Pterobairdia* from the Recent of the Solomon Islands which we will publish soon. Also, we have new distributional records from Indonesia of many of the *Triebelina* species.

The *Bairdia* Dynasty Review-Activities-Aspects

HEINZ MALZ
Forschungsinstitut Senckenberg, Frankfurt am Main, F.R. Germany



TEXT-FIG. 1—The homeland of the *Bairdia* dynasty.

Dynasties are created by men, and they are represented by mighty men.

By definition a dynasty is the reigning family, and "hallowed be thy name, thy kingdom come".

Dynasties are known from many parts of the world, from China as well as from Egypt. For instance, Rameses II. was one of the most famous representatives of the 19th dynasty during the New Kingdom in Egypt. He, during the 66 years of his reign, was not only famous for his many victories, but was also successful within his family, counting 198 children of his own: 106 girls and 92 boys. This brings me—to what I have entitled ⩾ The *Bairdia* Dynasty ⩽, an epic in seven pictures.

REVIEW (Text-fig.1)

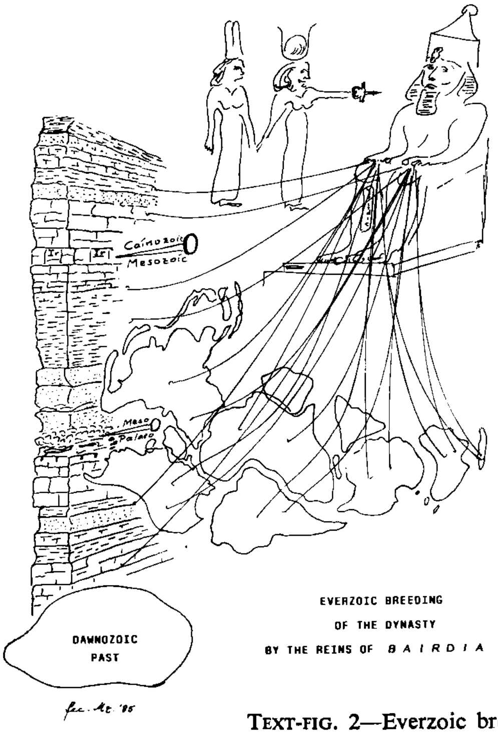
Ostracods, as you know, have many things in common with men: They grow, they feed, they breed and they develop dynasties. And that is where our story starts:

Although "long, long ago" applies to the beginning of fairy tales, it once happened in the early days of ostracod science that McCoy found a somewhat drop-shaped specimen in the Carboniferous of Ireland. In describing the specimen (1844) he referred to a cartouche on it that was not known at that time. Cartouches on other specimens had been deciphered already before as *"Cypris"* and *"Cythere"*, but the new cartouche was difficult to read. By hard comparative work he at last found out that the cartouche must read *"Bairdia"* the name of which refers to one of McCoy's famous British colleagues at that time. McCoy was not aware of the importance of his discovery then, for it often happens that great discoveries are evaluated much later. Presumably the *Bairdia* cartouche would even range among many others that are applied nowadays to short ranging units in the ostracod history or that are rejected for lack of information (as happened to the *Nesidea* cartouche dated by Costa (1846) on a badly illustrated specimen).

One lifespan after McCoy had found the *Bairdia* cartouche, the famous Norwegian G.O. Sars (1887) first fully recognized the importance of it. From now on the name *Bairdia* was no longer standing for a single genus, but for a whole dynasty: The *Bairdiidae* or (if you like) the Bairdiacea (which really do not have anything in common with any plants, as may be suggested by the misleading ending.)

THE REINS OF *Bairdia* (Text-fig. 2)

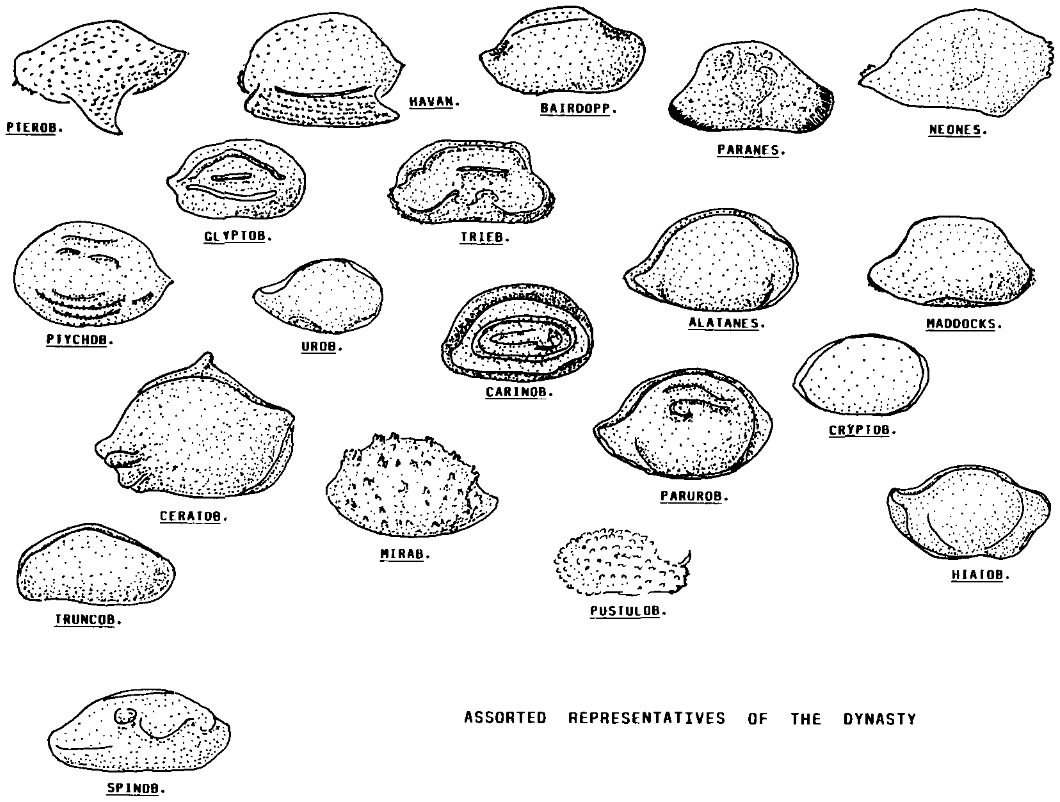
Nowadays, one hundred years later, the dynasty can be confirmed, for it is evidenced by many representatives from almost everywhere and from almost any geological time unit. In restricting the dynasty's distribution by the word "almost", I want to point out that there are still some gaps remaining to be filled by future research, but these aspects will be elucidated later on. Anyhow, you can see that the Godess Isis passes life to the *Bairdia* pharaoh for ever: "Hallowed be thy name".



TEXT-FIG. 2—Everzoic breeding of the dynasty by the reins of *Bairdia*.

ASSORTED CLANSMEN (Text-fig. 3)

In order to underpin and to improve the wide geographical and geological distribution of the dynasty, some of the prefixed and otherwise named Bairdias are briefly demonstrated by their outline. I willingly agree that, in the picture, the number of rather arbitrarily composed clansmen does not by far approach the number of the above mentioned Rameses' children. However, this selection stands as a *pars pro toto*, for one page is not sufficient to catch all the related clansmen.



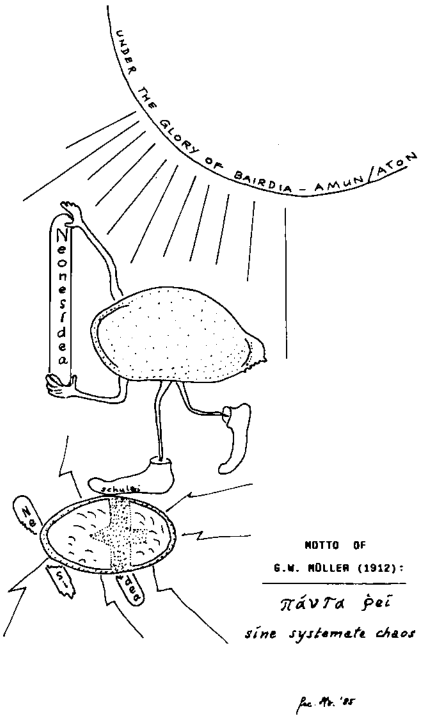
TEXT-FIG. 3—Assorted representatives of the dynasty.

GLORY OF *Bairdia* (Text-fig. 4)

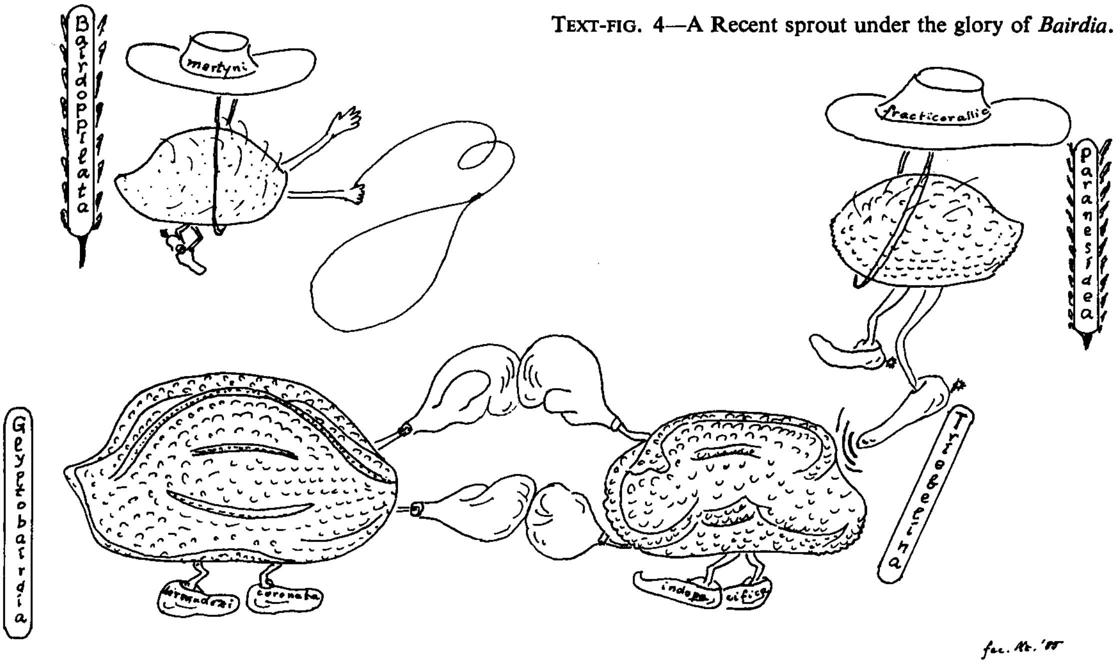
Although the dynasty achieved worldwide recognition, *Bairdia* itself remains nebulous.—Just as nebulous as *Nesidea*. *Nesidea* (Costa, 1846) that emerged as a competing Recent sprout beside *Bairdia,* is replaced now by the well-known *Neonesidea* (Maddocks, 1969). But, although *Neonesidea* plays trumps, *Bairdia* has still got the joker, for the glory of god Amun (or is it Aton?) is spreading its beams everywhere. Others beside and besides *Bairdia* are blinded. Thus, it may happen that a Recent ostracod belongs to *Neonesidea,* but by the help of Amun the Palaeozoic *Bairdia* is favoured for the determination. And therefore, by the help of nomenclature and taxonomy, living fossils are created. They keep everything running, and without systematics the whole system would become chaotic.

QUATERNARY EVENTS (Text-fig. 5; lower part)

A hard match, or nearly a fight, came up between *Triebelina* and *Glyptobairdia* in the late forties. Their rivalry started in 1946 and it still goes on. Interim results of this match (Text-fig. 6) are given here. Since the result comes out to fifty to fifty, bets can be arranged for the next round.



TEXT-FIG. 4—A Recent sprout under the glory of *Bairdia*.



QUATERNARY EVENTS

TEXT-FIG. 5 – Quaternary events.

Triebelina/Glyptobairdia MATCH (Text-fig. 5; upper part)

The match is over-shadowed by two more events. While the two are still competing, there are two related cartouches that claim for predominant reputation. Both these cartouches very much resemble Indian totem poles ornamented by birds' feathers, perhaps alluding to their Texan origin. The one is *Bairdoppilata* which, by its toothed hinge, tries to catch *Glyptobairdia.* The other is *Paranesidea.* Since its cartouche was found rather recently, it will not do any harm to *Triebelina.*

Results of Match

TEAMS:	*Glyptobairdia*	:	*Triebelina*
LEADERS:	STEPHENSON, 1946		v.d. BOLD, 1946
		0 : 1	(TRIEBEL, 1948)
		0 : 2	(KEY, 1954)
		0 : 3	(v. MORKHOVEN, 1958)
	(POKORNÝ, 1958)	1 : 3	
		1 : 4	(OSNOVY, 1960)
	(KOLLMANN, 1960)	2 : 4	
		2 : 5	(TREATISE, 1961)
		2 : 6	(v. MORKHOVEN, 1963)
	(MADDOCKS, 1969)	3 : 6	
		3 : 7	(BOLZ, 1971)
	(KEIJ, 1973)	4 : 7	
	(KEIJ, 1974)	5 : 7	
	(v.d. BOLD, 1974)	6 : 7	
		6 : 8	(PURI, 1974)
	(HARTMANN and PURI, 1974)	7 : 8	
		7 : 9	? (HARTMANN, 1975)
	(KEIJ, 1976)	8 : 9	
	(McKENZIE and KEIJ, 1977)	9 : 9	
		drawn	
	will be continued by prolongation (ISOP) in Japan 1985		
	(MALZ and LORD, 1985)	10 : 9	

SEPARATIST EFFORTS

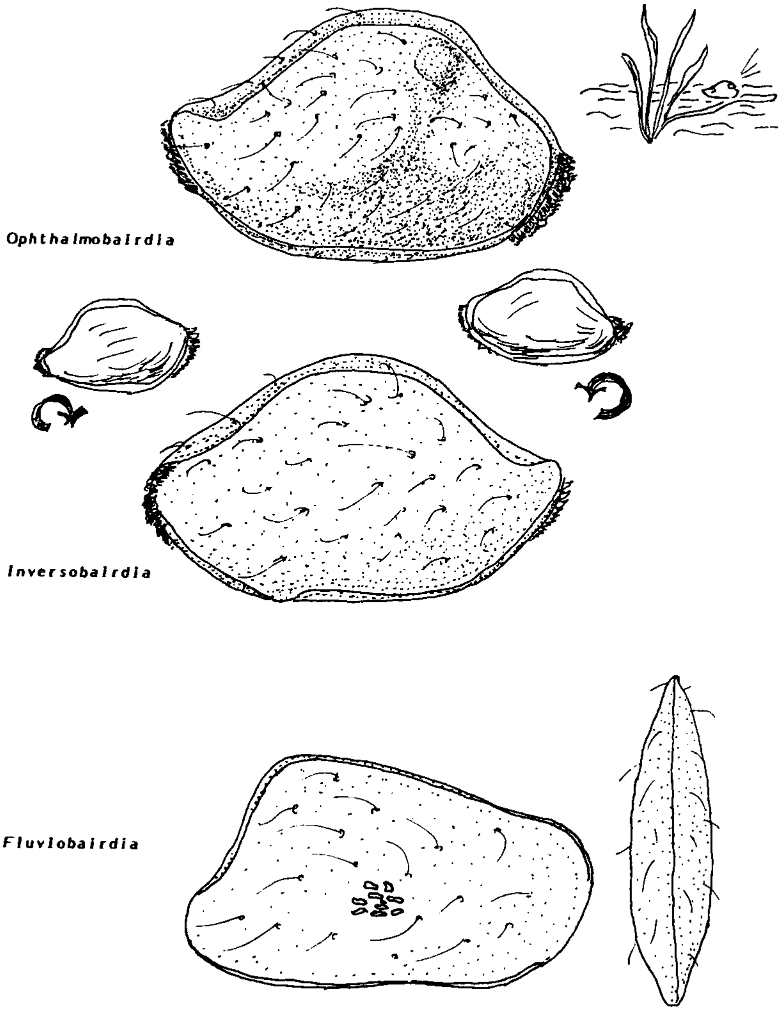
Since the early sixties of our century a rush on bairdiid cartouches can be noticed, mainly on Upper Triassic/Lower Jurassic ones. To demonstrate their relationship with the dynasty, most of them were prefixed by a characteristic feature (see also Text-fig. 3). This legion was then divided into 8 separate clans*, perhaps in order to find out different phylogenetic lineages, but the relationship was so close that separatist clanogene efforts shrunk by half.

ASPECTS (Text-fig. 6)

Researches on the dynasty continue and as has been stated before, many gaps remain to be

---

* Clans (= subfamilies) in alphabetical order; Alanellinae, Bairdiinae, Bairdoppilatinae, Bythocypridinae, Carinobairdiinae, Nodobairdiinae, Pussellinae, and Triebelininae.



TEXT-FIG. 6—Aspects for future research on speculative members of the *Bairdia* dynasty.

filled. Since we know two types of Recent winged Bairdias, we can conclude that the dynasty is on its best way to conquer a new biotope, the air (or even space). One of these winged forms which bears the *Havanardia* cartouche represents a more old-fashioned trial meant for gliding. The submarine coral platforms where it occurs can be suggested as ideal landing plains for strategical purposes. As we do not know anything about palaeo-strategy, this perhaps will be a future field of research. *Pterobairdia* which is the other winged cartouche represents the form of a modern streamline jet. The circumstances in which it was found in deeper water off Sumatra were explained (McKenzie and Keij, 1976) by post-mortem water transport, but why not consider it as a normal crash-down?

These aspects of new biotopes for Bairdias lead me to three more speculative cartouches: (1) *Ophthalmobairdia* (for only blind specimens are known up to now), (2) *Inversobairdia* (taking into account that reversal of overlap might be caused by the Corriolis effect), and (3) *Fluviobairdia* (which has certainly been misidentified as a freshwater *Candona*). Last, but not least, there is a chance for *Sinobairdia* which is waiting for identification from the endemic Bohai deposits.

Some Problems Associated with the Genus *Uroleberis*

JOHN W. NEALE AND PRATAP SINGH
University of Hull, England and
ONGC, Dehra Dun, India

ABSTRACT

The present interpretation of the genus *Uroleberis* is assessed and its stratigraphical distribution examined. S.E.M. stereographic paired photographs are given of some well known species including type specimens of seven species.

INTRODUCTION

During work on the Indian Tertiary faunas the authors became interested in the genus *Uroleberis* from the point of view of its stratigraphic potential as an age marker. The genus is widespread in the Palaeocene and Eocene faunas of the Indian sub-continent and the Middle East and is recorded as far afield as the Caribbean and Australia in rocks ranging in age from the late Cretaceous to Recent. Essentially a benthic shallow-water form, at least thirty species have been referred to the genus and a considerable number have also been recorded in the literature under open nomenclature. It quickly became apparent that what was conceived as a study of stratigraphical potential was overshadowed by the taxonomic problems involved. A thoroughgoing study and revision of this group of species is needed and the following contribution must be looked on merely as an interim report. Below we attempt to outline the problems and figure some of the well established species with SEM photographs. We are particularly indebted to Dr. O. Ducasse (France), Mr. R. Hodgkinson (Palaeontology) and Dr. G. Vauxhall and Miss Sheila Halsey (Zoology) of the B.M.N.H., London who kindly made available material from their collections.

TAXONOMY

The xestoleberid genus *Uroleberis* was established by Triebel in 1958 based on the Eocene *Eocytheropteron parnensis* Apostolescu, 1955 from the Lutetian of Parnes (Oise) in the Paris Basin as the type species. Triebel's principal figured material, also from the Lutetian of the Paris Basin, came from Liancourt-St-Pierre about 10 kilometres E.N.E. of Parnes, and from Grignon some 38 kilometres to the E.S.E. The particular characteristics of the genus are the development of a marked accommodation groove in the left valve and a small posterior caudal process coupled with a rather characteristic shape. As noted above, at least thirty species have been assigned to this genus as well as many left under open nomenclature. These range from Upper Cretaceous to Recent in age. The distribution of these, as known in the mid-seventies, has been ably covered by McKenzie (1977). This group of species shows a considerable range of variation from the type and covers forms such as the smooth Cretaceous species with rather poorly developed caudal process on the one hand to the strongly pitted Eocene and Recent forms of very characteristic shape such as *U. stagnosa* on the other. From this it appeared that some sub-division of the group might be possible.

At the same time, as knowledge of the Xestoleberididae has grown, a number of other genera and subgenera such as *Koilocythere* Deltel, 1963, *Ornatoleberis* Keij, 1975, *Pannonleberis* Krstic, 1974, *Pontoleberis* Krstic and Stancheva, 1967 and *Semixestoleberis* Hartmann, 1962 have been proposed over the last thirty years. None of these, except *Ornatoleberis*, is relevant to the present study. However, in 1980, Malz split the group and established *Foveoloberis* with Brady's *Xestoleberis foveolata* (Pl. 1, fig. 1; Pl. 2, fig. 4) as the type species (lectotype selected and figured by Puri and Hulings, 1976). This was to accommodate the latter and other species with a similar accommodation groove and shape to *Uroleberis* but characterised by a crenulate median hinge element. The two species figured by Malz (1980) also differ from the type species of *Uroleberis* in their strong pitting (foveolation). However, this latter feature need not necessarily be linked to a crenulate median hinge element. Originally in *U. angurium* (Pl. 2, fig. 8) and *U. stagnosa* (Pl. 1, figs. 12, 16; Pl. 2, fig. 3) Al-Furaih (1980) the median hinge element was described as smooth. This separated them from the co-eval *U. vulsa* Al-Furaih (1980) (Pl. 2, figs. 2, 5, 9) with its crenulate median element. The separation seemed artificial even though *U. vulsa* has a pustulose rather than a pitted ornament.

More recently Al-Furaih (1984) has returned to this group and has described them all as having a crenulate median bar, has transferred them to *Foveoleberis* and has added two more species from the Maastrichtian of Saudi Arabia, namely *F. ovata* and *F. trapezium*. *F. ovata* has a crenulate bar according to Al-Furaih (*op. cit.*) and fits well into the group with *U. angurium*, *U. stagnosa* and *U. vulsa*. *F. trapezium* is smooth, the nature of the hinge is unknown and it fits better with the *U. parnensis* group. The opposite situation is seen in the case of some smooth forms such as *Uroleberis batei* Neale, 1975 from the Santonian of W. Australia which was described as having a locellate hinge bar. On the other hand *U. batei* lacks a caudal process although this situation is also apparent in a number of European species usually placed in *Uroleberis*. This leads us to conclude that while the nature of the median element may be used to split the group of species hitherto assigned to *Uroleberis*, it is often difficult to determine, is not linked to ornamentation (foveolation) and may apparently separate what appear to be closely similar species and place them in

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PLATE 1—Stereoscopic paired photographs.

Fig. 1. *Foveoleberis foveolata* (Brady, 1880). Lectotype, BMNH 80.38.141. Right Valve, external view, Challenger Station 38.141 D8 off Booby Island. ×65.

Figs. 2,6. *U. striatopunctata* Ducasse, 1967. Univ. Bordeaux CO 2574. Carapace, Middle Eocene, Forage de Bassens, 83–91 m, France. 2. from right; 6. dorsal view. ×68.

Figs. 3,7. *U. globosa* Ducasse, 1967. Univ. Bordeaux CO 2572. Carapace, Middle Eocene, Blaye, France. 3. from right; 7. dorsal view. ×68.

Figs. 4,8. *U. subtrapezida* Ducasse, 1967. Univ. Bordeaux CO 2570. Right Valve, Middle Upper Eocene, Villeneuve de Blaye: Bois de Barbe, France. 4. external lateral view; 8. dorsal view. ×63.

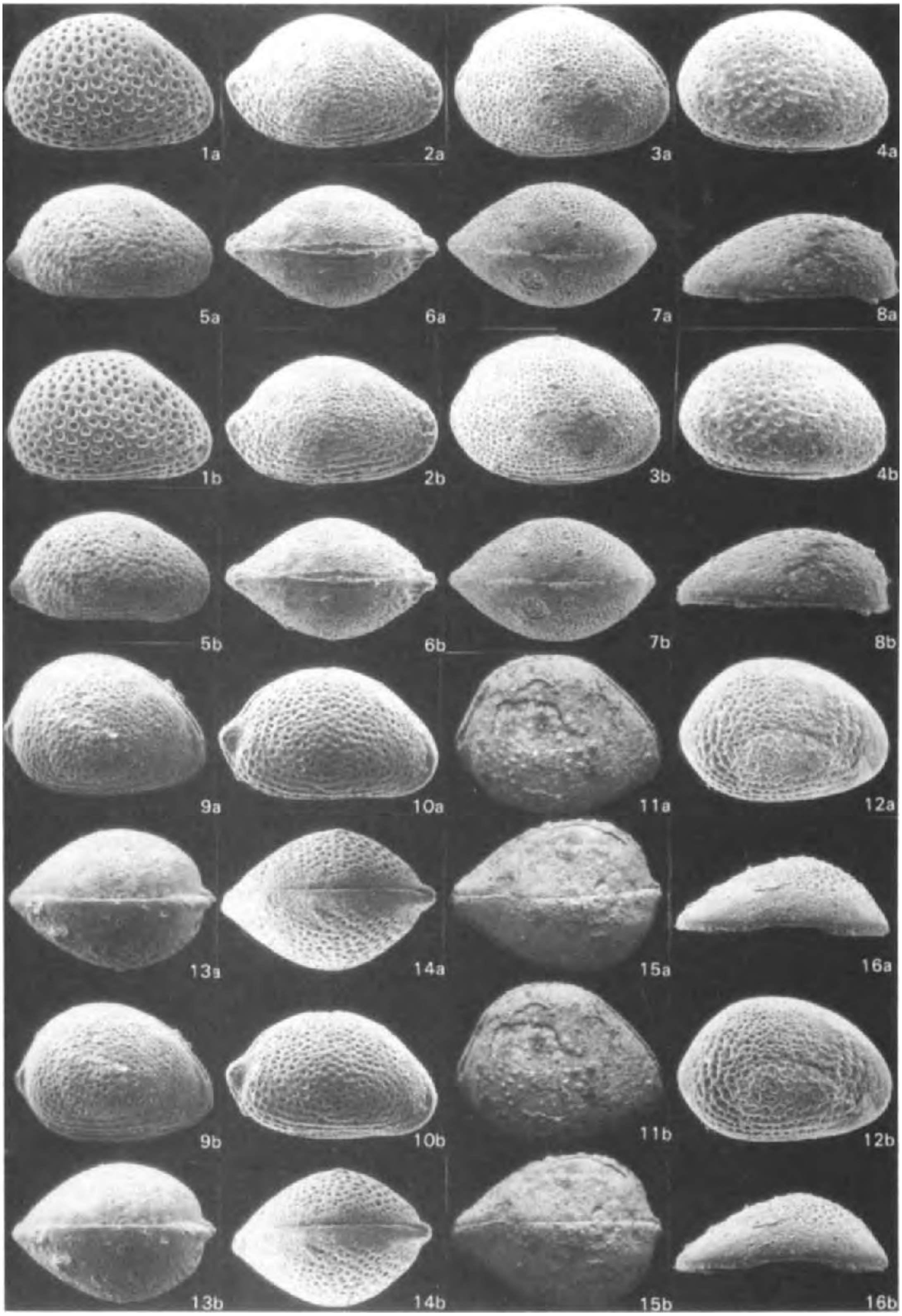
Fig. 5. *U. procera* (Deltel 1962). Univ. Bordeaux CO 2571. Right Valve external view, Stampian, Middle Oligocene, Tercis: Lesperon, France. ×50.

Figs. 9,13. *U. kymus* Ahmad MS. Holotype, BMNH OS 8189. Female carapace, FRCM 2033, Upper Eocene, Lindi Creek East Shore, Tanzania. 9. from right; 13. dorsal view. ×69.

Figs. 10,14. *U. armeniacum* Neale and Singh, 1985. Middle Eocene, Assam. 10. Holotype, IPE/H02/03/912. Male carapace from right; 14. Female carapace, IPE/B02/03/914, dorsal view. ×83.

Figs. 11,15. *U. ranikotiana* (Latham, 1938). Holotype, BMNH In. 37122. Carapace, Palaeocene, Pakistan. 11. from right; 15. dorsal view. ×52.

Figs. 12,16. *U. stagnosa* Al-Furaih, 1980. Holotype, BMNH Io. 5379, Female right valve, Lower Palaeocene, El-Alat W-1, 2044–2049 feet below surface, Saudi Arabia. 12. external lateral view; 16. dorsal view. ×58.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separate genera. There are three other disadvantages in the use of this criterion. Firstly, fossil *Uroleberis* most often turn up as closed carapaces and in consequence the nature of the median hinge element has not been ascertained in most species. However, it must be emphasised that if such a difference is considered to be of fundamental importance, difficulty of observation is no reason for not using it, although it can make taxonomic assignment very difficult. Secondly, the fact that the crenulation of the median hinge element is susceptible to erosion and post-depositional alteration is also a problem. In fossil forms this gives rise to considerable difficulty in anything but perfectly preserved material. Thirdly, and equally important, much depends on the mode of examination. Under optical microscopical examination a judgment may be made which becomes much more controversial with S.E.M. examination (Pl. 2, figs. 1–4). The Recent, well-preserved *Foveoleberis foveolata* (Brady) has a median element with well marked vertical striation although the positive and negative elements are not equally developed, the former being dominant (Pl. 2, fig. 4). This situation is seen less clearly and to varying degrees in the other examples figured. The median element in *U. subtrapezida* Ducasse (Pl. 2, fig. 1) has a fairly clear development of vertical striations with the positive and negative elements more comparable with each other than in *F. foveolata.* The same is true in *U. vulsa* Al-Furaih (Pl. 2, fig. 2). In *U. stagnosa* Al-Furaih (Pl. 2, fig. 3) the median hinge appears much smoother although it is possible to detect some vertical striation and particularly in stereoscopic view. It seems clear that this should be regarded as having a "crenulate" hinge. Under optical microscopic examination there is no doubt that the latter would be regarded as smooth as was the case in the original description. In the opposite valve (Left Valve) of *U. stagnosa* the median bar appears smooth even under S.E.M. examination and this appears to be a case where preservation and post-mortem history confuses the issue. For this reason it seems unwise to attach too much importance to whether the median hinge is crenulate or not. It is fair to say that under the optical microscope *U. batei* Neale appears to be crenulate. Under the S.E.M. it is very difficult to say whether this is the natural state or due to post-depositional history.

On the other hand, in its conception Malz's taxon does seem to encompass a closely related group of species. It would be useful to retain it and for this purpose one may consider the factors of shape and ornamentation. On this basis Al-Furaih's *U. angurium, A. stagnosa* and *U. vulsa* may be linked with Malz's *F. ymchengi* and others into a species group centred on *F. foveolata.* The group shows considerable variation in development of ornamentation and eye tubercle. Nevertheless, there are other forms, such as *U. oculata* Al-Furaih and *U. teiskotensis,* in which the carapace tapers posteriorly in side view and which are best accommodated in another species group which is not necessarily closely related to *Uroleberis* s.s.

It will be obvious that the common feature in the whole plexus is the well-developed accommodation groove in the left valve. The xestoleberid spot is important in confirming the wider relationship but is almost never seen in fossil material. Other features such as the nature of the median hinge element are difficult to verify and unknown in most fossil species and ornamentation, development of caudal process and eye tubercle show great variation. It is possible either to lump all the species together into *Uroleberis,* or to set up almost one genus per species which would obscure relationships and be self-defeating. Here we attempt to steer a middle course and to link species together into species groups which have some features in common. Because of the large number of poorly known species this must be regarded as provisional and we make no attempt to name them formally. To emphasise their inter-relationships it may be useful eventually to regard them as subgeneric groups of *Uroleberis* s.l. Because of the difficulties inherent in this group due to the number of poorly known taxa, we have used the name *Uroleberis* throughout, with the sole exception of the type species of *Foveoleberis foveolata,* and make some suggestions about species groups immediately after the following section before looking at their stratigraphical distribution.

Problematical forms

Some species which have been placed in *Uroleberis* in the past do not seem to belong there. In many cases it is difficult to be certain but *U. procerulus* Selensjova from the Campanian and Lower Maastrichtian of the Donbas does not appear to be a *Uroleberis* as far as it is possible to tell from her figures. *Cythere bimamillata* Brady, 1886, questionably referred to *Uroleberis* by Gramann (1975) who gave an excellent figure of a specimen from the Arakan Coast of Burma became the type species of the new genus *Ornatoleberis* Keij, 1975 being renamed *O. morkhoveni* because of problems of homonymy. Among other species which need re-investigation are *U. reticulata* Guha and Shukla, 1973 from the Lower Eocene of Tamilnadu and *U. oculata* Al-Furaih, 1980 from the Palaeocene of Saudi Arabia. Both these species have been compared with *U. teiskotensis* Apostolescu, 1961 from the Palaeocene of the Sudan. Unlike Apostolescu's other Sudan species *U. glabella* which is a good *Uroleberis, U. teiskotensis* is not typical and together with the two aforementioned species is best separated as a fourth species group which may be not closely related to *Uroleberis*. If further work sustains the idea that they are closely related the group can then be given formal taxonomic status. They are not considered further here. The forms figured as *Uroleberis*? from the Palaeocene of Greenland (Szczechura, 1971) and the Plio-Pleistocene of Vietnam (Herrig, 1978) were rightly treated with caution by those authors and belong elsewhere.

There are also a number of unfigured records which are of considerable interest but about which it is not possible to say anything meaningful. These include those of *Uroleberis* in the Eocene and Pliocene of China by Hou You-tang (1979) and those of Cirac and Peypouquet (1983) in Pleistocene cores in the Mediterranean near the Straits of Gibraltar.

American forms which range from the Lower Eocene of Guatemala and Belize to the Pleistocene of Jamaica are mainly Miocene and later and have proved difficult to assess since in the time available it has not been possible to examine any of the specimens. The same is true of Ye Chun Hui's species from Tibet.

The various taxa may be organised into a number of possible species groups.

Group I: Early, probably polyphyletic, species with reduced caudal process.

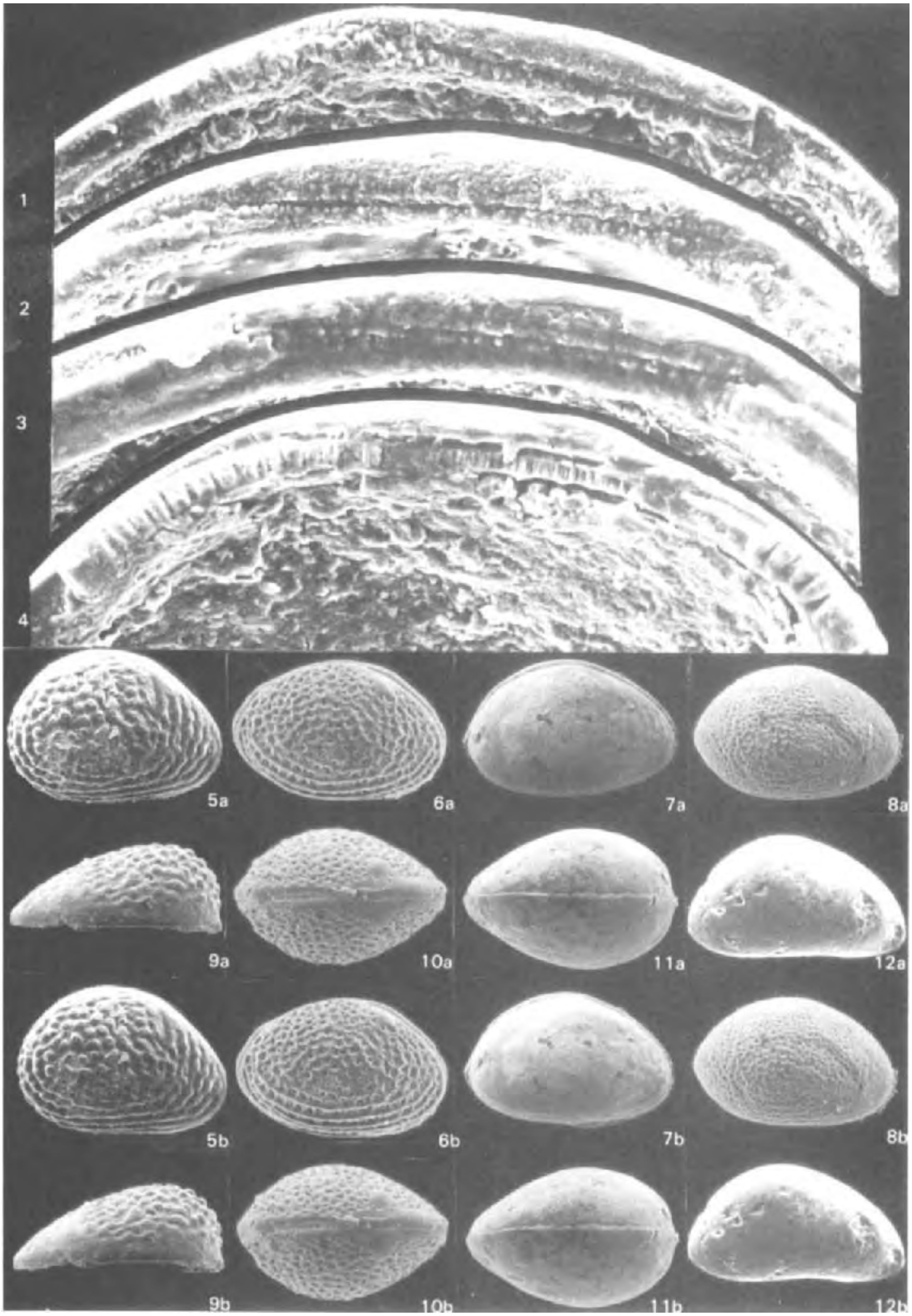
U. batei Neale, 1975. Santonian, W. Australia
U. marssoni (Bonnema, 1941). Maastrichtian, N. Europe
U. supplanata (Veen, 1936). Maastrichtian, N. Europe

Group II: Smooth forms with a typical caudal process. *"Uroleberis"*.

U. chamberlaini Sohn, 1970. Early Eocene, Pakistan
U. glabella Apostolescu, 1961. Palaeocene, Sudan
U. gopurapuramensis Guha and Shukla, 1973. Lower Eocene Virdachalam, Tamilnadu, South India.
U. kutchensis Guha, 1968. Middle Eocene, Kutch
U. nuda Ducasse, 1967. Middle Eocene, France
U. parnensis (Apostolescu, 1955). Eocene, Paris Basin
U. ranikotiana (Latham, 1938). Palaeocene, Pakistan.
U. shoragburensis (Bubikyan, 1958). Oligocene
U. trapezium (Al-Furaih, 1984). Maastrichtian, Saudi Arabia

Group III: Highly pitted and foveolate forms. Ornamentation and development of eye tubercle variable. *"Foveoleberis"*.

U. angurium Al-Furaih, 1980. Palaeocene, Saudi Arabia
U. armeniacum Neale and Singh, 1985. Middle Eocene, Assam
F. foveolata (Brady, 1880). Recent, Booby Island, N. of Australia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U. globosa Ducasse, 1967. Eocene, France and Spain
U. kynus Ahmad, MS. Upper Eocene, Tanzania
U. ovata (Al-Furaih, 1984). Maastrichtian, Saudi Arabia
U. procera Deltel, 1963. Stampian, M. Oligocene, France
U. pseudodemokrace Hu, 1982. Pleistocene, Taiwan
U. stagnosa Al-Furaih, 1980. Maastrichtian-Palaeocene, Saudi Arabia
U. striatopunctata Ducasse, 1967. Eocene, Aquitaine, France
U. subtrapezida Ducasse, 1967. Middle and Upper Eocene, Aquitaine, France
* *U. vulsa* Al-Furaih, 1980. Maastrichtian-Palaeocene, Saudi Arabia
U. ymchengi Malz, 1980. Pliocene/Pleistocene, S.W. Taiwan

* Perhaps better placed in Group V.

Group IV: Foveolate-reticulate species with or without eye tubercle. Probably polyphyletic. Tend to taper posteriorly in side view. Not necessarily closely related to *Uroleberis.*

U. oculata Al-Furaih, 1980. Palaeocene, Saudi Arabia
U. reticulata Guha and Shukla, 1973. Eocene, South India
* *U. teiskotensis* Apostolescu, 1961. Palaeocene, Sudan

* ? Related to *U. subtrapezida* Ducasse, 1967 (Group III)?

Group V: Heavy valves, almost vertical posterior margin, tendency to pustulose ornamentation. *Ornatoleberis Group.*

O. morkhoveni Keij, 1975 (= *Cythere bimamillatum* Brady, 1886). Recent, Sri Lanka, Burma
O. pustulatus Keij, 1975. Recent, South China Sea

Stratigraphical Distribution

The Cretaceous

Uroleberis first makes its appearence in the middle part of the Upper Cretaceous and is recorded in the Santonian and possibly Coniacian of Iran (Grosdidier, 1973) and the Santonian of Australia (Neale, 1975). Later in the European Maastrichtian a number of species occur and have been recorded in the works of Veen (1936), Bonnema (1941), Deroo (1966), Herrig (1966) and Szczechura (1965) ranging from Holland through the Island of Rugen to Poland.

The first records of Group III occur in the Upper Maastrichtian of Saudi Arabia (Al-Furaih, 1980) and this area and the adjacent part of the Indian sub-continent appears to have been the main centre of development and dispersal for the genus.

Species group I is only found in the Cretaceous and represents the early diversification of the *Xestoleberis* stock. *U. batei* Neale, 1975 (Pl. 2, fig. 12) from the Australian Santonian and *U. supplanata* (Veen, 1936) from the Maastrichtian of north-west Europe both lack a prominent caudal process but appear to have a crenulate bar in the LV hinge. Even so, Herrig (1966), who has

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PLATE 2—Figs. 1–4. Hinge in right valve. 1. *U. subtrapezida* Ducasse, 1967. Univ. Bordeaux CO 2570. ×425; 2. *U. vulsa* Al-Furaih, 1980. Holotype, BMNH Io. 5382. ×425; 3. *U. stagnosa* Al-Furaih, 1980. Holotype, BMNH Io. 5379. ×500; 4. *F. foveolata* (Brady, 1880). Lectotype, BMNH 80.38.141. ×425.

Figs. 5–12. Stereoscopic paired photographs.

Figs. 5,9. *U. vulsa* Al-Furaih, 1980. Holotype, BMNH Io. 5382, Female right valve, Lower Palaeocene, Abqaiq W-69, 1780–1790 feet below surface, Saudi Arabia. 5. external lateral view; 9. dorsal view. ×58.

Figs. 6,10. *U. oculata* Al-Furaih, 1980. Holotype, BMNH Io. 5375, Female carapace, Middle Palaeocene, El-Alat W-1, 1395–1397 feet below surface, Saudi Arabia. 6. from right; 10. dorsal view. ×68.

Figs. 7,11. "*U.*" *nuda* Ducasse, 1967. Univ. Bordeaux CO 2573. Carapace, Middle Eocene, Forage de Moulon: 156 m. 7. from right; 11. dorsal view. ×55.

Fig. 8. *U. angurium* Al-Furaih, 1980. Holotype, BMNH Io. 5372. Male right valve, Lower Palaeocene, Abqaiq W-69, 1870–1880 feet below surface, Saudi Arabia. External lateral view. ×73.

Fig. 12. *U. batei* Neale, 1975. Holotype, HU. 62.C.21. Female right valve, Santonian, Gingin, Western Australia. External lateral view. ×108.

published good figures of the latter remarks that it is "undeutlich gekerbte" while new SEM stereophotographs of *U. batei* are not entirely convincing. These two species appear to be more closely related to each other than to *U. marssoni* (also Maastrichtian north-west Europe) which has a fairly typical caudal process for the genus and a smooth median hinge element but appears to lack a prominent accommodation groove in the left valve. At the same time, typical members of pitted Group III appear in the Maastrichtian of Saudi Arabia such as *U. ovata* (Al-Furaih, 1984) and *U. stagnosa* Al-Furaih, 1980 (Pl. 1, figs. 12, 16; Pl. 2, fig. 3).

U. vulsa Al-Furaih, 1980 (Pl. 2, figs. 2, 5, 9) which is also placed here for the time being could equally well be placed in Group V on the basis of its heavy ornamentation, thick shell and steep posterior margin. The last two species continue into the Palaeocene. Al-Furaih (1984) is now of the opinion that *U. stagnosa* has a crenulate median hinge element but recent SEM photographs of the type figured here have not been able to resolve this satisfactorily because whilst there is no clear cut crenulation of the median hinge there is always the possibility that this may simply be a reflection of diagenesis, recrystallisation or other preservational phenomena. Grosdidier (1973) has figured two specimens from Iran as *"Uroleberis"*. These are difficult to interpet but his *"Uroleberis"* IR 08 (Pl. 4, fig. 30a–c) is a typical member of the group which comes from the Santonian. From the figures it appears to be finely pitted and so should perhaps be placed in Group II but to some extent this merely emphasises the artificial nature of the divisions. It represents the earliest occurrence of either Group II or Group III. Grosdidier's other specimen *"Uroleberis"* IR E14 (Pl. 4, fig. 32a–d) is even more difficult to interpret but should its assignment to the genus be upheld and its age (given as ?Coniacien) be confirmed this would make it the earliest known form.

The smooth *U. trapezium* (Al-Furaih, 1984) from Saudi Arabia is placed here in Group II and its hinge structure is unknown.

The Palaeocene

By Palaeocene times typical Group III forms such as *U. stagnosa* are well established. *U. angurium,* where ornamentation varies from smooth to pitted, is also tentatively assigned to Group III. *U. vulsa* also continues up from the Maastrichtian and as noted above could well be placed in Group V.

A widening of distribution occurs with the appearance in Pakistan of *U. ranikotiana* (Latham, 1938) (Pl. 1, figs. 11, 15) which is difficult to assign to a group. Latham's original figure shows quite coarse pitting but S.E.M. photographs of the holotype (Pl.1, figs. 11, 15) suggest that it is smooth or at most finely pitted. Notwithstanding the pustules on the posterior part of the shell and its infilling, which are interpreted provisionally as a post-mortem phenomenon, it is put in Group II. Smooth Group II forms are also represented by *U. glabella* of unknown hinge structure from the Sudan (Apostolescu, 1961) and Libya (Barsotti, 1963). This group is also represented in West Africa where the Nigerian *U.* aff. *U. glabella* of Reyment (1981) is very close to *U. ranikotiana.* Some species hitherto placed in *Uroleberis* are not typical in shape and are here placed in Group IV. These include *U. teiskotensis* Apostolescu, 1961 from Sudan and Libya (Barsotti, 1963) although this bears a considerable resemblance to the Eocene *U. subtrapezida* Ducasse 1967 which is somewhat tentatively placed in Group III. *U. oculata* Al-Furaih, 1980 from Saudi Arabia and the later Eocene *U. reticulata* Guha and Shukla, 1973 from South India are also placed in Group IV.

The Eocene

Together with the Palaeocene, the Eocene shows the maximum development of *Uroleberis* which is particularly widely recorded in the Indian sub-continent. In the Lower Eocene *U. chamberlaini* Sohn from Pakistan and *U. gopurapuramensis* Guha and Shukla from S. India are both Group

II species. *U. reticulata* Guha and Shukla, also from S. India, is placed in the problematical Group IV.

In the Middle Eocene *U. armeniacum* Neale and Singh (Pl. 1, figs. 10, 14) occurs in Assam (Group III) and *U. kutchensis* Guha in Kutch. The punctation described in the latter appears to be extremely fine and Guha's figure (Pl. 1, figs. 1, 4, 8) shows such a close resemblance to the typical smooth *Uroleberis* that it is put in Group II. Khosla (1968) figured as *Uroleberis* sp. what appears to be a typical Group II *Uroleberis* from the Eocene Kirthar Beds of Rajasthan.

Further afield Ahmad (1977 MS) described *U. kymus* from the Upper Eocene of Tanzania and Salahi (1966) has described typical Group II (*Uroleberis* n. sp. 1) and Group III (*Uroleberis* n. sp. 2) from the Lower and Upper Eocene respectively of Libya. The latter is very similar to *U. striatopunctata* Ducasse, 1967 from the Eocene of France.

In Western Europe, the Eocene (Lutetian) of the Paris Basin provides the type species *U. parnensis* (Apostolescu, 1955) of Group II. Group III are well represented in France by *U. striatopunctata* Ducasse (Pl. 1, figs. 2, 6) and *U. globosa* Ducasse (Pl. 1, figs. 3, 7) both mainly Middle Eocene. *U. subtrapezida* Ducasse (Pl. 1, figs. 4, 8; Pl. 2, fig. 1), commonest in the Upper Eocene of Aquitaine, is also placed in Group III and has much in common with *F. foveolata* although the shape is not entirely typical. *"U." nuda* Ducasse (Pl. 2, figs. 7, 11) was only tentatively referred to *Uroleberis* because the internal morphology was unknown. The internal morphology is still unknown and although the shape is not completely characteristic it is here provisionally placed in Group II.

In the western hemisphere, Bold (1946) recorded an almost smooth form from the Lower Eocene of Guatemala and Belize as *?X. ranikotiana.* Whilst probably not the Pakistan species it is not possible to shed further light on this at present.

Hornibrook (1952) lists the living species *F. foveolata* from the Eocene of New Zealand but does not figure it. One may assume that Group III *Uroleberis* occur but the species needs verification.

The Oligocene

Occurrences in the Oligocene are rather rare. Deltel (1963) described *U. procera* (Pl. 1, fig. 5) from the Middle Oligocene and Ducasse (1969) also found it in the basal Oligocene of France. Bubikyan (1958) described *X. schoragburensis,* which appears to be a typical Group II *Uroleberis,* from the Erevan Basin of the USSR, and McKenzie (1979) has noted that the genus occurs in the Janjukian Stage of the Willunga Embayment near Adelaide, Australia. *F. foveolata,* listed as occuring in every System from the Eocene onwards, was noted in the late Oligocene and early Miocene of offshore Bombay (Guha, 1975). Group III *Uroleberis* clearly occur although the species perhaps needs re-assessing.

The Miocene

Uroleberis is not common in the Miocene and most of the records are from the Americas. Bold (1973) recorded *Uroleberis* sp. from the Lower and Middle Miocene of Cuba but without figuring the specimens. His specimen of *Uroleberis* sp. from the Late Miocene of Puerto Rico and Cuba (Bold, 1969) shows a flattened ventral surface with distinct concentric ornamentation and can only be doubtfully referred to the genus.

The Pliocene

Pliocene *Uroleberis* are not generally well known. Under open nomenclature the genus has been recorded in China, Vietnam, S. Hispaniola and Haiti and *F. foveolata* listed from Guangdong, China. Bold (1968, 1971) lists *U. torquata* from the N. Dominican Republic and Cuba and *U. triangulata* from Jamaica and the N. Dominican Republic (Bold, 1971, 1975) but it has not been possible to make a satisfactory judgement of the genus or grouping.

The Pleistocene

Bold (1971) gives *U. angulata* (Brady) from Jamaica but it cannot be placed in any of the recognised groups and its genus is doubtful. Hu (1982) described the new *U. pseudodemokrace* from the Pleistocene of Taiwan which is here placed in Group III. The genus also occurs near the Straits of Gibraltar in cores (Cirac and Peypouquet, 1983).

Recent

Principal references are to *F. foveolata* whose type locality is 6–8 fathoms off Booby Island (10°36′S, 141°55′E) North of Australia. It is very common in this area and McKenzie (1976) notes that it occurs in 60% of samples from the Sahul Shelf. Gramann (1975) notes its occurrence in the Straits of Malacca and Ishizaki (1979) found it in the East China Sea. Smooth Group II *Uroleberis* do occur, however, as seen in the specimen from off the Australian coast near Adelaide figured in his original paper by Triebel (1958).

CONCLUSIONS

In late Cretaceous times the Xestoleberididae diversified to produce a group of forms whose common characteristics are a well-developed accommodation groove in the left valve, marked sexual dimorphism and "xestoleberid spot" (rarely seen). This plexus, to which the generic name "*Uroleberis*" may be loosely attached, shows great variation in the development of such features as shape, caudal process, median hinge element, eye tubercle and ornamentation. The group has previously been sub-divided on the basis of the smooth or crenulate nature of the median hinge element but this is difficult to determine satisfactorily for a variety of reasons and is unknown in the vast majority of species. For convenience we have provisionally recognised five groups of species some of which could probably be subdivided further. Further work will refine these groups and the species they contain. The question of subgeneric status or full generic status for them is a matter of personal preference and philosophy.

Group I is an early, probably polyphyletic group. Group II is centred on *Uroleberis* s.s. and Group III on *Foveoleberis*. Group IV is problematical and Group V synonymous with *Ornatoleberis*. As far as present knowledge goes, their greatest development occurs in the Palaeocene and Eocene of the Middle East, the Indian sub-continent and contiguous areas where they may prove stratigraphically useful.

We have clearly come to vastly different conclusions than those which we expected when we came to write this paper. Instead of being able to deal with the biostratigraphy, palaeoecology and palaeogeography we found that fundamental taxonomic problems were paramount. In consequence we have reviewed this aspect of the group with a view to directing attention to areas where a great deal of detailed work is still needed and hope to turn to other aspects on a later occasion.

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Tertiary and Recent Species of *Miocyprideis* from India

SUBHASH C. KHOSLA
University of Rajasthan, Udaipur, India

ABSTRACT

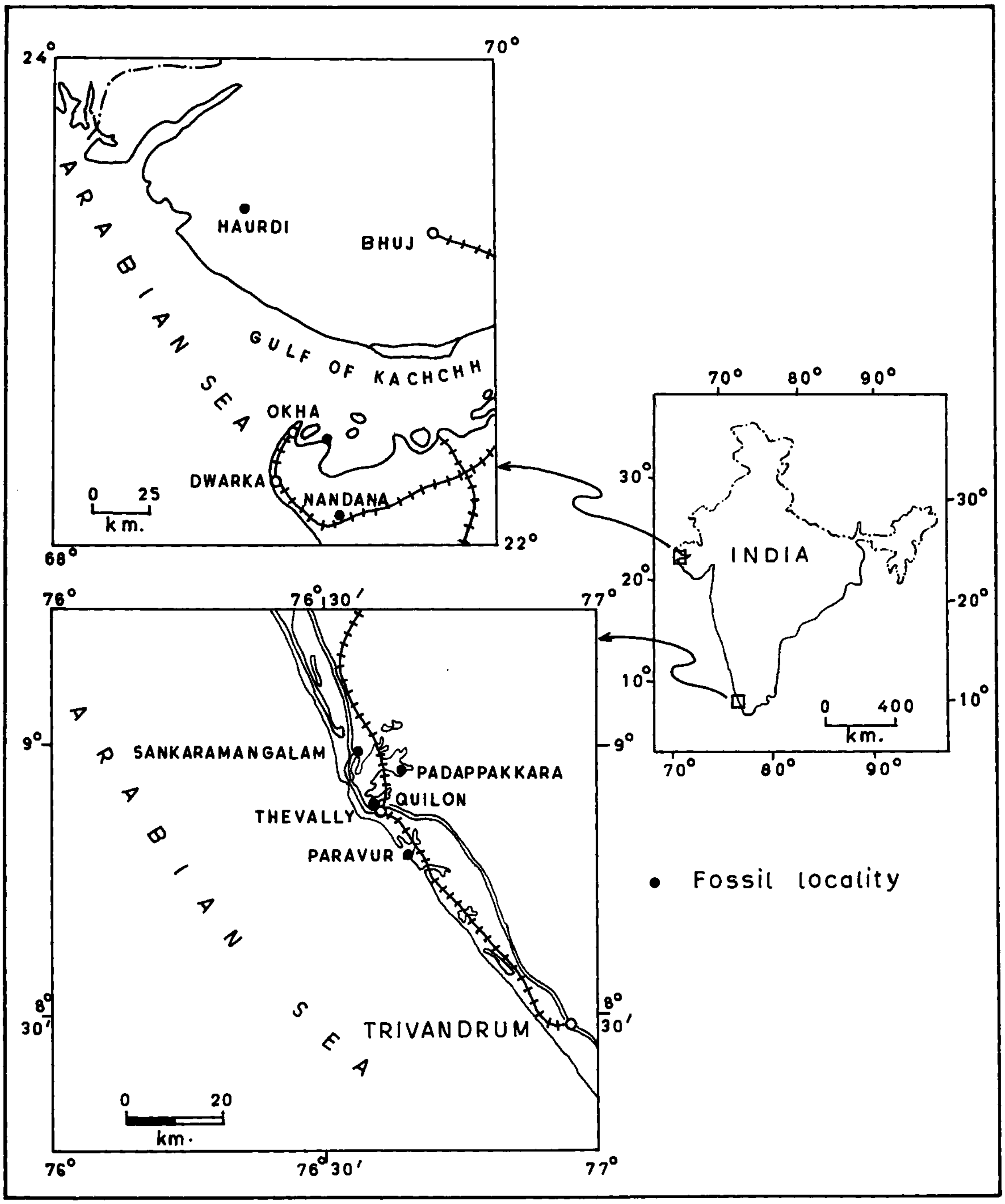
The genus *Miocyprideis* Kollmann, 1960, occurs commonly in the Tertiary and Recent sediments of India. Seven species, including four new, are recognised from these sediments. They are *Miocyprideis chaudhuryi* (Lyubimova and Guha, 1960), *M. kachchhensis* n.sp., *M. lyubimovae* Khosla, 1978, *M. okhaensis* n. sp., *M. paravurensis* n. sp., *M. punctata* n. sp., and *M. thirukkaruvensis* Guha and Rao, 1976. The last species is divided into three morphotypes on the basis of number of pits and their distribution pattern. These morphotypes are alike in all other characters and hence included in a single species.

In addition, the paper also reviews the taxonomic status of the three species *Cytheridea spinulosa* Brady, 1868, *Clithrocytheridea atjehensis* Kingma, 1948, and *Miocyprideis lyubimovae* Khosla, 1978, which were earlier assigned to the genus *Miocyprideis* and have been transferred to the genus *Bishopina* Bonaduce, Masoli and Pugliese, 1976, by Wouters (1981). These species clearly lack the marginal surface ridges, characteristic of *Bishopina*. The species are retained in *Miocyprideis* on the basis of their subovate to subrectangular lateral outline, presence of anterior and posterior marginal spines, merodont/entomodont hinge, two frontal scars and the characters of the marginal zone. Systematics of the species recorded are given in the paper.

INTRODUCTION

The genus *Miocyprideis* Kollmann, 1960 occurs commonly in the Tertiary and recent sediments of India. This is represented by seven species. Three of these are previously known taxa. These are *Miocyprideis chaudhuryi* (Lyubimova and Guha, 1960), *M. lyubimovae* Khosla, 1978, and *M. thirukkaruvensis* Guha and Rao, 1976. The other four species *Miocyprideis kachchhensis, M. okhaensis, M. paravurensis* and *M. punctata* are new.

The genus was introduced by Kollmann (1960) for Cytherideinae ostracods. Among others, he included the two species *Cytheridea spinulosa* Brady, 1868, and *Clithrocytheridea atjehensis* Kingma, 1948, in this genus. Many authors after him assigned these two species to the genus *Miocyprideis*. Recently Wouters (1981) describing the new species *Bishopina vangoethemi* stated that *Cytheridea spinulosa* and *Clithrocytheridea atjehensis* along with certain other species, including *Miocyprideis lyubimovae* Khosla, 1978, can be considered to belong to the genus *Bishopina* Bonaduce, Masoli and Pugliese, 1976. According to him species of *Bishopina* differ from the type species of *Miocyprideis* (*M. janoscheki* Kollmann, 1960) in being smaller, having a subrectangular shape



TEXT-FIG. 1—Map showing the fossil localities of *Miocyprideis* species in India.

instead of a rounded one, lacking the posteroventral right valve spine and in often having thick plate-like marginal denticles. Furthermore, in *Bishopina* species the greatest width in dorsal view is situated in the posterior half and some species show a very broad, subtruncate posterior extremity, often accentuated by a posterior transverse ridge consisting of irregular thickenings. A study of the type description of the genus *Bishopina* reveals that it is characterised by shape and ornamentation typical of the genus *Cytherelloidea.* In the type species—*Bishopina mozarti* Bonaduce, Masoli and Pugliese, 1976, the valve surface is ornamented by two marginal ridges; the outer one starts from the anterodorsal area and runs parallel to the anterior margin as far as the mid-ventral area; the othe ridge runs parallel, and inside, the first one contouring almost the entire valve; the posterior part of this ridge is almost vertical. At both sides of the interior ridge two chains of deep, elliptical foveolae are evident, especially anteriorly and ventrally. At the mid-height of the valves between the muscle scars and the posterior vertical ridge, two rows of deep foveolae are present.

The species *Cytheridea spinulosa, Clithrocytheridea atjehensis* and *Miocyprideis lyubimovae* clearly lack surface ridges. In the opinion of the present author these species are not congeneric with *Bishopina* as suggested by Wouters (1981). On the basis of their subovate to subrectangular lateral outline, presence of anterior and posterior marginal spines, merodont/entomodont hinge, two frontal scars and characters of the marginal zone the species are retained in the genus *Miocyprideis.* Systematics of the species recorded are given in the paper.

Location of Samples

The material from which species of *Miocyprideis* are being recorded comes from 4 localities in Kerala and 3 in Gujarat. Details of the localities are given below and also in Text-fig. 1.

Kerala
- A. The Quilon beds (Burdigalian) exposed at the base of cliff sections:
  - (i) about 1.5 kilometres northwest of Padappakkara village (8° 58′ N: 76° 38′ E) on the bank of Asthamundi Kayal (lake);
  - (ii) 2.25 kilometres west of Paravur village (8° 49′ N: 76° 40′ E).
- B. The Quilon beds encountered in subsurface sections:
  - (iii) Sankaramangalam well 4 (8° 59′45″ N: 76° 32′15″ E);
  - (iv) Thevally well (8° 53′45″ N: 76° 34′45″ E).

Gujarat
- (v) The Lower Miocene beds (Burdigalian) exposed near Nandana village (22° 07′46″ N: 69° 17′ 14″ E), Saurashtra;
- (vi) The Ramania Stage (Lattorfian-Rupelian) exposed in the Rakhdi Stream south of Harudi village (23° 20′30″ N: 68° 41′10″ E), Kachchh;
- (vii) Shallow water sediments (1–2 metres), near Okha (22° 06′ N: 69° 07′ E), Gulf of Kachchh.

For details of stratigraphy reference may be made to Khosla (1978), Khosla and Pant (1982), and Khosla and Nagori (1985).

Repository

All the illustrated specimens are deposited in the Museum of the University of Rajasthan, Department of Geology, and references to them are designated by RUGDMF catalogue numbers in the text and plate explanations.

SYSTEMATIC DESCRIPTION

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925
Subfamily CYTHERIDEINAE Sars, 1925
Genus MIOCYPRIDEIS Kollmann, 1960

MIOCYPRIDEIS CHAUDHURYI (Lyubimova and Guha, 1960)

(Pl. 1, fig. 1)

Cyprideis chaudhuryi Lubimova and Guha, in LUBIMOVA, GUHA and MOHAN, 1960, p. 30–31, Pl. 2, fig 9.
Miocyprideis chaudhuryi: GUHA, 1961, Pl. 2, Text-figs. 3, 19; GUHA *et al.*, 1965, p. 4, Pl. 3, fig. 4; GUHA, 1968, p. 212, Pl. 1, figs. 13, 24; KHOSLA, 1978, p. 273, Pl. 2, fig. 11, Pl. 6, fig. 8.

Illustrated specimen.—A right valve, RUGDMF No. 294 (Pl. 1, fig. 1; L. 650 μm; H. 350 μm).

Diagnosis.—Carapace elongate, subovate in lateral outline, left valve overlaps right valve all along margin; dorsal margin convex, sloping down posteriorly; ventral margin slightly convex in left valve and straight in right valve; anterior margin broadly rounded; posterior margin less so; both fringed with minute spines; valve surface smooth to sparsely pitted.

Remarks.—This species has so far been recorded from the Lower Miocene beds of Kachchh (Lyubimova, Guha and Mohan, 1960; Guha, 1961; Mehra, 1980), Saurashtra (Guha, 1967a; Khosla, 1978), the Cauvery basin (Guha *et al.*, 1965; Guha, 1968), Kerala (Guha and Rao, 1976; Dutta, 1976; Rao and Datta, 1980), the Oligocene beds of Cambay (Guha, 1967b) and the Late Oligocene beds of the Bombay High (Guha, 1975).

MIOCYPRIDEIS KACHCHHENSIS n. sp.

(Pl. 1, figs. 2, 3; Text-fig. 2)

Etymology.—After the district of Kachchh, Gujarat, India.

Type.—Holotype, a male carapace, RUGDMF No. 295 (Pl. 1, fig. 2; L. 550 μm; H. 290 μm; W. 250 μm) from olive green shales, Ramania Stage (Lattorfian-Rupelian) of Rakhdi Stream, Kachchh.

Illustrated specimens.—Paratype I, a male carapace, RUGDMF No. 296 (Pl. 1, fig. 3; L. 550 μm; H. 290 μm; W. 250 μm). Paratype II, a female left valve, RUGDMF, No. 297 (Text-fig. 2; L. 580 μm; H. 370 μm).

Material.—Ten carapaces, 93 open valves.

Diagnosis.—Carapace subovate in lateral outline; valve surface densely pitted, pits near anterior and posterior ends arranged in rows parallel to margin.

Description.—Carapace subovate in lateral outline, with greatest height near middle; left valve larger than right valve, overlapping distinctly along dorsal and ventral margins; dorsal margin arched; ventral margin slightly convex in left valve and straight in right valve; anterior margin

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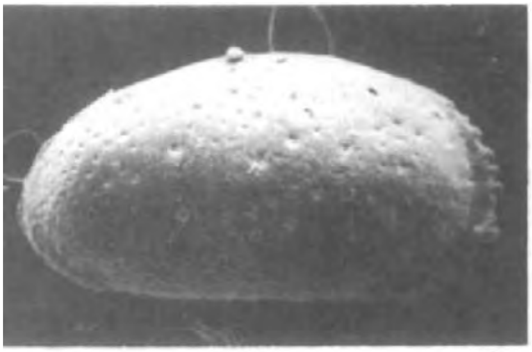
PLATE 1—Fig. 1. *Miocyprideis chaudhuryi* (Lyubimova and Guha). Lateral view of right valve (RUGDMF No. 294). ×96.

Figs. 2–3. *Miocyprideis kachchhensis* n. sp. 2. Right valve view of male carapace (holotype, RUGDMF No. 295). ×95; 3. Dorsal view of male carapace (paratype I, RUGDMF No. 296). ×96.

Figs. 4–6. *Miocyprideis okhaensis* n. sp. 4. Right valve view of female carapace (holotype, RUGDMF No. 298). ×95; 5. Internal view of female left valve (paratype I, RUGDMF No. 299). ×95; 6. Dorsal view of male carapace (paratype II, RUGDMF No. 300). ×92.

Figs. 7–8. *Miocyprideis paravurensis* n. sp. 7. Lateral view of left valve (holotype, RUGDMF No. 301). ×89; 8. Lateral view of right valve (paratype I, RUGDMF No. 302). ×88.



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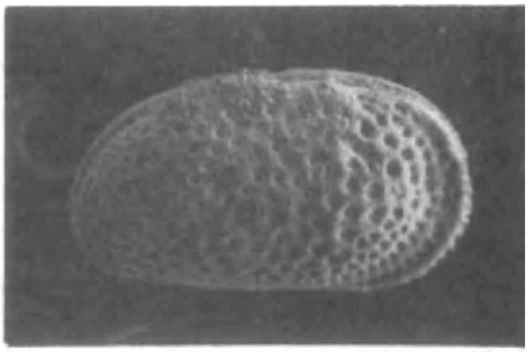

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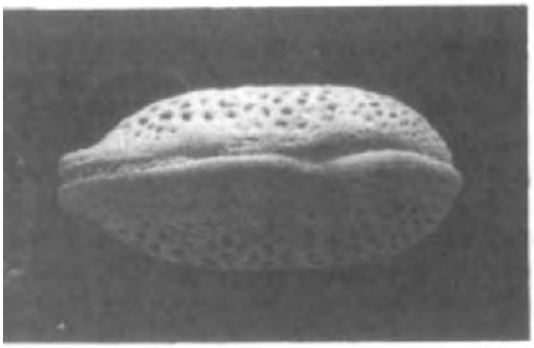

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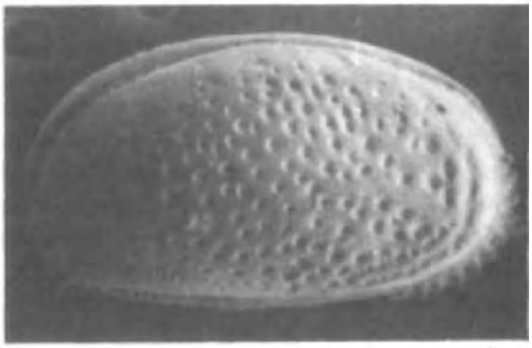

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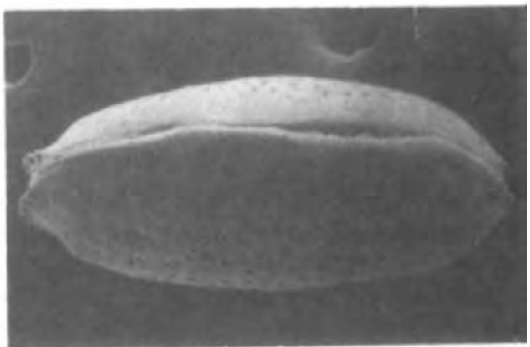

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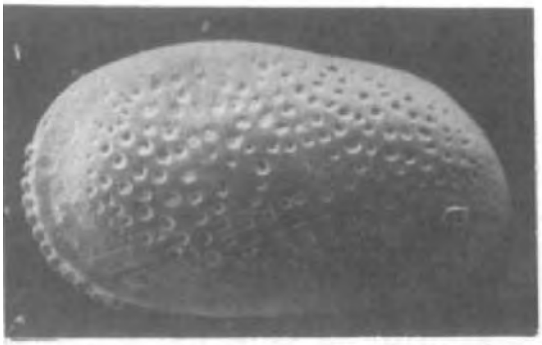

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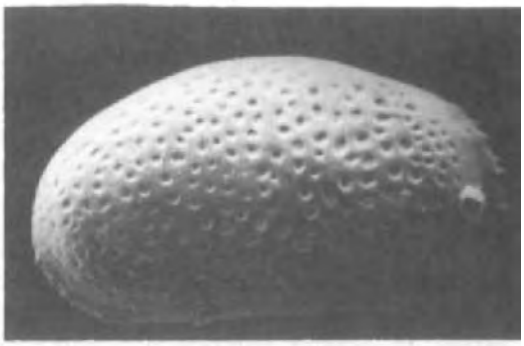

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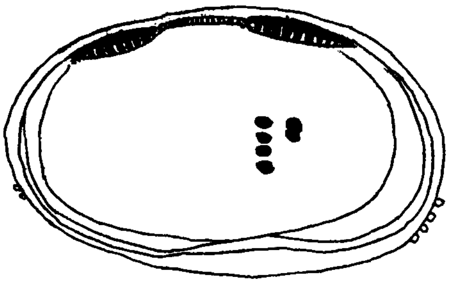


TEXT-FIG. 2—*Miocyprideis kachchhensis* n. sp. internal view of a left valve (RUGDMF no. 297).

broad and evenly rounded, fringed with 12–13 minute spines; posterior margin narrow, sloping downwards in upper half and rounded in lower; in dorsal view anterior end compressed, carapace otherwise biconvex, with maximum width posterior to middle. Surface of each valve densely pitted, pits near anterior and posterior ends parallel to margin.

Inner lamella widest anteriorly and narrow along ventral and posterior margins; line of concrescence and inner margin coincide; selvage subperipheral; marginal pore canals numerous, straight and thin; central muscles comprise a vertical row of four adductor scars, and two frontal scars. Hinge merodont/entomodont; in the left valve it consists of an elongate, loculate anterior socket, followed by a short finely crenulate median bar and then a long loculate posterior socket; hinge complementary in right valve.

Remarks.—In outline the present species resembles *Miocyprideis chaudhuryi* (Lyubimova and Guha, 1960), originally described from the Lower Miocene beds of Kachchh, but differs in being smaller in size and having a densely pitted surface. In *M. chaudhuryi* the valve surface is either smooth or sparsely pitted.

Occurrence.—This species occurs commonly in the Ramania Stage of Bermoti series of Kachchh.

MIOCYPRIDEIS LYUBIMOVAE Khosla, 1978

Miocyprideis lyubimovae KHOSLA, 1978, p. 273, Pl. 2, figs. 14–15, Pl. 6, fig. 9.

Diagnosis.—Carapace subrectangular in lateral outline, with greatest height anterior to middle; left valve larger than right valve, overlapping almost all along margin; anterior margin fringed with 14 thick spines and posterior margin with five to seven spines; in dorsal view extremities compressed, sides slightly converging anteriorly, maximum width near posterior end; surface of each valve ornamented by pits, and a weak elevation near posterior end.

Remarks.—This species has previously been described only from the Lower Miocene beds of Saurashtra by Khosla (1978). The species closely resembles *Miocyprideis thirukkaruvensis* Guha and Rao, 1976, in lateral outline but can be easily differentiated by the absence of a median vertical depression.

MIOCYPRIDEIS OKHAENSIS n. sp.

(Pl. 1, figs. 4–6)

Etymology.—After the port of Okha, Gulf of Kachchh, Gujarat, India.

Type.—Holotype, a female carapace, RUGDMF No. 298 (Pl. 1, fig. 4; L. 690 μm; H. 390 μm; W. 310 μm) from near Okha, Gulf of Kachchh, India, Recent.

Illustrated specimens.—Paratype I, a female left valve, RUGDMF No. 299 (Pl. 1, fig. 5; L. 700 μm; H. 390 μm). Paratype II, a male carapace, RUGDMF No. 300 (Pl. 1, fig. 6; L. 690 μm; H. 370 μm; W. 270 μm).

Material.—Fifty-five carapaces and 30 open valves.

Diagnosis.—Carapace elongate-subovate in lateral view; valve surface coarsely pitted; anterior margin fringed with 10–11 denticles and posterior margin with seven or eight spines.

Description.—Sexual dimorphism present, males being more elongate, less high and wide than females; carapace elongate, subovate in lateral outline, with greatest height slightly anterior to middle; left valve larger than right valve and except for anterior margin overlapping all along margin; dorsal margin gently arched in left valve and convex in right valve; ventral margin nearly straight; anterior margin evenly rounded and fringed with 10–11 spines in lower half; posterior margin sloping down in upper part and rounded in lower part bearing seven or eight spines; in dorsal view carapace biconvex with maximum width near middle in males and posteriorly in females. Valve surface coarsely pitted, marginal region smooth.

Inner lamella widest along anterior margin and narrow along ventral and posterior margins; line of concrescence and inner margin coincide; selvage subperipheral; marginal pore canals simple and straight, 17–18 along anterior margin; central muscle scars comprise a vertical row of four ovate scars and two frontal scars. Hinge merodont/entomodont; in right valve it consists of an elongate tooth with eight or nine denticles, followed by a finely locellate median groove and then a posterior tooth bearing five or six denticles. Hinge complementary in right valve.

Discussion.—*Miocyprideis okhaensis* n.sp. resembles *Miocyprideis atjehensis* described by Kingma (1948) from the Pliocene beds of the Malayan region in outline but differs in being coarsely pitted. In the latter species the surface is rather smooth with many irregularly placed pits.

Occurrence.—*M. okhaensis* occurs commonly in shallow water near Okha, Gulf of Kachchh, Gujarat, India.

MIOCYPRIDEIS PARAVURENSIS n. sp.

(Pl. 1, figs. 7, 8; Text-fig. 3)

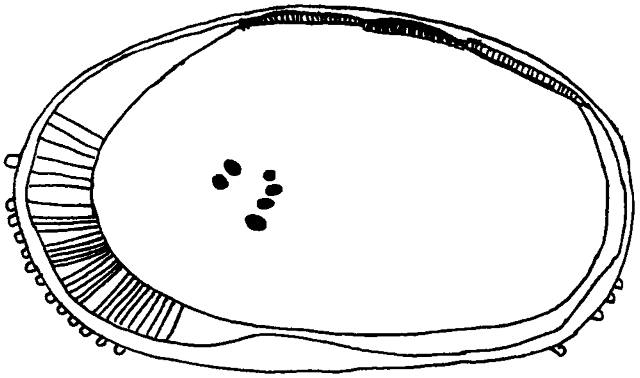
Etymology.—After the village of Paravur, Quilon district, Kerala, India.

Type.—Holotype, a left valve, RUGDMF No. 301 (Pl. 1, fig. 7; L. 720 μm; H. 410 μm) from Sample PR/2, bluish-grey, soft fossiliferous calcareous clay, Quilon beds, Lower Miocene, Paravur, Kerala, India.

Illustrated specimen.—Paratype I, a right valve, RUGDMF No. 302 (Pl. 1, fig. 8; L. 690 μm; H. 390 μm). Paratype II, a right valve, RUGDMF No. 303 (Text-fig. 3; L. 780 μm; H. 470 μm).

Material.—Three carapaces and 47 valves.

Diagnosis.—Carapace subovate in lateral outline; valve surface ornamented with numerous oval-shaped pits, region near anterior margin smooth.



TEXT-FIG. 3—*Miocyprideis paravurensis* n. sp. internal view of a right valve (RUGDMF No. 303).

Description.—Carapace subovate in lateral outline, with greatest height slightly anterior to middle; left valve larger than right valve; overlapping all along margin; dorsal margin convex and sloping down posteriorly in left valve, evenly arched in right valve; ventral margin nearly straight; anterior margin broadly rounded and fringed with 12–13 spines; posterior margin sloping in upper part and rounded in lower part in left valve, evenly rounded in right valve; in dorsal view carapace elongate-pyriform, maximum width near posterior end, anterior end compressed and sides slightly converging forward. Valve surface ornamented with numerous oval-shaped pits, region near anterior margin smooth.

Inner lamella widest anteriorly and narrow along ventral and posterior margins; line of concrescence and inner margin coincide; selvage subperipheral; marginal pore canals simple, rarely bifurcating, about 30–32 along anterior margin and 12 along posterior margin; central muscle scars comprise a vertical row of four adductor scars and two frontal scars. Hinge merodont/entomodont; in right valve it consists of an elongate anterior tooth with about 20 crenulations, followed by a short median groove with 14 denticles and then a long posterior tooth with 17 crenulations; hinge complementary in left valve.

Remarks.—*Miocyprideis paravurensis* n. sp. resembles *Miocyprideis chaudhuryi* (Lyubimova and Guha, 1960) in overall outline but differs in having a distinctly pitted surface. The species also differs from *Miocyprideis janoscheki* Kollmann, 1960, in lateral outline and in having 12–13 spines along the anterior margin, whereas there are about 30 in Kollmann's species.

Occurrence.—This species occurs in the Paravur, Sankaramangalam and Thevally sections of Kerala.

MIOCYPRIDEIS PUNCTATA n. sp.

(Pl. 2, figs. 1–4)

Etymology.—From Latin *punctus*, meaning dotted; with reference to its surface ornamentation.

Type.—Holotype, a complete carapace, RUGDMF No. 304 (Pl. 2, figs. 1, 2; L. 570 μm; H. 310 μm; W. 250 μm) from Sample S/6, 113.69–116.73 metres below the surface, grey sticky clay and sands with shells, Quilon beds, Lower Miocene, Sankaramangalam well 4, Kerala, India.

Illustrated specimen.—Paratype, a right valve, RUGDMF No. 305 (Pl. 2, figs. 3, 4; L. 590 μm; H. 330 μm).

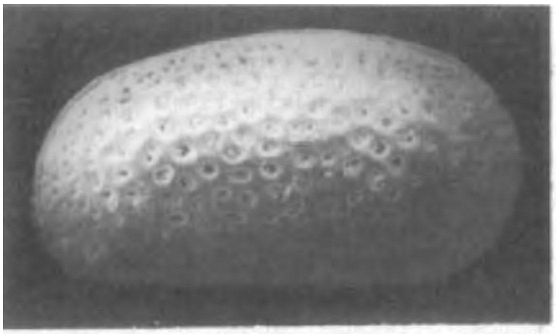
Material.—Thirteen carapaces and 124 valves.

Diagnosis.—Carapace subrectangular in lateral outline, with greatest height slightly anterior to middle; valve surface ornamented by rounded to subrounded deep pits, coarse in middle and fine along margins.

Description.—Carapace subrectangular in lateral outline, with greatest height slightly anterior to middle; left valve larger than right valve, overlapping all along margin except for anterior end; dorsal margin weakly convex; ventral margin straight; anterior margin rounded and fringed with 16–17 minute spines; posterior margin sloping in upper half and rounded in lower, with eight or nine minute spines; in dorsal view carapace elongate-pyriform, with maximum width posterior to middle, anterior end compressed, sides slightly converging forward. Valve surface ornamented by rounded to subrounded deep pits, coarse in middle and fine along margins.

PLATE 2—Figs. 1–4. *Miocyprideis punctata* n. sp. 1. Right valve, view of carapace (holotype, RUGDMF No. 304). ×114; 2. Dorsal view of carapace (holotype, RUGDME No. 304). ×87; 3. Internal view of right valve (paratype, RUGDMF No. 305). ×89; 4. Central muscle scars of right valve (paratype, RUGDMF No. 305). ×500.

Figs. 5–8. *Miocyprideis thirukkaruvensis* Guha and Rao. 5. Lateral view of left valve (morphotype A, RUGDMF No. 306). ×118; 6. Dorsal view of carapace (morphotype A, RUGDMF No. 307). ×121; 7. Lateral view of left valve (morphotype B, RUGDMF No. 308). ×127; 8. Lateral view of left valve (morphotype C, RUGDMF No. 309). ×128.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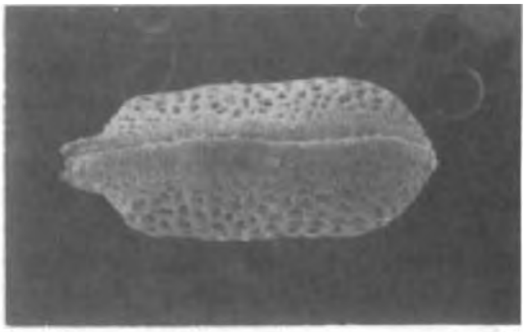
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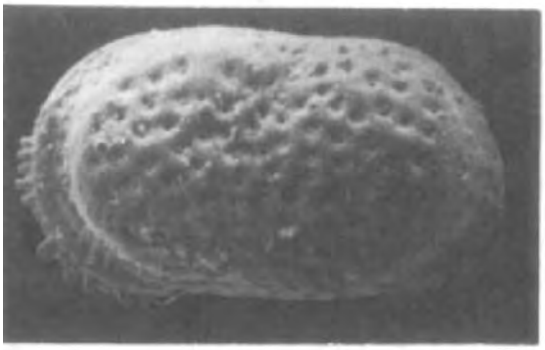
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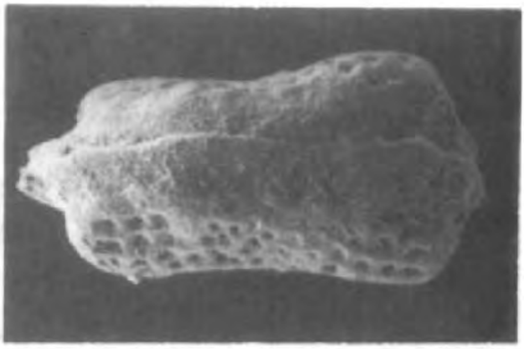
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Inner lamella widest anteriorly and narrow along ventral and posterior margins; selvage subperipheral; line of concrescence and inner margin coincide; marginal pore canals simple, rarely bifurcating, 35–37 anteriorly, 15–16 posteriorly; central muscle scars comprise a vertical row of four adductor scars and two frontal scars. Hinge merodont/entomodont; in right valve anterior and posterior teeth with about 25 and 17 crenulation respectively and median groove with 17 denticles.

Remarks.—The present species differs from *Miocyprideis thirukkaruvensis* Guha and Rao, 1976, in having a deeply pitted surface and in lacking a vertical depression in the middle and a swelling/ hump in the posterior region.

Occurrence.—*M. punctata* occurs abundantly in the Padappakkara, Paravur, Sankaramangalam and Thevally sections of Kerala.

MIOCYPRIDEIS THIRUKKARUVENSIS Guha and Rao, 1976

(Pl. 2, figs. 5–8)

Miocyprideis thirukkaruvensis GUHA and RAO, 1976, p. 94, 95, Pl. 1, figs. 2–4.

Diagnosis.—Carapace subrectangular in lateral outline, with greatest height anterior to middle; left valve larger than right valve, distinctly overlapping along dorsal and ventral margins; anterior margin fringed with 13–15 spines and posterior with five or six spines; in dorsal view carapace roughly pyriform, anterior end compressed, maximum width near posterior end; valve surface variably pitted and marked by a broad, shallow vertical depression in middle and a swelling/ or hump in posterior region.

Remarks.—This species has so far been recorded from the Quilon beds of Kerala by Guha and Rao (1976). The species may be divided into the following three morphotypes on the basis of the number of pits and their distribution pattern. These morphotypes are alike in all other characters and hence included in a single species.

Morphotype A

(Pl. 2, figs. 5, 6)

Illustrated specimens.—A left valve, RUGDMF No. 306 (Pl. 2, fig. 5; L. 550 μm; H. 310 μm). A carapace, RUGDMF No. 307 (Pl. 2, fig. 6; L. 510 μm; H. 0.310 μm; W. 0.270 μm).

Diagnosis.—This morphotype is characterised by the presence of dense pitting, the pits being disposed uniformly over the entire surface.

Morphotype B

(Pl. 2, fig. 7)

Illustrated specimen.—A left valve, RUGDMF No. 308 (Pl. 2, fig. 7; L. 490 μm; H. 290 μm).

Diagnosis.—This morphotype is characterised by sparse pitting. About 40 to 45 pits occur over the middle of valve; the marginal area is smooth.

Morphotype C

(Pl. 2, fig. 8)

Illustrated specimen.—A left valve, RUGDMF No. 309 (Pl. 2, fig. 8; L. 510 μm; H. 290 μm).

Diagnosis.—This morphotype is characterised by a few pits (20–25) in the median depression of the valve, the rest of the surface area smooth.

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DISCUSSION

Keyser: I am referring to your last statement on the morphotypes that you encountered. Do you have any evidence that this could be related to the Ca content of the water?

Khosla: No. The three morphotypes come from the same samples. I don't think calcium contents of the water would influence some individuals and not others.

De Deckker: I wish to further comment on what Dietmar Keyser said. The fact that you identified three different morphotypes is important. These are the types of ostracods which will be useful in palaeontology. These ostracods have an "unstable" morphology but belong to the same species. If we understand these morphological changes, then they will be of use to the palaeoecologist.

Siddiqui: What is the range of variation in the number of anterior marginal pore canals in your species?

Khosla: The number of anterior marginal pore canals varies from 15–35.

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The Genus *Stigmatocythere* from the Quilon Beds (Lower Miocene) of Kerala, India

SUBHASH C. KHOSLA AND M.L. NAGORI
University of Rajasthan, Udaipur, India

ABSTRACT

Nine species of the genus *Stigmatocythere* Siddiqui, 1971, including six new, are described and illustrated from the Quilon beds (Lower Miocene) of Kerala, India. Of these, four species have normal overlap and hinge structure as given by Siddiqui, while the other five species show reversal of overlap and hinge structure. In the latter species the right valve is larger than the left valve, and anterior and posterior teeth, anteromedian socket and posteromedian groove are present in the left valve, and complementary hinge structure in the right valve. These species constitute a distinct group and deserve a separate designation in odrer to differentiate them from the species with normal overlap and hinge structure. Accordingly a new subgenus *Bhatiacythere* is erected to accommodate the former group of species and the latter species are assigned to the subgenus *Stigmatocythere* s.s. The checklist of the species recorded in this paper is as follows: *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961), *S.* (*S.*) *latebrosa* (Lyubimova and Guha, 1960), *S.* (*S.*) *multicostata* n. sp., *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp., *S.* (*B.*) *interrupta* n. sp., *S.*(*B.*) *rete* n. sp., *S.* (*B.*) *reversa* Khosla, 1976, and *S.* (*B.*) *spinosa* n. sp. Biostratigraphical and geographical distributions and evolutionary relationships of the above species are also discussed in the paper.

INTRODUCTION

The genus *Stigmatocythere* was established by Siddiqui (1971) from the Middle and Upper Eocene beds of the Sulaiman Range, Pakistan for a group of highly ornamented Trachyleberididae. It is characterised by the presence of two ridges springing from the eye tubercle, one to form a high anterior marginal rim, the other curving sharply round to join the subcentral tubercle. According to Siddiqui the genus has normal overlap, *i.e.* left valve slightly over-reaches right valve in the region of the anterior cardinal angle and at the posterodorsal slope, and hinge structure. In the right valve, the hinge consists of a strongly projecting anterior tooth followed by an anteromedian socket, a posteromedian locellate groove or a reduced narrow shelf, and a projecting reniform or pessular posterior tooth; the hinge in the left valve is complementary. Subsequently Khosla (1976), extending both the stratigraphical range and geographical limits of the genus, described three species from the Lower Miocene beds of Saurashtra, India. Two of these species — *Stigmatocythere chaasraensis* (Guha, 1961) and *S. latebrosa* (Lyubimova and Guha, 1960) — show the overlap and hinge structure of the type described by Siddiqui, while the third *Stigmatocythere reversa* Khosla, 1976 exhibits an interesting example of reversal of overlap and hinge structure. In this species the right valve is larger than the left valve, and anterior and posterior teeth, anteromedian socket and posteromedian groove are present in the left valve with complementary hinge structure in the right valve. The above three species along with another new species of *Stigmatocythere* were later recorded from the Lower Miocene beds of Kachchh by Mehra (1980).

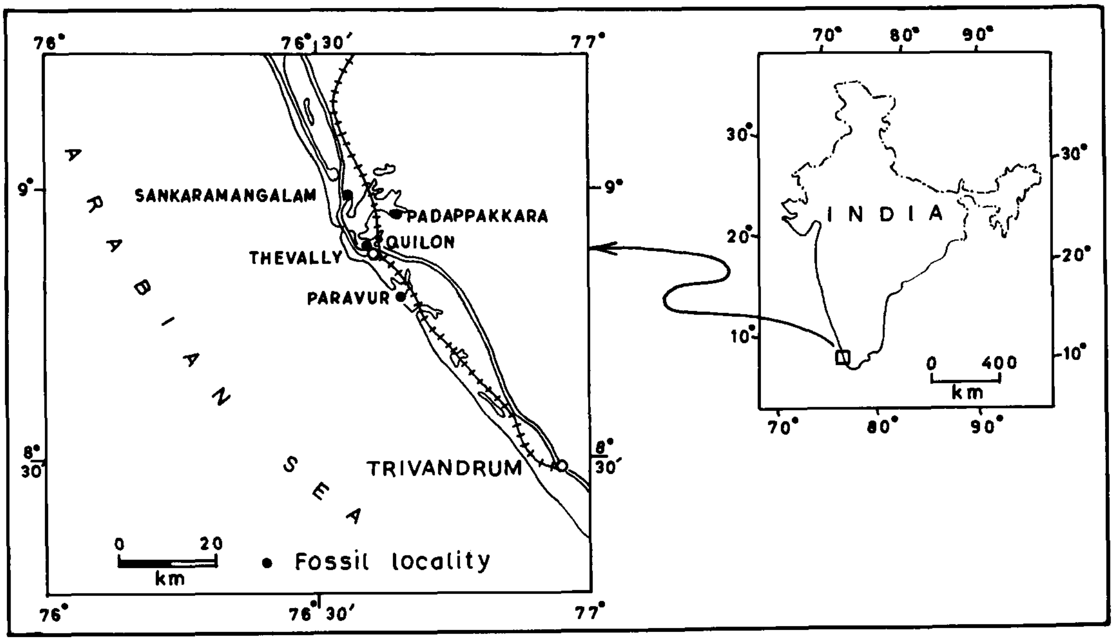
During the course of the study of ostracods from the Quilon beds (Lower Miocene), Kerala the present authors have come across nine species of *Stigmatocythere,* six of which are new. Of these, four species have normal overlap and hinge structure, while the other five species show reversal of overlap and hinge structure. It now appears certain that the latter species constitute a distinct group and deserve a separate designation in order to differentiate them from the species with normal overlap and hinge structure. Accordingly a new subgenus *Bhatiacythere* is erected to accommodate the former group of species and the latter species are assigned to subgenus *Stigmatocythere* s.s. The systematics, biostratigraphical and geographical distributions and evolutionary relationships of the above nine species are discussed in this paper.

STRATIGRAPHY

The material from which the *Stigmatocythere* species were obtained comes from two surface sections and two subsurface sections. The location of these sections is given below and also in the Text-fig. 1.

Surface sections

Padappakkara (8° 58′N: 76° 38′E): cliff section (locally known as 'Chunna Kodi', meaning calcareous point) about 1.5 kilometres northwest of Padappakkara village on the bank of Asthamundi Kayal (lake).



TEXT-FIG. 1—Map showing the fossil localities of *Stigmatocythere* species in Kerala.

Paravur (8° 49′N: 67° 40′E): cliff section 2.25 kilometres west of Paravur village.

Subsurface sections

Sankaramangalam well 4 (8° 59′45″N: 76°32′15″E).

Thevally well (8° 53′45″N: 76° 34′45″E).

Of these sections the best developed succession, rich in ostracods, is found in Sankaramangalam well 4. Here the succession is divisible into two lithostratigraphic units, the lower Quilon beds (31.39 to 247.79 metres depth), and the upper Warkalli beds (0 to 31.39 metres depth). The Quilon beds in the lower part (113.69 to 247.79 metres depth) are dominated by argillaceous and arenaceous facies and comprise clays with peat/carbonaceous matter and sand. In the upper part (31.39 to 113.69 metres depth) the beds are dominated by calcareous facies and consist of limestone and clays with sands. Ostracods occur commonly in the Quilon beds, on the basis of which the beds can be tentatively divided into two assemblage zones. These are, in ascending order:

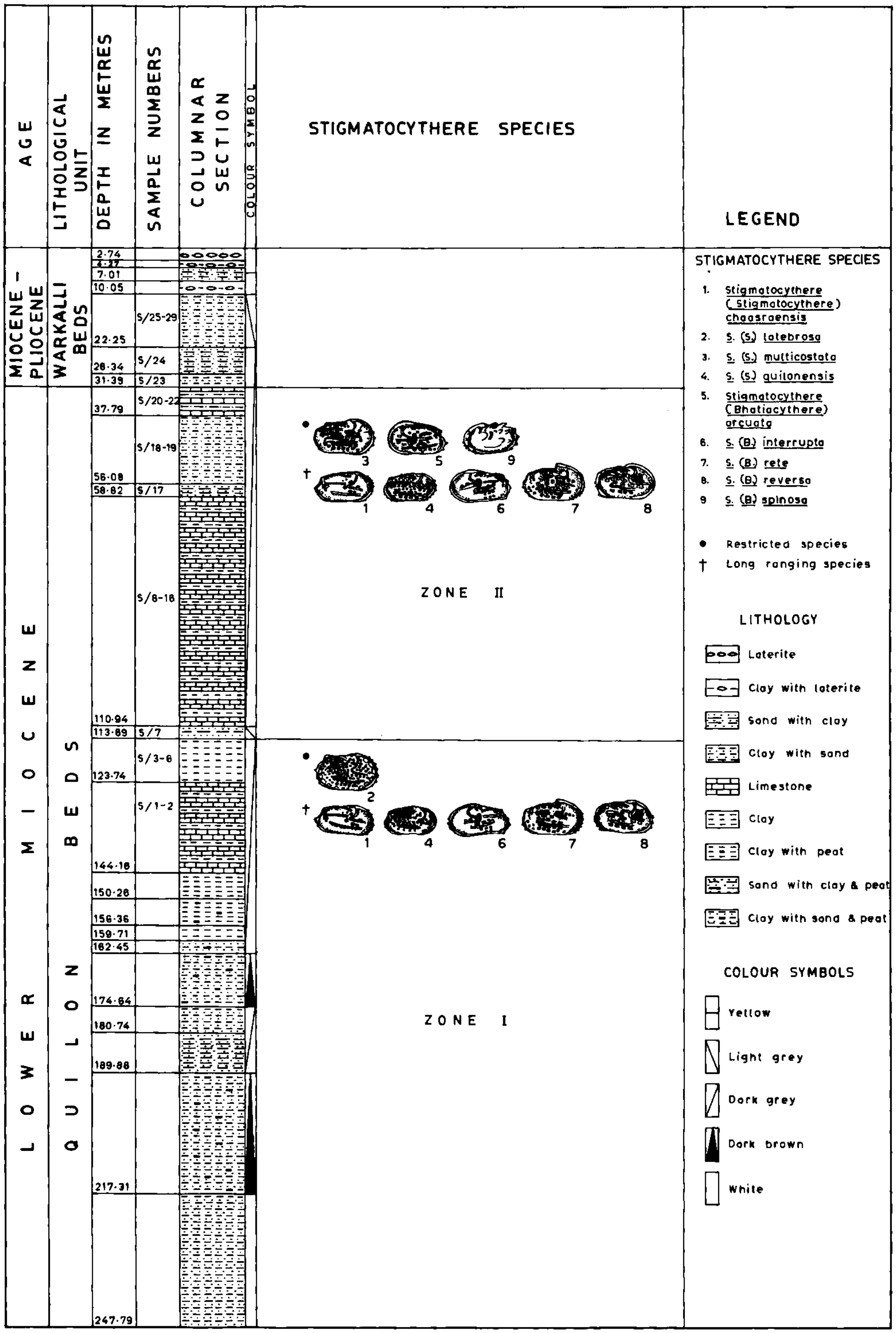
Zone I: This zone extends downward from 113.69 metres depth. *Stigmatocythere* (*Stigmatocythere*) *latebrosa* (Lyubimova and Guha, 1960) is confined to this zone. Other *Stigmatocythere* species occurring in the zone are: *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961), *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp., *S.* (*B.*) *rete* n. sp., and *S.* (*B.*) *reversa* Khosla, 1976. The associated ostracods restricted to Zone I are: *Gujaratella* sp., *Hemicyprideis kachharai* Khosla, *Ornatoleberis* sp., *Pokornyella pindaraensis* Khosla, and *Pokornyella* sp.

Zone II: This zone is 82.30 metres thick, occurring from 31.39 to 113.69 metres depth below the surface. *Stigmatocythere* (*Stigmatocythere*) *multicostata* n. sp., *Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp., and *S.* (*B.*) *spinosa* n. sp. are confined to this zone. Other *Stigmatocythere* species occurring in this zone include *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961), *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp., *S.* (*B.*) *rete* n. sp., and *S.* (*B.*) *reversa* Khosla, 1976. The associated ostracods restricted to Zone II are: *Alocopocythere* sp., *Bradleya* (*Quasibradleya*) sp., *Cytherelloidea costatruncata* Lyubimova and Mohna, 1960, *Cytherelloidea* sp., *Loxoconchella* sp., *Neomonoceratina* sp., *Paracytheridea perspicua* Lyubimova and Guha, and *Paracytheridea* sp.

The stratigraphic succession of Sankaramangalam well 4 and distribution of *Stigmatocythere* species are shown in Text-fig. 2.

A succession more or less similar to that of Sankaramangalam well 4 was found in Thevally well. It is divisible into three lithostratigraphic units, in ascending order: Quilon beds (28.34 to 247.79 metres depth), Warkalli beds (6.09 to 28.34 metres depth), and Sub-Recent beds (0 to 6.09 metres depth). Like Sankaramangalam well 4, the Quilon beds in their lower part (128.93 to 247.79 metres depth) comprise mainly clay with peat/carbonaceous matter and sands, while in their upper part (28.34 to 128.93 metres depth) consist of alternate bands of limestone and clays with sands. The beds are divisible into two ostracod assemblage zones. *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961). *S.* (*S.*) *latebrosa* (Lyubimova and Guha, 1960), *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp., *S.* (*B.*) *rete* n. sp., and *S.* (*B.*) *reversa* Khosla, 1976, occur in Zone I (86.25 to 247.79 metres depth) and *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961), *S.* (*S.*) *multicostata* n. sp., *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp., *S.* (*B.*) *interrupta* n. sp., *S.* (*B.*) *rete* n. sp., and *S.* (*B.*) *reversa* Khosla, 1976, occur in Zone II (28.34 to 86.25 metres depth).

A very thin succession of the Quilon beds is exposed in the surface sections. At Padappakkara it comprises light yellow sandy clay (0.8 metre) at the base successively overlain by grey clay (0.5 metre), black carbonaceous clay (0.5 metre), greenish-grey clay (1 metre) and greenish-grey limestone (0.5 metre). The following *Stigmatocythere* species occur in these beds: *Stigmatocythere*



TEXT-FIG. 2—Stratigraphical succession of Sankaramangalam Well 4, Kerala.

(*Stigmatocythere*) *chaasraensis* (Guha, 1961), *S.* (*S.*) *latebrosa* (Lyubimova and Guha, 1960), *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp., *S.* (*B.*) *rete* n. sp., and *S.* (*B.*) *reversa* Khosla, 1976.

At Paravur the Quilon beds are composed of greenish-grey hard limestone (1 metre) at the base, overlain by similar looking soft clays (2 metres). *Stigmatocythere* species occurring at this locality are as follows: *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961), *S.* (*S.*) *latebrosa* (Lyubimova and Guha, 1960), *S.* (*S.*) *quilonensis* n. sp., *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp., *S.* (*B.*) *rete* n. sp., and *S.* (*B.*) *reversa* Khosla, 1976.

The Quilon beds of Padappakkara and Paravur can be correlated with Zone I of Sankaramangalam well 4 and Thevally well.

GEOGRAPHICAL DISTRIBUTION OF *Stigmatocythere*

The genus occurs commonly in the Indian subcontinent. It has been recorded from the Eocene beds of the Sulaiman Range, Pakistan (Siddiqui, 1971), Rajasthan (authors' personal observation), the Middle Eocene to Lower Miocene beds of Kachchh (Lyubimova, Guha and Mohan, 1960; Guha, 1961; Mehra, 1980; Khosla and Pant, 1981), the Lower Miocene beds of Saurashtra (Guha, 1967; Khosla, 1976), the Upper Oligocene-Early Miocene beds of the Bombay High (Guha, 1975), the Quilon beds of Kerala (Dutta, 1976; Guha and Rao, 1976; Rao and Datta, 1980), and the Lower Miocene beds of the Cauvery basin (Guha, 1968). The distribution of the various species is given in Table 1.

EVOLUTION OF *Stigmatocythere*

The origin of the genus is not known but it was well established during Eocene time. In Oligocene time it split into two subgenera—*Stigmatocythere* s.s. and *Bhatiacythere* n. subgen. Studies of species from the Quilon beds indicate certain clear lineages within the genus. Among the subgenus

TABLE 1—DISTRIBUTION OF *Stigmatocythere* SPECIES IN THE TERTIARY BEDS OF THE INDIAN SUBCONTINENT.

Species	Pakistan	Rajasthan	Kachchh	Saurashtra	Kerala	Cauvery Basin
Stigmatocythere (*Stigmatocythere*) *calia* Siddiqui, 1971	M. Eocene	—	—	—	—	—
S. (*S.*) *chaasraensis* (Guha, 1961)	—	—	L. Miocene	L. Miocene	L. Miocene	—
S. (*S.*) *delineata* Siddiqui, 1971	M. Eocene	—	—	—	—	—
S. (*S.*) *latebrosa* (Lyubimova and Guha, 1960)	—	—	L. Miocene	L. Miocene	L. Miocene	L. Miocene
S. (*S.*) *lumaria* Siddiqui, 1971	M. and U. Eocene	—	—	—	—	—
S. (*S.*) *multicostata* n. sp.	—	—		—	L. Miocene	—
S. (*S.*) *obliqua* Siddiqui, 1971	L. Eocene	L. Eocene	—	—	—	—
S. (*S.*) *portentum* Siddiqui, 1971	M. Eocene	—	M. Eocene	—	—	—
S. (*S.*) *quilonensis* n. sp.	—	—	—	—	L. Miocene	—
Stigmatocythere (*Bhatiacythere*) *arcuata* n. sp.	—	—	—	—	L. Miocene	—
S. (*B.*) *interrupta* n. sp.	—	—	—	—	L. Miocene	—
S. (*B.*) *rete* n. sp.	—	—	—	—	L. Miocene	—
S. (*B.*) *reversa* Khosla, 1976	—	—	L. Miocene	L. Miocene	L. Miocene	—
S. (*B.*) *spinosa* n. sp.	—	—	—	—	L. Miocene	—

L. = Lower; M. = Middle; U. = Upper.

Stigmatocythere s.s., *S.* (*S.*) *multicostata* n.sp. is closely related to *S.* (*S.*) *latebrosa* (Lyubimova and Guha, 1960). It occurs in stratigraphically younger beds and may have evolved from *S.* (*S.*) *latebrosa* by development of additional longitudinal ridges. *S.* (*S.*) *quilonensis* n. sp. is closely related to *S.* (*S.*) *chaasraensis* (Guha, 1961), differing only in the presence of surface reticulation, and appears to have evolved from it. In the subgenus *Bhatiacythere, S.* (*B.*) *reversa* Khosla, 1976 appears to be the most central type. One lineage to evolve from it is *S.* (*B.*) *interrupta* n. sp. by splitting of the dorsal ridge into two ridges, which in *S.* (*B.*) *spinosa* n. sp. is reduced to only two spines. Another lineage to evolve from *S.* (*B.*) *reversa* is *S.* (*B.*) *arcuata* n. sp. by disappearance of surface reticulation. *S.* (*B.*) *rete* n. sp. also appears to have evolved from *S.* (*B.*) *reversa* by developing prominent reticulation with suppression of the median longitudinal ridge.

Repository

All the illustrated specimens are deposited in the Museum of the University of Rajasthan, Department of Geology. Their RUGDMF catalogue numbers are used in the text and plate explanations.

SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948
Tribe COSTAINI Hartmann and Puri, 1974
Genus STIGMATOCYTHERE Siddiqui, 1971

Diagnosis.—Highly ornamented Trachyleberididae in which two ridges spring from eye tubercle, one to form a high anterior marginal rim, the other curving sharply round to join the subcentral tubercle.

Type species.—Stigmatocythere obliqua Siddiqui, 1971

Subgenus STIGMATOCYTHERE sensu stricto

Diagnosis.—Stigmatocythere with normal overlap and hinge structure.

Stratigraphic range.—Middle Eocene to Lower Miocene.

Remarks.—Stigmatocythere (*Stigmatocythere*) s.s. occurs in the Eocene beds of Pakistan and the Eocene-Miocene beds of India. The following species are included in this subgenus:

Stigmatocythere (*Stigmatocythere*) *calia* Siddiqui, 1971
S. (*S.*) *chaasraensis* (Guha, 1961)
S. (*S.*) *delineata* Siddiqui, 1971
S. (*S.*) *latebrosa* (Lyubimova and Guha, 1960)
S. (*S.*) *lumaria* Siddiqui, 1971
S. (*S.*) *multicostata* n. sp.
S. (*S.*) *obliqua* Siddiqui, 1971
S. (*S.*) *protentum* Siddiqui, 1971
S. (*S.*) *quilonensis* n. sp.

Only the species occurring in Kerala are described in this paper.

STIGMATOCYTHERE (STIGMATOCYTHERE) CHAASRAENSIS (Guha, 1961)

(Pl. 1, fig. 1)

Occultocythereis chaasraensis Guha, 1961, p. 4, 5, figs. 8, 10, 13.
Stigmatocythere chaasraensis; Khosla, 1976, p. 136, 137, Pl. 1, figs. 7–9; Khosla, 1978, p. 271, Pl. 5, fig. 2, Pl. 6, fig. 16.

Illustrated specimen.—A female right valve, RUGDMF No. 273 (Pl. 1, fig. 1; L. 550 μm; H. 290 μm).

Diagnosis.—The species is characterised by the presence of two ridges originating from the eye tubercle, diagnostic of the genus, three longitudinal ridges, dorsal, median and ventral, the first two joined posteriorly by a vertical ridge; rest of area smooth.

Remarks.—The present specimens from Kerala are identical with the types of the species described by Guha (1961) from the Lower Miocene beds of Chaasra, Kachchh. The species has also been recorded from the Lower Miocene beds of Saurashtra (Guha, 1967; Khosla, 1976, 1978), and Kachchh (Mehra, 1980).

Occurrence.—The species occurs commonly in all the four sections studied.

STIGMATOCYTHERE (STIGMATOCYTHERE) LATEBROSA (Lyubimova and Guha, 1960)

(Pl. 1, fig. 2)

Cythereis latebrosa Lubimova and Guha, in Lubimova, Guha and Mohan, 1960, p. 34, 35, Pl. 3, fig. 2.
Bradleya latebrosa; Guha, 1968, p. 216, Pl. 2, figs. 19, 21.
Stigmatocythere latebrosa; Khosla, 1976, p. 137, Pl. 1, figs. 10, 11; Khosla, 1978, p. 271, Pl. 5, fig. 1, Pl. 6, fig. 18.

Illustrated specimen.—A female right valve, RUGDMF No. 274 (Pl. 1, fig. 2; L. 620 μm; H. 390 μm).

Diagnosis.—The species has a subquadrate lateral outline, distinctly concave ventral margin and strongly reticulate valve surface with five ridges, two of which originate from the eye tubercle, the other three being longitudinal.

Remarks.—This species has been previously recorded from the Lower Miocene beds of Kachchh (Lyubimova, Guha and Mohan, 1960; Mehra, 1980), Saurashtra (Guha, 1967; Khosla, 1976, 1978), Cauvery basin (Guha, 1968), and Kerala (Guha and Rao, 1976; Dutta, 1976; Rao and Datta, 1980).

Occurrence. — *S.* (*S.*) *latebrosa* occurs commonly in the Sankaramangalam section and rarely in the other three sections studied.

STIGMATOCYTHERE (STIGMATOCYTHERE) MULTICOSTATA n. sp.

(Pl. 1, figs. 3–6)

Etymology.—From the Latin *multus*, much + *costa*, ribs; with reference to the surface ridges.

Type.—Holotype, a complete male carapace, RUGDMF No. 275 (Pl. 1, fig. 3; L. 620 μm; H. 330 μm; W. 310 μm) from sample S/12, 77.11–83.21 metres below the surface, bluish-grey soft clay with fossiliferous limestone, Quilon beds, Lower Miocene, Sankaramangalam well 4, Kerala, India.

Illustrated specimens.—Paratype I, a complete male carapace, RUGDMF No. 276 (Pl. 1, fig. 4; L. 650 μm; H. 370 μm; W. 320 μm). Paratype II, a complete female carapace, RUGDMF No. 277 (Pl. 1, fig. 5; L. 570 μm; H. 370 μm; W. 330 μm). Paratype III, a female left valve, RUGDMF No. 278 (Pl. 1, fig. 6; L. 570 μm; H. 370 μm).

Material.—Forty-six complete carapaces and 72 open valves.

Diagnosis.—Carapace subquadrate in lateral outline; ventral margin distinctly concave; valve surface ornamented with reticulation and seven ridges, two originating from the eye tubercle, five longitudinal.

Description.—Sexual dimorphism distinct, males being more elongate, less high and wide than females; carapace subquadrate in lateral outline, with greatest height at anterior cardinal angle; left valve slightly larger than right valve, overlapping at anterior cardinal angle and along posterodorsal slope. Dorsal margin straight concealed posteriorly by overhanging ridge; ventral margin distinctly concave in middle; anterior margin broad and evenly rounded, with 6–7 denticles; posterior margin in left valve straight in upper part and convex in lower part, in right valve subangulate; posterior cardinal angle distinct. In dorsal view carapace rather compressed, with maximum width posterior to middle. Eye and subcentral tubercles distinct. Valve surface ornamented by reticulation and seven ridges; two ridges originate from the eye tubercle, one ridge forms a high rim along the anterior margin and also continues along the ventral and posterior margins, the other ridge turns sharply round to the subcentral tubercle where it recurves and runs anteriorly. The five longitudinal ridges consist of a dorsal ridge which originates below the eye tubercle, making an arc overhangs part of the margin and then turns downward in the posterodorsal region; a median ridge runs posterior to the subcentral tubercle and joins the dorsal ridge; two short ridges occur between the median and ventral ridges; a ventral ridge extends from the anteroventral region in a posterior direction.

Inner lamella wide along anterior margin, narrow along posterior; line of concrescence and inner margin coincide; selvage submarginal. Marginal pore canals simple and straight, 19–20 along anterior margin, and 9–10 along posterior margin. Hinge amphidont/heterodont; in right valve consisting of an anterior tooth, a postjacent anteromedian socket, followed by a posteromedian groove and then a posterior tooth; hinge complementary in left valve, posteromedian bar finely crenulate.

Remarks.—*Stigmatocythere* (*Stigmatocythere*) *multicostata* n. sp. resembles *Stigmatocythere* (*Stigmatocythere*) *latebrosa* (Lyubimova and Guha, 1960) in lateral outline but differs in having five longitudinal ridges instead of three as in the case of the latter species. *S.* (*S.*) *latebrosa* possibly represents the ancestral form of *S.* (*S.*) *multicostata.*

Occurrence.—The species occurs commonly in the Sankaramangalam and Thevally sections.

STIGMATOCYTHERE (STIGMATOCYTHERE) QUILONENSIS n. sp.

(Pl. 1, figs. 7–10)

Etymology.—After the district of Quilon, Kerala, India.

Type.—Holotype, a female right valve, RUGDMF No. 279 (Pl. 1, figs. 7, 10; L. 570 μm; H. 310 μm) from Sample T/21, 61.87–64.92 metres below surface, Quilon beds, Lower Miocene, Thevally well, Kerala, India.

Illustrated specimens.—Paratype I, a complete female carapace, RUGDMF No. 280 (Pl. 1, fig. 8; L. 570 μm; H. 310 μm; W. 250 μm). Paratype II, a male left valve, RUGDMF No. 281 (Pl. 1, fig. 9; L. 600 μm; H. 290 μm).

PLATE 1 —Fig. 1. *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961). Lateral view of female right valve (RUGDMF No. 273). ×73.

Fig. 2. *Stigmatocythere* (*Stigmatocythere*) *latebrosa* (Lyubimova and Guha, 1960). Lateral view of female right valve (RUGDMF No. 274). ×77.

Figs. 3–6. *Stigmatocythere* (*Stigmatocythere*) *multicostata* n. sp. 3. Lateral view of complete male carapace (holotype, RUGDMF No. 275). ×76; 4. Dorsal view of complete male carapace (paratype I, RUGDMF No. 276). ×74; 5. Lateral view of female complete carapace (paratype II, RUGDMF No. 277). ×75; 6. Internal view of female left valve (paratype III, RUGDMF No. 278). ×85.

Figs. 7–10. *Stigmatocythere* (*Stigmatocythere*) *quilonensis* n. sp. 7. Lateral view of right female valve (holotype, RUGDMF No. 279). ×70; 8. Dorsal view of complete female carapace (paratype I, RUGDMF No. 280). ×79; 9. Lateral view of male left valve (paratype II, RUGDMF No. 281). ×75; 10. Internal view of female right valve (holotype, RUGDMF No. 279). ×70.

Figs. 11–13. *Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp. 11. Lateral view of left male valve (holotype, RUGDMF No. 282). ×75; 12. Dorsal view of complete female carapace (paratype, RUGDMF No. 283). ×78; 13. Internal view of male left valve (holotype, RUGDMF No. 282). ×70.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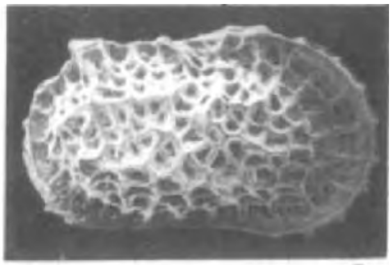
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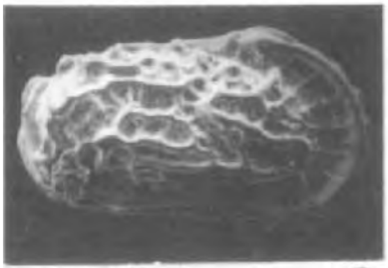
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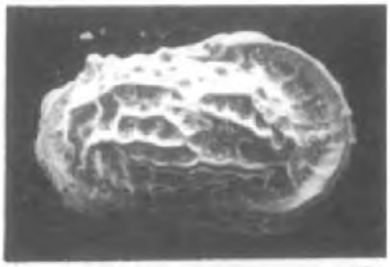
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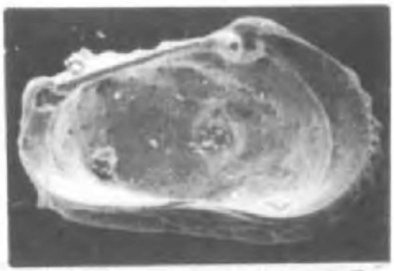
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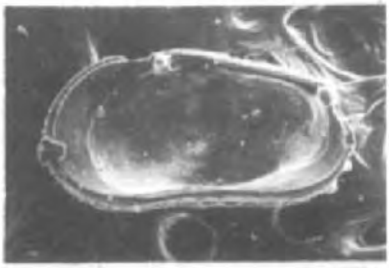
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Material.—Nineteen complete carapaces and 23 open valves.

Diagnosis.—Carapace subrectangular in lateral outline; ventral margin slightly concave in middle; valve surface ornamented by distinct reticulation and five ridges, two spriging from the eye tubercle, three longitudinal.

Description.—Sexual dimorphism pronounced, males being more elongate, less high and wide than females. Carapace subrectangular in lateral outline, with greatest height at anterior cardinal angle; left valve slightly over-reaches right valve in region of anterior cardinal angle and posterodorsal slope. Dorsal margin straight, concealed posteriorly by overhanging ridge; ventral margin slightly concave near middle; anterior margin broadly rounded, with 20–21 minute denticles; posterior margin concave in upper part and convex in lower, with 2–3 denticles. In dorsal view carapace rather compressed, maximum width posterior to middle in females and near middle in males. Eye and subcentral tubercles present. Surface of each valve ornamented by distinct reticulation and ridges; two ridges springing from the eye tubercle, one forming a high rim along the anterior, ventral and lower part of posterior margins and bearing 6 and 3 nodes along anterior and posterior margins respectively, the other curves sharply round and meets the subcentral tubercle. There are three longitudinal ridges, dorsal, median and ventral; the dorsal ridge originates a little below eye tubercle, making an arc overhangs part of margin and then turns downward at right angles in the posterodorsal region; the median ridge runs posterior to the subcentral tubercle and meets dorsal ridge; the ventral ridge starts from the anteroventral region and slopes up posteriorly.

Inner lamella of moderate width; line of concrescence and inner margin coincide; selvage at some distance from outer margin in right valve, and peripheral in left valve; a distinct flange groove in right valve. Marginal pore canals simple, straight and about 17–18 along anterior margin; Hinge amphidont/heterodont. Eye sinus present.

Remarks.—*Stigmatocythere* (*Stigmatocythere*) *quilonensis* n. sp. resembles *Stigmatocythere* (*Stigmatocythere*) *chaasraensis* (Guha, 1961) in outline and surface ridge pattern but differs in having a distinctly reticulated surface. The latter species is devoid of reticulation and appears to be the ancestral form of *S.* (*S.*) *quilonensis.*

Subgenus BHATIACYTHERE n. subgen.

Etymology.—The subgenus is named in honour of Dr. S. B. Bhatia, Professor of Geology, Panjab University, Chandigarh, India.

Diagnosis.—*Stigmatocythere* with reversal of overlap and hinge structure; right valve larger than left valve; hinge amphidont/heterodont; in left valve consisting of projecting anterior tooth, a postjacent anteromedian socket, followed by a posteromedian groove and then a projecting reniform posterior tooth; hinge complementary in the right valve.

Type species.—*Stigmatocythere* (*Bhatiacythere*) *reversa* Khosla, 1976.

Stratigraphic range.—Oligocene to Lower Miocene.

Remarks.—The subgenus occurs commonly in the Oligocene-Lower Miocene beds of Kachchh and the Lower Miocene beds of Kerala and Saurashtra of India. It is represented by the following species:

Stigmatocythere (*Bhatiacythere*) *arcuata* n. sp.
S (*B.*) *interrupta* n. sp.
S.(*B.*) *rete* n. sp.
S.(*B.*) *reversa* Khosla, 1976
S.(*B.*) *spinosa* n. sp.

Another unpublished species which belongs to this subgenus is *Stigmatocythere* (*Bhatiacythere*) *bermotiensis* recorded by Pant (1981) from the Oligocene beds of Kachchh, India.

STIGMATOCYTHERE (BHATIACYTHERE) ARCUATA n. sp.
(Pl. 1, figs. 11–13)

Etymology.—From the Latin *arcuatus,* arch; with reference to the arc-shaped dorsal ridge.

Type.—Holotype, a male left valve, RUGDMF No. 282 (Pl. 1, figs. 11, 13; L. 600 μm; H. 370 μm) from Sample S/19, 40.54–46.63 metres below the surface, bluish-grey sticky fossiliferous clay, Quilon beds, Lower Miocene, Sankaramangalam well 4, Kerala, India.

Illustrated specimen.—Paratype, a complete female carapace, RUGDMF No. 283 (Pl. 1, fig. 12; L. 590 μm; H. 390 μm; W. 310 μm).

Material.—Three complete carapaces and 3 open valves.

Diagnosis.—Valve surface ornamented by two ridges springing from eye tubercle; three longitudial ridges, dorsal, median and ventral; dorsal ridge making a broad arc overhangs margin; two small oblique ridges between median and ventral ridges; rest of surface with indistinct reticulation.

Description.—Sexual dimorphism distinct, males being more elongate, less high and wide than females. Carapace subrectangular in lateral outline, with greatest height at anterior cardinal angle; right valve slightly larger than left valve, overlapping at anterodorsal and posteroventral margins. Dorsal margin partly concealed by overhanging ridge, otherwise straight, sloping down posteriorly; ventral margin concave; anterior margin broadly rounded and fringed with 13–14 short spines; posterior margin concave in upper part and convex in lower part, with 4–5 spines. In dorsal view carapace rather compressed, maximum width posterior to middle. Eye and subcentral tubercles distinct. Surface of each valve ornamented by two ridges springing from the eye tubercle, one forms a high rim along the anterior margin and also continues along the ventral and posterior margins, the other turns sharply to the subcentral tubercle where it recurves and runs anteriorly. There are three longitudinal ridges, dorsal, median and ventral. The dorsal ridge originates a little below the eye tubercle and, making a broad arcoverhangs the margin; in the posterodorsal region it turns downward at right angle and bears three distinct nodes. The median ridge is short, runs posteriorly to the subcentral tubercle and does not join the dorsal ridge. The ventral ridge starts in the anteroventral region and slopes up posteriorly. There are two small oblique ridges between the median and ventral ridges. The rest of the surface is smooth or with indistinct reticulation.

Inner lamella of moderate width; line of concrescence and inner margin coincide; selvage near periphery in right valve and at some distance from outer margin in left valve; a distinct flange groove in left valve along anterior and ventral margins. Marginal pore canals simple and straight, about 19–21 along anterior margin and 8–9 along posterior margin. Hinge amphidont/heterodont; in left valve it consists of an anterior tooth, a postjacent anteromedian socket, followed by a posteromedian groove and then a posterior tooth; hinge complementary in right valve. Eye sinus present.

Remarks.—*Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp. resembles *Stigmatocythere* (*Bhatiacythere*) *reversa* Khosla, 1976; in outline and overall surface ornamentation, but differs in the absence of reticulation and presence of an arcuate dorsal ridge. The present species appears to have evolved from the latter species.

Occurrence.—This species has only been recorded from the Sankaramangalam section.

STIGMATOCYTHERE (BHATIACYTHERE) INTERRUPTA n. sp.
(Pl. 2, figs. 1–4)

Etymology.—From the Latin *interruptus,* broken apart; with reference to the break in the dorsal ridge.

Type.—Holotype, a male left valve, RUGDMF No. 284 (Pl. 2, figs. 1, 4; L. 600 μm; H. 350 μm) from Sample S/14, 68.88–71.02 metres below surface, bluish-grey sticky clay with hard fossiliferous limestone, Quilon beds, Lower Miocene, Sankaramangalam well 4, Kerala, India.


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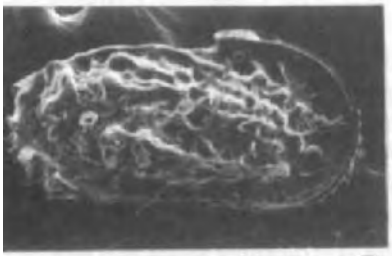
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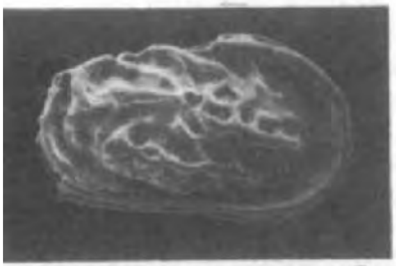
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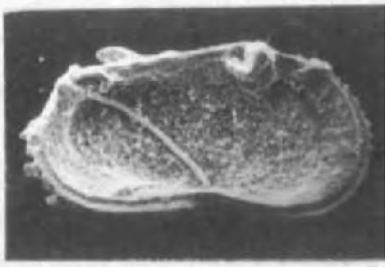
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Illustrated specimen.—Paratype, a female right valve, RUGDMF No. 285 (Pl. 2, figs. 2, 3; L. 590 μm; H. 390 μm).

Material.—Twenty-one complete carapaces and 40 open valves.

Diagnosis.—Valve surface ornamented by two ridges springing from the eye tubercle and four longitudinal ridges of which two are dorsal, one median and one ventral. Rest of surface either smooth or with indistinct reticulation.

Description.—Sexual dimorphism distinct, males being more elongate, less high and wide than females. Carapace similar to *Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp. in outline. Anterior margin fringed with 13–14 spines and posterior margin with 4–5 spines. Eye and subcentral tubercles present. Surface of each valve ornamented by two ridges springing from the eye tubercle, one forms a high rim along the anterior, ventral and posterior margins, the other turns sharply round to the subcentral tubercle where it recurves and runs anteriorly. There are four longitudinal ridges, of which two are dorsal, one median and one ventral. The upper dorsal ridge originates a little below the eye tubercle and runs up to the mid-dorsal margin; the lower dorsal ridge extends from the posterodorsal corner of the subcentral tubercle to the dorsal margin where it overhangs part of margin, and then turns downward at right angles in the posterodorsal region and bears three nodes. The median ridge runs posteriorly to the subcentral tubercle and does not join the lower dorsal ridge. The ventral ridge starts in the anteroventral region and rises posteriorly. The rest of the surface is either smooth or with indistinct reticulation.

Inner lamella of moderate width; line of concrescence and inner margin coincide; selvage near periphery in right valve and at some distance from outer margin in left valve; flange groove present along anterior, ventral and lower part of posterior margins in left valve. Marginal pore canals simple and straight, about 18–20 along anterior margin and 8–10 along posterior margin. Hinge amphidont/heterodont. Eye sinus present.

Remarks.—This species resembles *Stigmatocythere* (*Bhatiacythere*) *reversa* Khosla, 1976, in overall shape and surface ornamentation. It differs, however, in having two dorsal ridges instead of a single dorsal ridge and in lacking distinct reticulation. The species may have evolved from *S.* (*B.*) *reversa.*

Occurrence.—*S. interrupta* occurs in all the sections studied.

STIGMATOCYTHERE (BHATIACYTHERE) RETE n. sp.

(Pl. 2, figs. 5–8)

Etymology.—From the Latin *rete,* net; with reference to the surface ornamentation.

Type.—Holotype, a female right valve, RUGDMF No. 286 (Pl. 2, fig. 5; L. 630 μm; H. 410 μm) from Sample PR/4, bluish-grey, soft fossiliferous calcareous clay, Quilon beds, Lower Miocene, Paravur, Kerala, India.

Illustrated specimen.—Paratype I, a male right valve, RUGDMF No. 287 (Pl. 2, fig. 6; L. 690 μm;

PLATE 2—Figs. 1–4. *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp. 1. Lateral view of male left valve (holotype, RUGDMF No. 284). ×77; 2. Dorsal view of female right valve (paratype, RUGDMF No. 285). ×78; 3. Lateral view of female right valve (paratype, RUGDMF No. 285). ×76. 4; Internal view of male left valve (holotype, RUGDMF No. 284). ×73.

Figs. 5–8. *Stigmatocythere* (*Bhatiacythere*) *rete* n. sp. 5. Lateral view of female right valve (holotype, RUGDMF No. 286). ×71; 6. Lateral view of male right valve (paratype I, RUGDMF No. 287). ×70; 7. Dorsal view of complete male carapace (paratype II, RUGDMF No. 288). ×68; 8. Internal view of female right valve (paratype III, RUGDMF No. 289). ×75.

Figs. 9–10. *Stigmatocythere* (*Bhatiacythere*) *reversa* Khosla. 9. Right valve view of female complete carapace (RUGDMF No. 290). ×68; 10. Internal view of female left valve (RUGDMF No. 291). ×80.

Figs. 11–13. *Stigmatocythere* (*Bhatiacythere*) *spinosa* n. sp. 11. Lateral view of left valve (holotype, RUGDMF No. 292). ×75; 12. Dorsal view of complete carapace (paratype, RUGDMF No. 293). ×75; 13. Internal view of left valve (holotype, RUGDMF No. 292). ×80.

H. 390 μm). Paratype II, a complete male carapace, RUGDMF No. 288 (Pl. 2, fig. 7; L. 680 μm; H. 370 μm; W. 290 μm). Paratype III, female right valve, RUGDMF No. 289 (Pl. 2, fig. 8; L. 640 μm; H. 410 μm).

Material.—Forty complete carapaces and 33 open valves.

Diagnosis.—Valve surface ornamented by strong reticulation, reticule meshes arranged concentrically; two ridges spring from the eye tubercle; three longitudinal ridges of which the median is the least distinct.

Description.—Sexual dimorphism distinct, males being more elongate less high and wide than females. Carapace similar to *Stigmatocythere* (*Bhatiacythere*) *arcuata* n. sp. and *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp. in outline; anterior margin fringed with 16–18 spines, posterior margin with 4–5 spines. Eye and subcentral tubercles present. Surface of each valve ornamented by strong reticulation, reticule meshes arranged concentrically. Two ridges spring from the eye tubercle, one forms a high rim along the anterior and ventral margins, the other turns sharply round to the subcentral tubercle and then curves round to run anteriorly. A dorsal ridge originates a little below the eye tubercle, making an arc overhangs part of the margin, turns downward at right angle in the posterodorsal region and bears three nodes; the less distinct median ridge runs posterior to the subcentral tubercle and does not join the dorsal ridge; the ventral ridge starts from the anteroventral region and rises posteriorly.

Inner lamella moderately wide along anterior margin and narrow along ventral and posterior margins; line of concrescence and inner margin coincide; selvage near periphery in right valve and at some distance from outer margin in left valve; a distinct flange groove in left valve. Marginal pore canals simple and straight, about 20–22 anteriorly and 7–8 posteriorly. Central muscle scars as for the genus. Hinge amphidont/heterodont.

Remarks.—This species resembles *Stigmatocythere* (*Bhatiacythere*) *reversa* Khosla, 1976 in overall outline and surface ornamentation but differs in having strong reticulation, a weak median ridge and in the lack of an inclined ridge extending downward from the middle of the dorsal ridge. This species may have evolved from *S.* (*B.*) *reversa.*

Occurrence.—*S. rete* occurs in all the four sections.

STIGMATOCYTHERE (BHATIACYTHERE) REVERSA Khosla, 1976
(Pl. 2, figs. 9, 10)

Stigmatocythere reversa KHOSLA, 1976, p. 137, 138, Pl. 1, figs. 1–6; KHOSLA, 1978, p. 271, Pl. 5, figs. 3–5; Pl. 6, fig. 17.

Illustrated specimens.—A complete female carapace, RUGDMF No. 290 (Pl. 2, fig. 9; L. 620 μm; H. 390 μm; W. 350 μm). A male left valve, RUGDMF No. 291 (Pl. 2, fig. 10; L. 640 μm; H. 390 μm).

Diagnosis.—A species characterised by sparse reticulation, the edges of reticule meshes being raised in low ridges giving rugged appearance; two ridges originate from the eye tubercle; three longitudinal ridges, dorsal, median and ventral, first two not joining posteriorly; a short inclined ridge extends from the middle of the dorsal ridge towards the subcentral tubercle.

Remarks.—The present specimens from Kerala are identical with the types described by Khosla (1976) from the Lower Miocene beds of Saurashtra. The species has also been recorded from the Lower Miocene beds of Kachchh by Mehra (1980).

Occurrence.—*S. reversa* occurs commonly in all the four sections.

STIGMATOCYTHERE (BHATIACYTHERE) SPINOSA n. sp.
(Pl. 2, figs. 11–13)

Etymology.—From the Latin *spinosus,* spine; with reference to the surface spines.

Type.—Holotype, a left valve, RUGDMF No. 292 (Pl. 2, figs. 11, 13; L. 590 μm; H. 290 μm) from Sample S/15, 64.92–68.88 metres below the surface, bluish-grey clay with fossiliferous limestone, Quilon beds, Lower Miocene, Sankaramangalam well 4, Kerala, India.

Illustrated specimen.—Paratype, a complete carapace, RUGDMF No. 293 (Pl. 2, fig. 12; L. 570 μm; H. 350 μm; W. 270 μm)

Material.—Four complete carapaces and 3 open valves.

Diagnosis.—Valve surface ornamented by two ridges springing from the eye tubercle; dorsal and median line of ornamentation composed of spines/nodes, ventral a low ridge terminating in a spine; a crescent-shaped depression occurs posterior to the subcentral tubercle; rest of surface smooth.

Description.—Carapace similar to other species of the subgenus recorded herein. Anterior margin fringed with 13–14 spines and posterior with 3–4 spines. Eye and subcentral tubercles well developed. Valve surface ornamented by ridges and spines/nodes. Two ridges spring from the eye tubercle. One forms a high marginal rim along the anterior, ventral and posterior margins and above the anterior margin it bears 7 minute spines/nodes. The other ridge is small, curves downward and does not reach the subcentral tubercle. Dorsal and median lines of ornamentation composed of spines/nodes, two spines/nodes in the dorsal row, both extending beyond margin and three spines/nodes in the median row. The ventral line of ornamentation consists of a low ridge terminating in a spine. A crescent-shaped depression occurs posterior to the subcentral tubercle and the rest of the surface is smooth.

Inner lamella of moderate width; line of concrescence and inner margin coincide; selvage near periphery in right valve and at some distance from outer margin in left valve. Marginal pore canals simple and straight, about 24–26 along anterior margin and 13–15 along posterior margin. Hinge amphidont/heterodont. Eye sinus present.

Remarks.—This species clearly differs from other species of the subgenus *Bhatiacythere* in having dorsal and median lines of ornamentation composed of spines/nodes, instead of complete ridges. *S. spinosa* appears to have evolved from *Stigmatocythere* (*Bhatiacythere*) *interrupta* n. sp.

Occurrence.—This species occurs only in the Sankaramangalam well.

ACKNOWLEDGEMENTS

The authors are grateful to Mr. R. K. Nair, Senior Hydrogeologist, Kerala State Ground Water Department, Trivandrum, for kindly providing subsurface samples from Sankaramangalam and Thevally; to the Physical Research Laboratory, Ahmedabad for S.E.M. facilities for taking photographs of the ostracod specimens and to the University Grants Commission for financial assistance to carry out the study. One of us (SCK) is also grateful to the University of Rajasthan for providing a travel grant to attend the symposium.

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DISCUSSION

Lundin: In those which show reversal of overlap, do all specimens of each population show it or is it true for only some specimens?

Khosla: All specimens of each population show reversal of overlap and hinge structure without any exception.

Krstic: You are talking not only about reverse overlapping, but about reversed hingement also. Are the populations with reversed specimens controlled by the palaeochemistry of the environment, or something of that sort?

Khosla: I don't know.

On Ostracod Biofacies and Five New Genera in Korean Seas

KAE-LIM CHOE
Marine Geology Division, Korea Institute of Energy and Resources, Seoul, Korea

ABSTRACT

Out of 200 samples, a total of 222 species in 96 genera were recognized. Based on the composition and distribution of the ostracod fauna, 4 biofacies and 6 subdivisions were recognized. Five genera: *Semidarwinula*, *Ekpectocythere*, *Paikcythere*, *Chejucythere*, *Gamagyangnella*, and 5 species are described as new.

INTRODUCTION

I present the first report on ostracods of Korea and furnish a foundation for biological and palaeontological study of Korean ostracods. The Korean Peninsula is located so close to China and Japan that a considerable number of species occur in common. Therefore the study of Korean ostracods will contribute to the biogeographical study of East Asia.

GENERAL FEATURES OF THE STUDY AREA

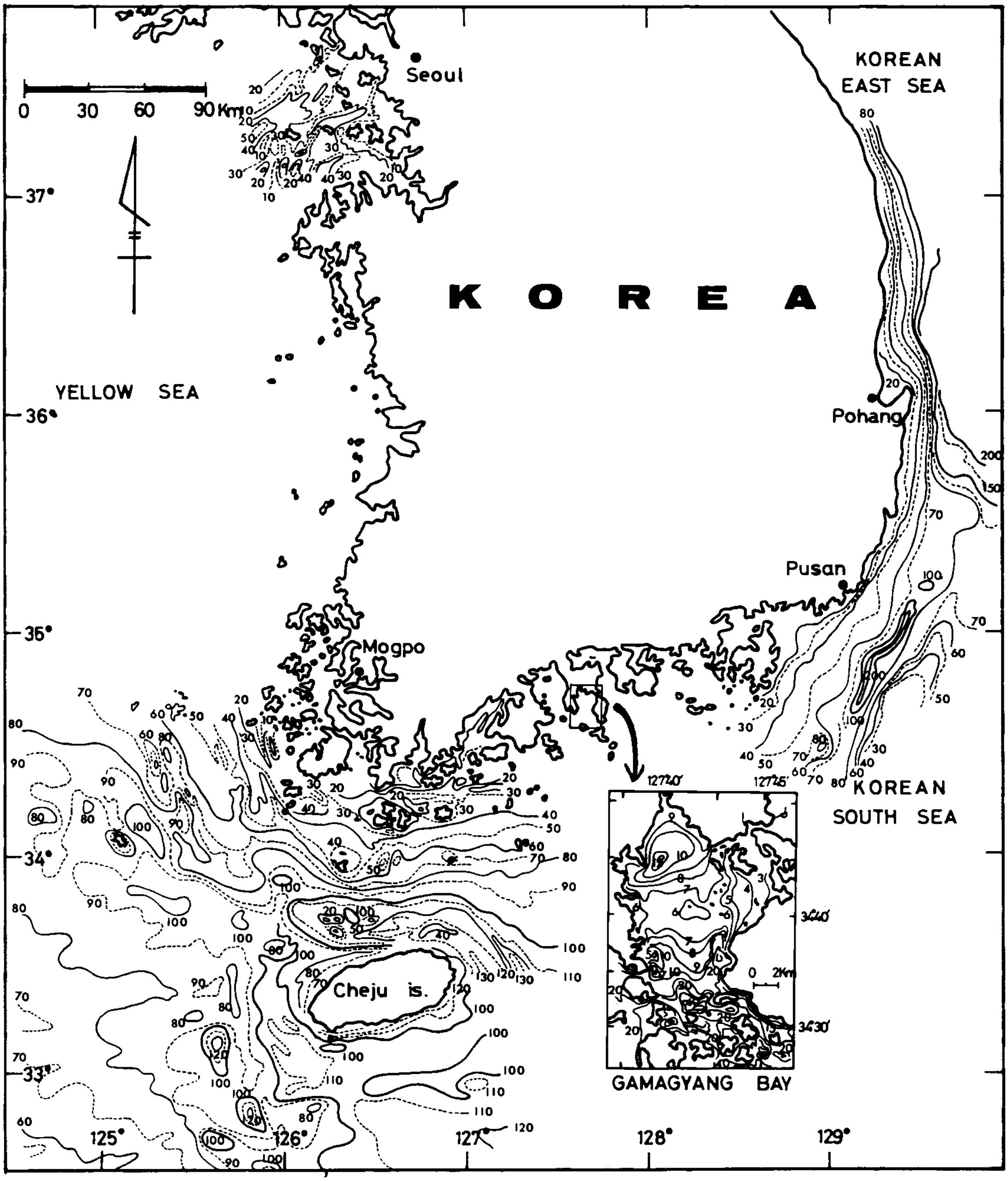
The epicontinental Yellow Sea is shallow and rather flat, and deepens progressively towards the southeast (Text-fig. 1). The western part of the Yellow Sea is bordered by the deltas of both the Hwangho and Yangtze Rivers. The eastern coast is characterised by tidal flats.

In the southwestern part of the study area the bottom cold water of low salinity originating from the Yellow Sea flows to the South Sea (Kim, 1980). A branch of the Kuroshio Current, identified by its high temperature, high salinity and low dissolved oxygen, enters the Cheju Strait from the south (Kim, 1980).

The southern ria-type coast of the peninsula is characterised mostly by post-glacial rocky embayments. The relatively flat nearshore shelf of the South Sea deepens to 90 m toward the south and the bottom of the outer shelf stretching over Cheju Strait is characterised by a steep slope with a number of isolated depressions.

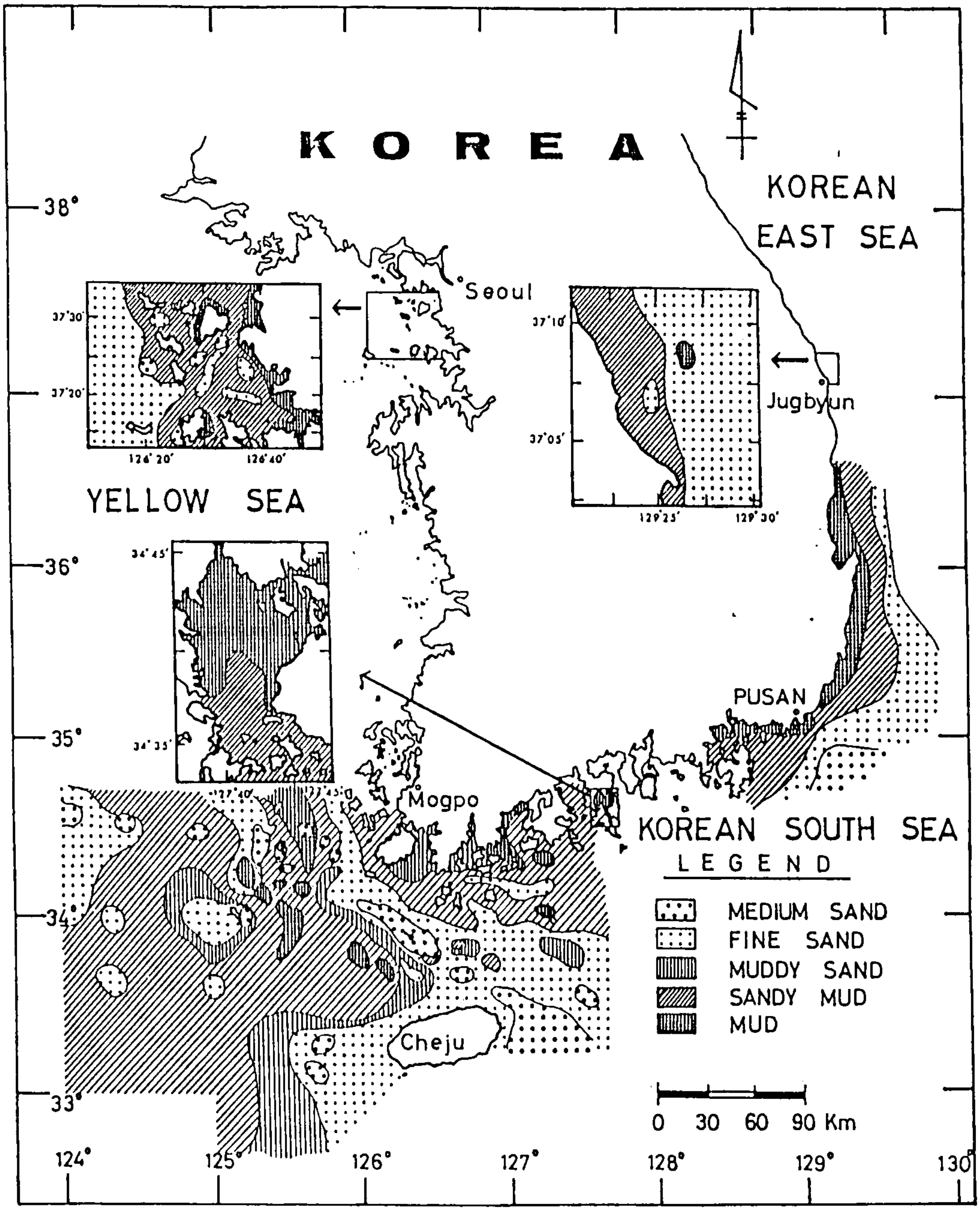
The East Sea deepens abruptly seaward forming a narrow continental shelf. The shoreline is largely straight. The Kuroshio Current passes toward the East Sea through the Cheju and Korea Straits whilst the North Korean cold water flows towards the south along the eastern coast.

The study area occupies the continental shelf off the south coast, the inner shelf off the eastern coast near Jugbyun, Gyunggi Bay and Gamagyang Bay.



TEXT–FIG. 1—Bathymetric chart.

The fine-grained sediments in the broad western part of the Yellow Sea are derived mainly from the Chinese rivers (Text-fig. 2). Sediments in the narrow eastern part originate largely from the short rivers of Korean Peninsula and are coarse-grained (Chough, 1983). In Gyunggi Bay, the sediments become, in general, finer toward the bay margin. The influence of the Kuroshio Current in transporting sediments into the Yellow Sea is minimal. Dispersal of these sediments in the eastern Yellow Sea is dominated by a clockwise nearshore current in winter and a counterclockwise trend



TEXT-FIG. 2—Distribution of the bottom surface sediments.

in summer (Chough and Kim, 1981).

Muddy sediments are dominant in the southwestern area except in the nearshore area and around the islands where strong tidal currents winnow away fine materials. Sandy sediments prevail in the outer part of the shelf in response to winnowing of finer sediments by the Kuroshio Current.

On the southeastern shelf, fine-grained sediments are restricted to the nearshore inner shelf forming a band parallel to the coastline. Sediment distribution in this area is controlled by a current which winnows away finer materials into deeper water (Chough, 1983). Thus sediments become coarser toward the outer shelf.

Gamagyang Bay, which is located on the ria-type southern coast, is connected in the south to the South Sea. The bay is relatively shallow (mean depth about 9 m). The northern part of the bay is covered with mud and the southern part with sandy mud. Sedimentation is dominated by tidal currents with no significant sediment contributed by the surrounding drainage area (Chough, 1983).

DISTRIBUTION OF KOREAN OSTRACODS

Ninty-six genera and 222 species of ostracods were recognized in the total 200 samples. All samples were collected using a grab-sampler. The systematic descriptions of them have been completed by Choe (1985): Eighty-nine genera and 97 species of them are already known and 5 genera and 54 species are considered to be new; two genera and 71 species are described under open nomenclature. Five new genera will be described horein.

In general, the composition of the ostracod fauna in this study area is closely related to that of Japanese late Cenozoic. The distribution of the ostracod fauna seems to be controlled largely by environmental factors (mainly water currents) and by geographical barriers.

Based on the composition and distribution of ostracod fauna, the following four biofacies and six subdivisions are recognized in the study area (Text-fig. 3).

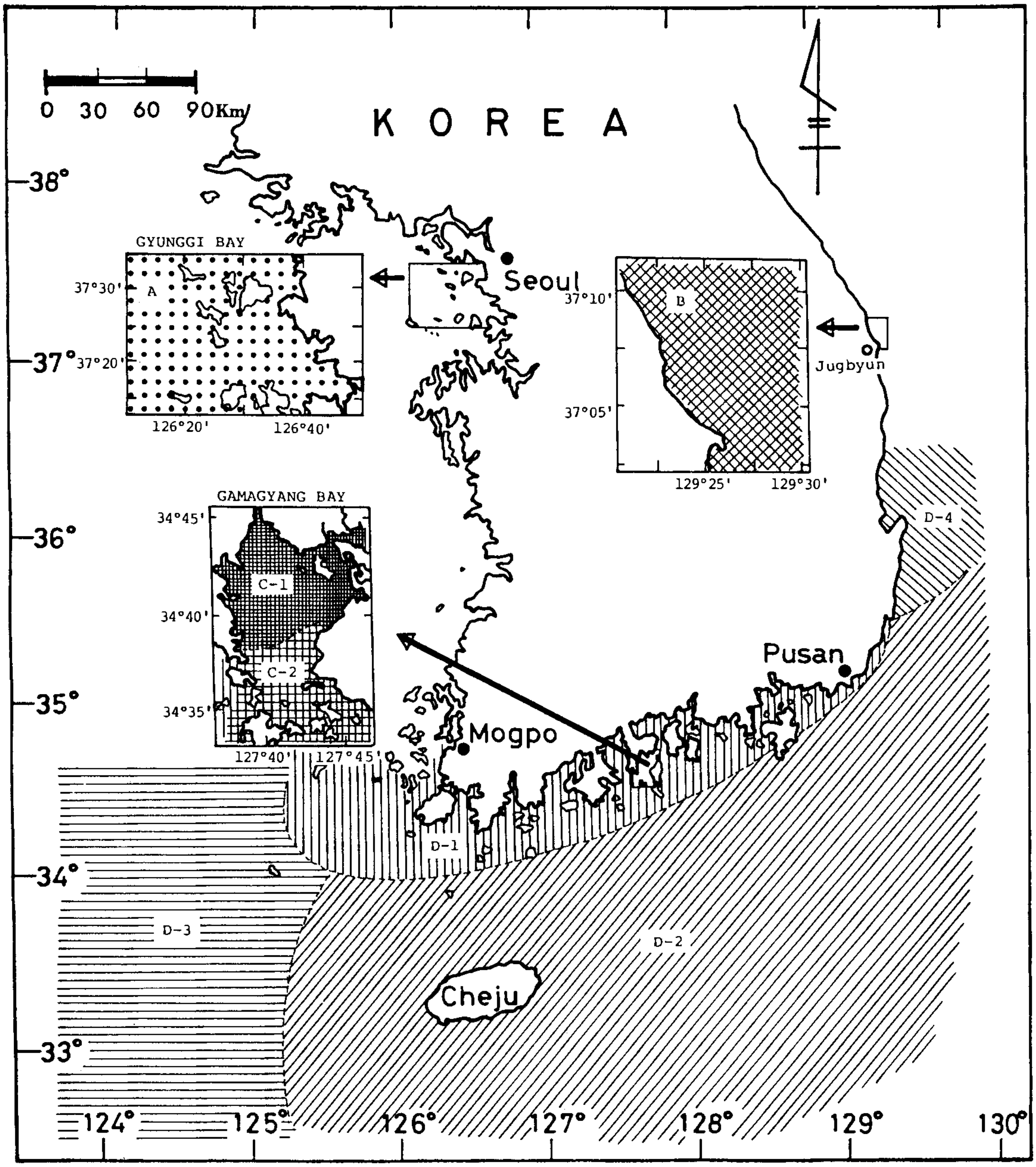
A) Tidal flat Gyunggi Bay Biofacies
B) Inner shelf East Sea Biofacies
C) Gamagyang Bay Biofacies
  1) Inner bay area
  2) Outer bay area
D) Continental shelf South Sea Biofacies
  1) Nearshore area
  2) Off-shore Cheju and Tsushima Straits area
  3) Epicontinental western area
  4) Northeastern area

Although Gyunggi Bay is connected on the west to the Yellow Sea, the composition of the ostracod fauna of Gyunggi Bay and of the southeastern part of the Yellow Sea are different from each other. Warm water species are completely absent in the Gyunggi Bay and the fauna is characterised by abundant endemic species and by the dominance of *Aglaiocypris* sp. Ostracods are extremely rare, but the distribution of ostracod fauna is uniform.

The ostracod fauna in the southeastern part of the Yellow Sea includes members of both the Chinese and of Japanese ostracod fauna, and is characterised by the low density of ostracod specimens and low species diversity in both the off-shore and nearshore types of species. The fauna seems to be a southward extension of the Yellow Sea fauna. This area is characterised by the dominance of *Metacytheropteron* sp.

The nearshore area along the southern coast of the Korean Peninsula is characterised by high species diversity and high density of ostracod specimens as well as by the dominance of nearshore type species *Bicornucythere bisanensis* (Okubo, 1975).

The off-shore Cheju and Tsushima Straits area is characterised by the dominance of off-shore types of species which occur commonly in the East China Sea. The ostracod fauna in this area is closely related to the Japanese and southeast Asian fauna, whereas the bay type, the inner shelf



TEXT-FIG. 3—Four biofacies and 6 subdivisions based on the composition and distribution of ostracod fauna.

type and the characteristic Yellow Sea fauna are found sparsely. No cold-water types of species occur in this area. Dominant species in this area is *Cytherelloidea senkakuensis* Nohara, 1976 and *Macrocypris* sp.

Cold water types of species occur simultaneously with the warm water types of species in the southern part of the East Sea near Ulsan.

The ostracod fauna in the East Sea near Jugbyun is composed of cold water types of species and is related to the Japanese cold water fauna of North Honshu and the Kuril Islands. The southeast

Asian and Chinese faunas are not found in this area. *Palmenella limicola* (Norman, 1865) and *Robertsonites* sp. 1 are dominant species in this area.

Gamagyang Bay is characterised by the dominance of bay types of species *Spinileberis quadriaculeata* (Brady, 1880). Few off-shore types of species occur in the outer bay area influenced by the influx of the open sea water.

SYSTEMATIC DESCRIPTION OF FIVE NEW GENERA

Order PODOCOPIDA Sars, 1866
Suborder PODOCOPINA Sars, 1866
Superfamily DARWINULACEA Brady and Norman, 1889
Family DARWINULIDAE Brady and Norman, 1889
Genus SEMIDARWINULA n. gen.

Type-species.—*Semidarwinula terraenuxforma* n. sp.

Diagnosis.—Darwinulidae with reticulate surface and broader anterior margin than posterior in lateral view.

Remarks.—Characteristic muscle scar of rosette type, simple hinge and no marginal zone suggest that the genus is related to Darwinulidae, in spite of the apparent difference in surface ornamentation. The new genus is distinguishable from both *Darwinula* Brady and Robertson, 1885 and *Darwinuloides* Mandelstam, 1956 by its reticulate surface and broadly rounded anterior margin in lateral view. Although more detailed anatomy of appendages is desirable to clarify the relationship between these genera, difference in surface ornamentation and lateral outline is so distinct as to discriminate this new genus from other genera of Darwinulidae.

SEMIDARWINULA TERRAENUXFORMA n. sp.

(Pl. 1, figs. 1, 2, 3)

Etymology.—from "terraenux" [Latin, "peanut"]

Type.—Holotype, a complete carapace, PLKU-O-6 (Pl. 1, figs. 1, 2, 3; L, 420 μm; H, 180 μm; W, 280 μm), St. Jb-1.

Diagnosis.—A species of *Semidarwinula* n. gen. characterised by elongate, oblong outline, with straight dorsal and medially concave ventral and obliquely rounded anterior margins. Left valve larger than right. Muscle scar comprising eight elongate, radially arranged spots.

Description.—Shell small, elongate, oblong, highest at anterior cardinal angle. Left valve larger than right. Anterior margin obliquely rounded, more broadly rounded than posterior. Dorsal

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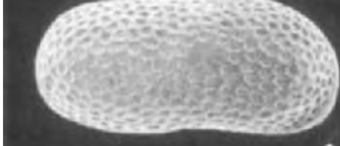
PLATE 1—Figs. 1–3. *Semidarwinula terraenuxforma* n. gen. and n. sp. 1. Lateral view of right valve (PLKU-O-6). ×95; 2. Inner view of left valve (PLKU-O-6). ×95; 3. Muscle scar (PLKU-O-6). ×390.

Figs. 4–6, 15, 20. *Paikcythere gyunggiensis* n. gen. and n. sp. 4. Lateral view of right valve (PLKU-O-56). ×86; 5. Inner view of left valve (PLKU-O-55). ×86; 6. Inner view of right valve (PLKU-O-56). ×89; 15. Simple normal pore (PLKU-O-55). ×3720; 20. Hinge of left valve (PLKU-O-55). ×137.

Figs. 7, 8, 17, 21. *Chejucythere choughi* n. gen. and n. sp. 7. Lateral view of left valve (PLKU-O-127). ×82; 8. Inner view of left valve (PLKU-O-128). ×96; 17. Dorsal view of a complete carapace (UMUT RA16973). ×96; 21. Normal pore opening and surface ornamentation on posterocentral part of left valve (PLKU-O-127). ×748.

Figs. 9, 10, 18. *Ekpectocythere plana* n. gen. and n. sp. 9. Lateral view of right valve (PLKU-O-47). ×76; 10. Inner view of left valve (PLKU-O-47). ×67; 18. Hinge of left valve (PLKU-O-47). ×120.

Figs. 11–14, 16, 19. *Gamagyangnella abei* n. gen. and n. sp. 11. Lateral view of left valve (PLKU-O-253). ×57; 12. Lateral view of right valve (PLKU-O-252). ×57; 13. Inner view of right valve (UMUT RA17079). ×57; 14. Inner view of left valve (UMUT RA17078). ×57; 16. Muscle scars on right valve (UMUT RA17079). ×225; 19. Hinge of right valve (UMUT RA17079). ×113.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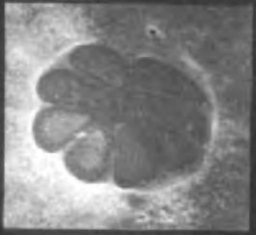
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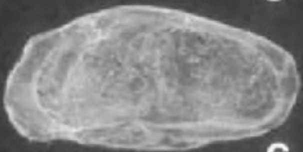
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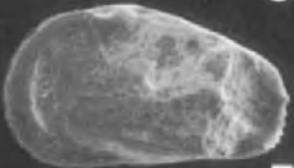
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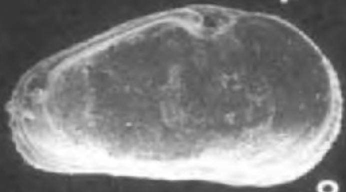
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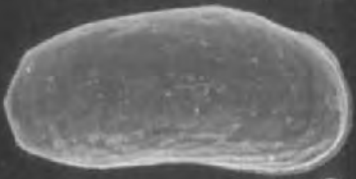
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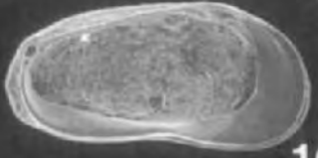
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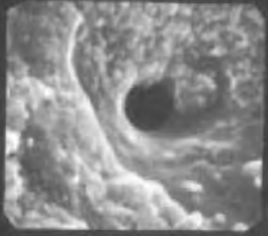
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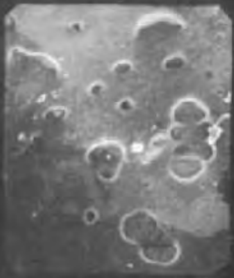
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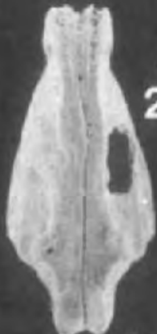
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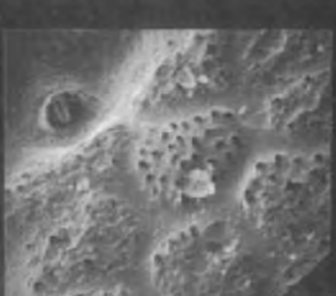
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margin straight, ventral margin slightly concave at middle. Viewed dorsally, sides tapering acutely toward anterior, and abruptly toward posterior. Greatest thickness in posterior half of carapace. Along hinge margin dorsal edge of right valve fitting into shallow groove of left valve. Surface reticulate. Adductor muscle scar field locating at anterior to mid-length. Muscle scar of rosette type, consisting of eight elongate, radially arranged spots. Normal pores simple, few, located on muri. No marginal infold.

Remarks.—This species is close to *Darwinula malayica* reported by Menzel (1923) in having similarly arranged muscle scars, but the radical difference between the two species in surface ornamentation and lateral outline suggests that the basic distribution pattern of muscle scars is a relatively conservative character within the Family Darwinulidae.

Occurrence.—Two specimens were found at St. Jb-1.

Superfamily CYTHERACEA Baird, 1850

Family EUCYTHERIDAE Puri, 1954

Subfamily PECTOCYTHERINAE Hanai, 1957

Genus EKPECTOCYTHERE n. gen.

Etymology.—ek- [Greek, "out of"] + *Pectocythere*

Type-species.—*Ekpectocythere plana* n. sp.

Diagnosis.—Pectocytherinae characterised by elongate subrectangular lateral outline, surface without marginal ridge, broad marginal infold, narrow zone of concrescence, and by presence of posterior projection.

Remarks.—This genus differs from other pectocytherid genera in having a relatively thin carapace, no marginal ridge on the surface, and a distinct posterior projection. Here it is tentatively assigned to the Pectocytherinae because it possesses a pentodont hinge. In comparison with the hinge of *Pectocythere* and *Munseyella*, in which antero- and postero-median teeth in left valve are separated into upper and lower elements, the undivided teeth of this genus are characteristic.

Ekpectocythere is closely related to the genera *Arcacythere* Hornibrook, 1953, *Tetracytherura* Ruggieri, 1952, and *Dolocythere* Mertens, 1956 in hinge structure, but the diagnostic characters mentioned in the preceding lines will easily differentiate this genus from these genera. Large J-shaped frontal scar, four adductor muscle scars, straight and few marginal pore canals, and crescent shaped vestibule of the genus are all closely similar to those of *Pectocythere*, the type-genus of the Pectocytherinae, but the unseparated antero- and posteromedian teeth in left valve, and the thin carapace with a posterior projection and without a marginal ridge will serve as the distinguishable characters. Absence of marginal ridge, unseparated antero- and posteromedian teeth in left valve, and four adductor muscle scars of the genus are similar to those of *Dolocythere*, but the present genus differs in having anterior and posterior vestibules, J-shaped frontal scars and a posterior projection.

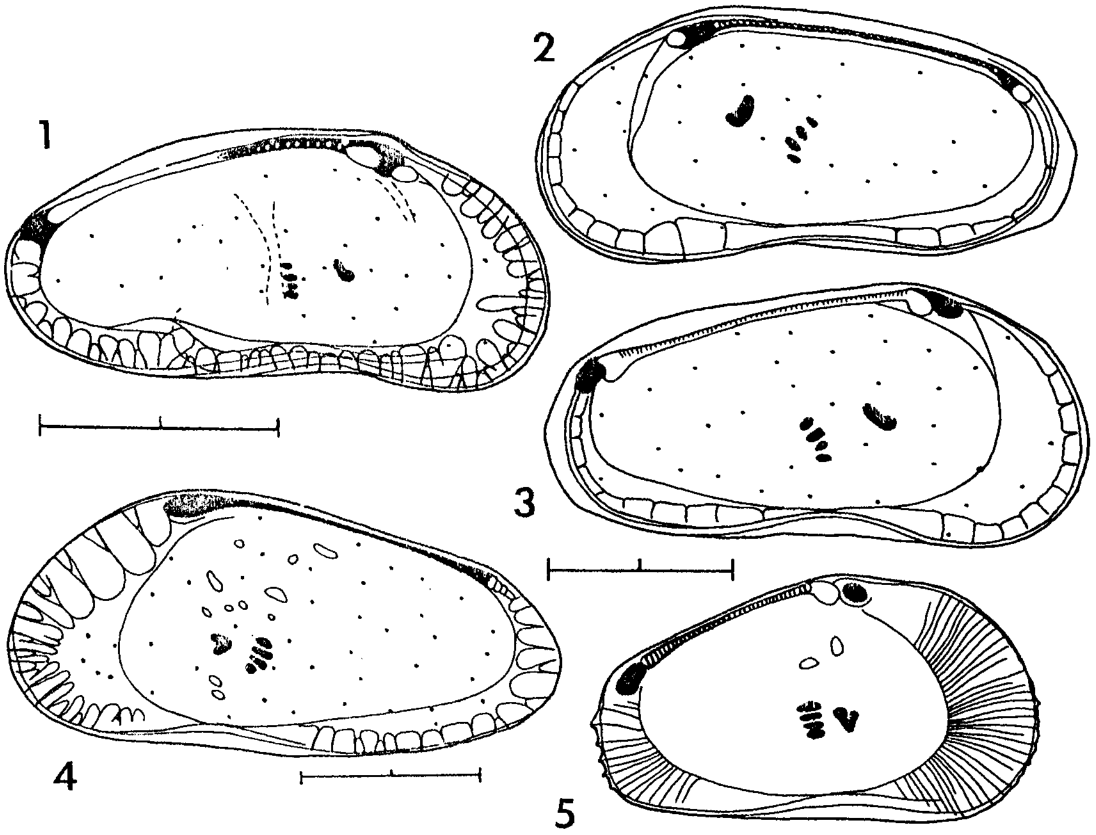
EKPECTOCYTHERE PLANA n. sp.

(Pl. 1, figs. 9, 10, 18; Text-figs. 4–2, 4–3)

Type.—Holotype, a complete carapace, PLKU-O-47 (Pl. 1, figs. 9, 10, 18, figs. 4–2, 4–3; L, 590 μm; H, 280 μm), St. Jb-14.

Diagnosis.—An *Ekpectocythere* characterised by a smooth surface with faint wrinkles along the periphery of the carapace, broadly, slightly and obliquely rounded anterior margin with marginal fringe, and posterior angular projection.

Description.—Carapace relatively thin, elongate subrectangular in lateral outline, highest at the anterior cardinal angle, and with a posterior projection. Dorsal margin nearly straight. Ventral margin concave at middle. Anterior margin broadly and obliquely rounded with marginal fringe.



Text-fig. 4—Internal views (scale: 200 μm).
4–1. *Paikcythere gyunggiensis* n. sp., left valve (PLKU-O-55); 4–2. *Ekpectocythere plana* n. sp., right valve (PLKU-O-47); 4–3. *Ekpectocythere plana* n. sp., left valve (PLKU-O-47); 4–4. *Gamagyangnella abei* n. sp., right valve (PLKU-O-252); 4–5. *Chejucythere choughi* n. sp., left valve (PLKU-O-127).

Posterior contact margin narrowly rounded. Posterior margin with posterior angular projection. Viewed dorsally, sides nearly parallel and gently tapering toward each end. Surface smooth with scattered punctations of normal pore canal openings and with faint wrinkles at the periphery of the carapace. Hinge pentodont, left valve consisting of anterior and posterior sockets which open interiorly, and a crenulate median bar. Anterior and posterior terminations of median bar swell into knob-like projections which are not separated into upper and lower elements. Marginal infold broad anteriorly, moderate posteroventrally and narrow posteriorly and ventrally. Vestibule crescent shaped and deep anteriorly, and shallow posteroventrally, thus the zone of concrescence is narrow along the entire free margin. Marginal pore canals short, simple, straight, moderate in number, approximately ten along the anterior margin. Normal pore canals few, widely scattered. Adductor muscle scars consisting of an oblique row of four scars with a large, of J-shaped frontal scar.

Remarks.—Since *Ekpectocythere* is so far a monospecific genus, it is difficult to give a diagnostic characters of the species. In the Pectocytherinae, however, the lateral outline of the carapace, the features observable on the carapace surface and of the marginal infold are usually considered as specific characters.

Occurrence.—Only one specimen occurs at St. Jb-14, of sandy mud bottom, 50 m deep.

Family LEPTOCYTHERIDAE Hanai, 1957

Genus PAIKCYTHERE n. gen.

Etymology.—In honor of K. H. Paik, Korea University.

Type-species.—*Paikcythere gyunggiensis* n. sp.

Diagnosis.—Carapace elongate ellipsoid in lateral view, highest at anterior cardinal angle, with semicircular posteroventral tubercle and anterodorsal and dorsomedian sulci. Muscle scars consisting of a vertical row of four adductor scars and a J-shaped frontal scar. Hinge of left valve consists of a deep anterior socket, crenulate anteromedian groove, smooth posteromedian bar, and deep and oblong posterior socket. Anteromedian groove gradually shallows and is connected to the posteromedian bar at a point near middle of median hinge element. Anti-slip tooth lies at anterior end of anteromedian groove. An anti-slip tooth like projection is present in front of the anterior socket. Marginal infold broad anteriorly and moderate ventrally and posteriorly. Marginal pore canals polyfurcated. Vestibule present.

Remarks.—The characteristic hinge structure of *Paikcythere* mentioned in the diagnosis is different from hinges generally found in leptocytherids, but here the new genus is assigned to the Leptocytheridae because of the general leptocytherid outline of carapace and polyfurcated marginal pore canals. Most genera of Leptocytheridae have a crenulate and two-fold median hinge element, although in *Amnicythere* Devoto, 1965, median hinge element is smooth and not two-fold. In *Paikcythere* the median hinge element is crenulate in its anterior half and smooth in its posterior half. Both this character and the gradual change of anteromedian groove to posteromedian bar in the left valve do not allow this new genus to be included in any other genus of Leptocytheridae. The dorsal flange projects prominently above the anterodorsal groove, and merges posteriorly into the posteromedian bar which appears as if it were the dorsal flange, which is a feature worth describing.

PAIKCYTHERE GYUNGGIENSIS n. sp.

(Pl. 1, figs. 4, 5, 6, 15, 20; Text-fig. 4–1)

Etymology.—Gyunggi Bay.

Type.—Holotype, a left valve, PLKU-O-55 (Pl. 1, figs. 5, 15, 20, fig. 4–1; L, 460 μm; H, 210 μm), St. Gg-81087; Paratype, a right valve, PLKU-O-56 (Pl. 1, figs. 4, 6; L, 0.43; H, 0.21), St. Gg-81087.

Diagnosis.—*Paikcythere* characterised by a smooth surface with obtuse anterior ridges, compressed antero- and posteromarginal areas, and elongate carapace with maximum height less than half the length.

Description.—Carapace thin, elongate ellipsoid in lateral outline, highest at the anterior cardinal angle. Antero- and posteromarginal area flattened. Semicircular posteroventral tubercle and ventral inflation distinct. Dorsal margin broadly convex. Ventral margin sinuate anterior to the mid-length, and subparallel to the dorsal margin. Anterior margin broadly and obliquely rounded. Posterior margin narrowly rounded and forming an obtuse posterior cardinal angle with the dorsal margin. Ventral sinuation is obscured by ventral inflation. Viewed dorsally the carapace is spindle shape, thickest posterior to the mid-length owing to the posteroventral tubercle, each end acute owing to compressed anterior and posterior marginal areas. Surface smooth with anterodorsal and dorsomedian sulci, two obtuse anterior marginal ridges, and faint anteroventral undulations.

Inner anterior marginal ridge starting at anterior cardinal angle and terminating in the anteroventral area. Outer anterior marginal ridge shorter and lying at the middle of the anterior margin. Anterodorsal groove running parallel to anterior marginal ridge, and diminishing ventrally at one-third of the carapace height. Dorsomedian sulcus wedge-shaped, with inside minor ridge. Hinge, muscle scars, marginal pore canals and vestibule as for the genus. Normal pore canals few, widely scattered and of simple type.

Remarks.—It is difficult to give diagnostic characters of the species of a monospecific genus. In Leptocytheridae, the general outline and surface ornamentation of the carapace are generally considered as specific characters, and hinge structures and characters of the marginal area as generic characters.

Occurrence.—This species occurs at St. Gg-81087 of sandy mud bottom.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily BUNTONIINAE Apostolescu, 1961
Genus CHEJUCYTHERE n. gen.

Etymology.—Cheju, name of island in Korean South Sea.

Type-species.—*Chejucythere choughi* n. sp.

Diagnosis.—Buntoniinae characterised by a small, thick carapace of reniform lateral outline, sagittate in dorsal view, obtuse marginal rim along anterior, wide marginal infold without vestibule, simple and numerous radial pore canals and denticulate posterior margin. Hinge amphidont, right valve with strong round anterior tooth, postjacent deep socket, serrated posteromedian groove and reniform posterior tooth. Muscle scars consisting of a vertical row of four closely spaced adductor muscle scars and a hook-shaped frontal scar.

Remarks.—This genus is closely related to the genera *Harringtonia* Bertels, 1975 and *Phacorhabdotus* Howe and Laurencich, 1958 in its dorsal outline of arrow-head shape, but the obtuse anterior and posterior margins will easily differentiate this genus from the other two genera which are characterised by their sharp margin. *Chejucythere* resembles *Ambocythere* Van den Bold, 1957 in lateral outline, broad marginal infold, thick anterior marginal rim and numerous radial pore canals, but differs in dorsal view and in the absence of a longitudinal ridge on the carapace surface and a posteroventral projection or flange.

CHEJUCYTHERE CHOUGHI n. sp.
(Pl. 1, figs. 7, 8, 17, 21; Text-fig. 4–5)

Etymology.—Named in honor of S. K. Chough, Seoul National University.

Type.—Holotype, a left valve, PLKU-O-127 (Pl. 1, figs. 7, 21, fig. 4–5; L, 460 μm; H, 260 μm), St. J-31; Paratype, a left valve, PLKU-O-128 (Pl. 1, fig. 8; L, 440 μm; H, 240 μm), St. J-32; a complete carapace, UMUT RA16973 (Pl. 1, fig. 17; L, 430 μm; H, 240 μm; W, 190 μm), St. J-30.

Diagnosis.—A *Chejucythere* with feeble reticulation and sieve-like micropunctation on the fossae.

Description.—Carapace thick, reniform in lateral outline, highest at the anterior cardinal angle. Anterior margin broadly rounded with thick anterior marginal rim. Gently arched dorsal margin and slightly concave ventral margin convergent posteriorly. Posterior margin narrowly rounded with approximately seven denticles. Viewed dorsally, sagittate with obtuse and compressed anterior and posterior ends, widest posteromedially. Surface feebly reticulate with thick, smooth anterior marginal rim and marginal furrow just behind marginal rim. Almost smooth surface except for anterior marginal rim and on muri characterised by sieve-like micropunctation. Hinge amphidont of genus, posteromedian hinge bar faintly serrated anteriorly in left valve. Marginal infold broad anteriorly, moderate posteriorly, without vestibule. Radial pore canals simple, nearly straight, approximately 35 along anterior margin. Muscle scars as for genus. Normal pore canal openings moderate in number, scattered, consisting of two types: simple and sunken sieve types, situated on muri. Eye tubercle obscure.

Remarks.—Since *Chejucythere* is so far a monospecific genus, it is difficult to give diagnostic characters of the species. In Buntoniinae the detailed hinge structure, lateral outline of the carapace and the features observable on the carapace surface and in the marginal infold are generally used as a specific characters.

Occurrence.—This species occurs at St. Soh-29, J-30, J-31, Soh-14, eJ-9, eJ-72 and eJ-76, associated with a sandy mud to medium-grained sand bottom, 85 to 110 m deep.

Family Uncertain

Genus GAMAGYANGNELLA n. gen.

Type-species.—*Gamagyangnella abei* n. sp.

Diagnosis.—Elongate subtriangular carapace with smooth surface. Subacutely tapered posterior margin with caudal process. Hinge of right valve with elongate anterior socket, narrow and smooth median groove and posterior tooth. Posterior tooth serrate, consisting of four toothlets which become smaller posteriorly. Left valve with complementary hinge elements. Muscle scars consist of an oblique row of four adductor scars, a crescent-shaped frontal scar, two mandibular scars and several dorsal scars. Marginal infold broad anteriorly, moderate posteriorly and posteroventrally. Radial pore canals polyfurcate, moderately numerous.

Remarks.—*Gamagyangnella* has a certain similarity to *Javanella* Kingma, 1948, in external appearance, but the presence of a posterior tooth and the absence of an anti-slip tooth in the right valve and polyfurcate marginal pore canals easily differentiate *Gamagyangnella* from the latter. To my knowledge, the hinge structure of this genus seems to be completely different from known genera.

GAMAGYANGNELLA ABEI n. sp.

(Pl. 1, figs. 11, 12, 13, 14, 16, 19; Text-fig. 4–4.)

Etymology.—Named in honor of K. Abe, University of Tokyo.

Type.—Holotype, a right valve, PLKU-O-252 (Pl. 1, fig. 12, fig. 4–4; L, 620 μm; H, 300 μm), St. G-75; Paratype, a left valve, PLKU-O-253 (Pl. 1, fig. 11; L, 640 μm; H, 320 μm), St. G-75; a left valve, UMUT RA17078 (Pl. 1, fig. 14; L. 650 μm; H, 310 μm), St. G-75; a right valve, UMUT RA17079 (Pl. 1, figs. 13, 16, 19; L, 640 μm; H, 310 μm), St. G-75.

Diagnosis.—*Gamagyangnella* with smooth surface, keel-like feeble ventrolateral edge, caudal process in lower part of posterior margin.

Dscription.—Carapace thin, elongate subtriangular in lateral view. Anterior margin obliquely broadly rounded. Dorsal margin nearly straight with slight sinuation posterodorsally. Ventral margin broadly rounded in left valve, slightly sinuate anterior of the middle in the right valve. Dorsal and ventral margins taper towards rear. Posterior margin subacutely tapered, its upper margin straight. Caudal process distinct, in the lower part of the posterior margin. Viewed dorsally, sides parallel, tapering gently toward each end. Surface smooth. Keel-like ventrolateral edge developing somewhat feebly, parallel to ventral margin. Hinge structure and muscle scar pattern as for the genus. Marginal infold broad anteriorly, moderate posteroventrally and posteriorly. Vestibule deep anteriorly, shallow posteroventrally and posteriorly. Marginal pore canals moderately numerous, somewhat densely spaced anteroventrally, polyfurcate, especially in the anterior region. Normal pore canals moderate in number, evenly distributed. Four to five small denticles present below the ventral selvage. Eye tubercle and sexual dimorphism indiscernible.

Remarks.—Since *Gamagyangnella* is so far a monospecific genus, it is difficult to give a diagnostic character of the species.

Occurrence.—The species occurs at St. G-75 and S-17, of mud bottom, 21.5 to 75 m deep.

ACKNOWLEDGEMENTS

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On the Recent *Aurila* Species from Japan*

ICHIRO OKUBO
Shujitsu Joshi University, Okayama, Japan

ABSTRACT

The copulatory organ of the genus *Aurila* is composed of two parts. The distal part is made up of three structures: the clasping apparatus with the finger guard, an "ejaculatory duct" and a "holding plate". The last two are characteristic of the species and show no variation within a species. Therefore, they are good characters for the discrimination of species.

The usefulness of the copulatory organ in identifying species is shown, taking the species of *Aurila* as an example. Recent *Aurila* species from Japan have been examined mainly on the basis of the valves so that some of them are misnamed. Synonyms of *A. cymba, A. hataii, A. munechikai* and others are corrected in part, and a new checklist for the recent species of *Aurila* reported before 1982 is proposed.

Two new species, *Aurila okayamensis* sp. nov. and *A. ikeyai* sp. nov., are described. Both species were formerly called *A. hataii.* One further new species remains unnamed because its valves have not yet been examined.

INTRODUCTION

The valve is important for the study of ostracods. Moreover, it is generally the only material that palaeontologists have to work with. Some investigators, therefore, are liable to identify even Recent species by their valves alone. As the valves within one genus are similar in the shape to each other, identification based solely on the valves has sometimes been responsible for misjudgments.

The male copulatory organ is useful in identifying species. It is characteristic of a species, showing no variation within one species. Furthermore, it is often large enough to examine. When valves deposited on the sea floor are inspected, living specimens should be searched for nearby.

Incidentally, searching for the living ostracods will enable us to establish their real "occurrence". Valves in bottom sediments may be deposited by tidal currents or by chance. The known occurrence of most Japanese species is reported as sand-mud, though a relatively few species may be found alive in sand-mud.

The genus *Aurila* includes more than ten species, which inhabit coastal areas throughout Japan. Living specimens can be assembled with ease, but few have been utilized. As *Aurila* species have been identified mainly by their valves, there is some confusion about their specific identification. I have collected some species from the type localities and elsewhere, and traced the relationship of the specific identification.

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* Marine Ostracoda of Japan–4

I wish to express my thanks to Mr. Okamura of JEOL Ltd. for taking the scanning electron microscope photographs.

MALE COPULATORY ORGAN OF *Aurila* SPECIES

The copulatory organ of the genus *Aurila* is composed of a basal part and a distal part. The basal part, being homologous to the peniferum figured by Hart and Hart (1969), is a round, membrane-like plate. It is bordered by the cardos and the zygum, and connects with the tropis and sterinx. At its lower centre there is a small structure like the penis of *Entocythere* which connects with the finely-striped spermatic tube.

The distal part is made up of three structures which are separated from the basal one. A heavily-sclerotized, complicated one near the base may be the clasping apparatus with the finger guard, because it has the horizontal ramus with denticles and the rod-shaped projection of a finger guard. The duct is two-segmented and heavily sclerotized. Hart and Hart called such a duct the spermatic tube in the copulatory organ of their *Hemicythere*. However, it does not seem to be homologous with the spermatic tube of *Entocythere* because it follows the "penis". It may play a role in ejaculating sperm from the penis. The plate is made up of two membranes that are pasted along both margins. The inner membrane articulates with the clasping apparatus and the outer one with the peniferum. Two groups of "muscles" on the peniferum focus on these joints. This plate is situated outside the duct, and would function in holding down the female during the copulation.

It is difficult to compare the copulatory organ of *Aurila* with that of *Entocythere*, before many kinds of ostracods have been examined. It seems, however, that the duct and the plate may be homologous to Hart and Hart's "fingers"; the duct is possibly the ventral finger and the plate is the dorsal finger. Unlike the motionless parasitic *Entocythere*, free-living *Aurila* species may need such a duct and plate for copulation. In this paper the duct is called the "ejaculatory duct" and the plate the "holding plate".

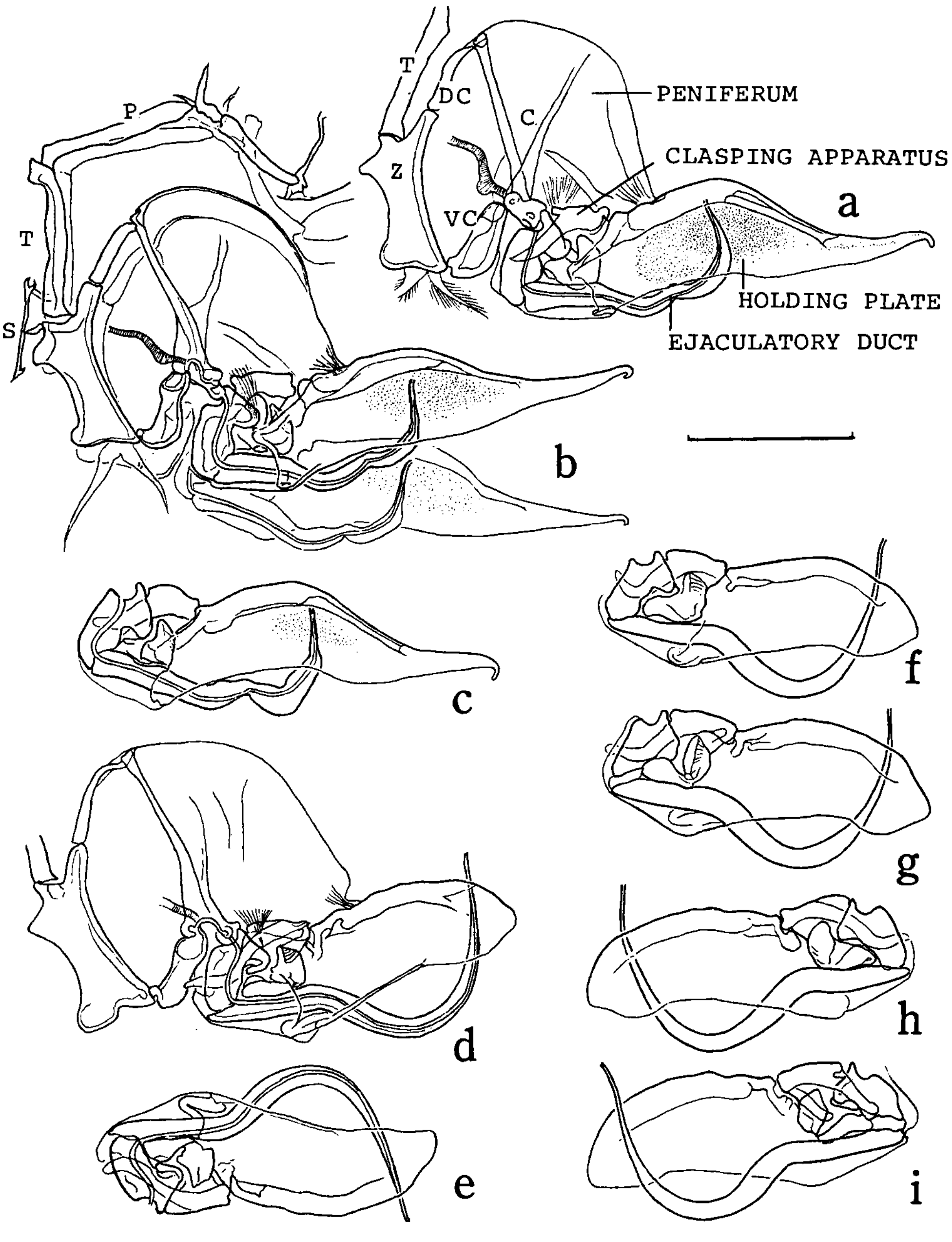
In *Aurila* species, the ejaculatory duct and the holding plate, as well as the valves, are the best characteristics for identification. They are large enough to dissect and observe, and will discriminate between the species at a glance. Moreover, there is little variation in the copulatory organs within one species. *A. cymba* from the Inland Sea, *A. miii* from Uranouchi and *A. subconvexa* from Misaki have the same copulatory organ. The ejaculatory ducts and the holding plates of *A. hataii*, *A. munechikai* and *A. corniculata* from two distant areas also show little variation. Of course, specimens from one area have no variation, as shown in *A. ikeyai* (Text-fig. 1).

There is a little variation between *A. hataii* from the Japan Sea and that from the Pacific. The ejaculatory duct in the former is slightly wider than in the latter. They are thought to fall within the limits of specific variations, however.

RECENT *Aurila* SPECIES FROM JAPAN

Recent *Aurila* species reported from Japan before 1982 are shown in Text-fig. 2.

Brady (1880) found nine ostracod species in dredged samples collected from the Inland Sea by the "Challenger". These included *Cythere cymba*, now *Aurila cymba* whose type specimens he had discovered at Hong Kong in 1869. This species is common in Japan, and Ishizaki (1981) found it also in the East China Sea, which lies halfway between the type locality and Japan. It is thus probable that the Japanese species is identical with the type from Hong Kong. It has appeared in the literature under such names as *A. subconvexa*, *A. miii* and so on.

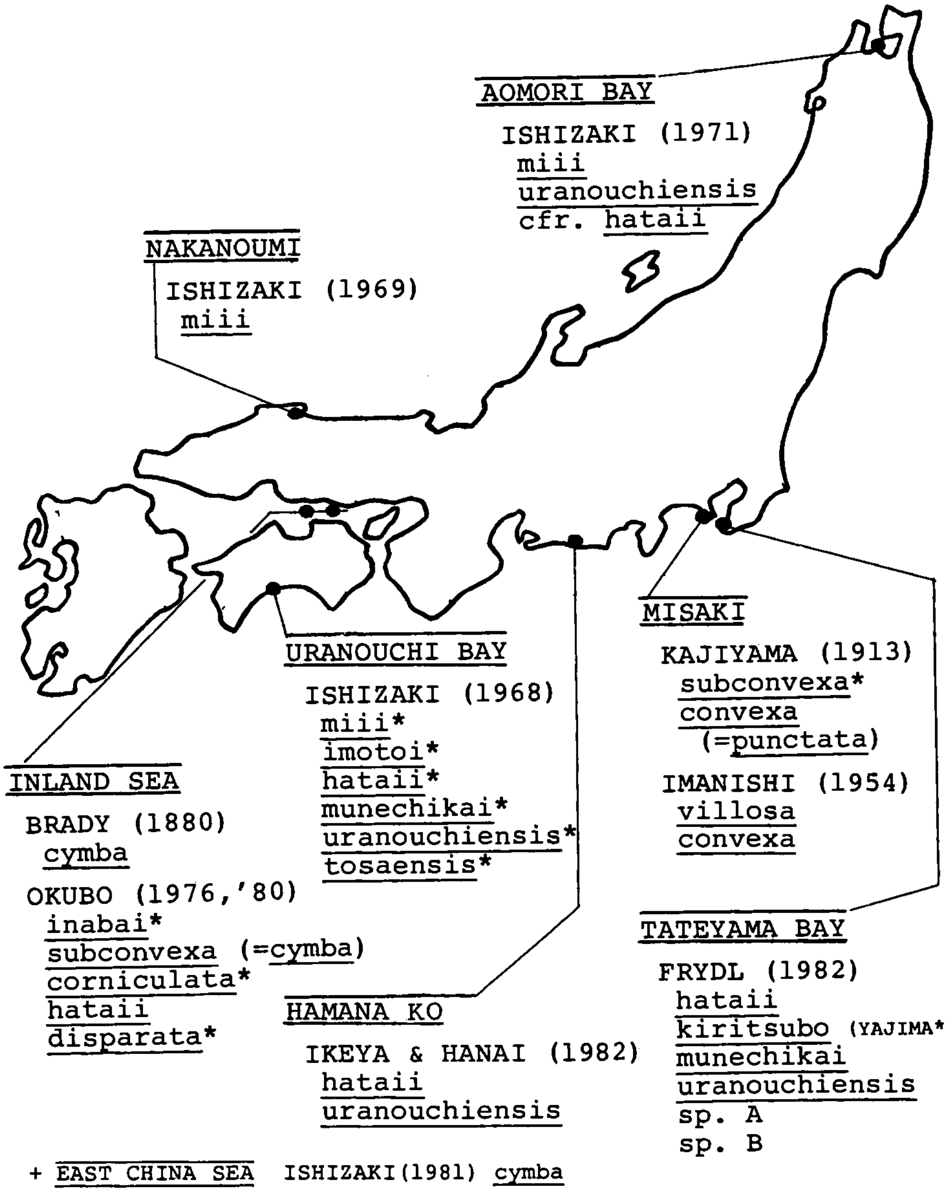


TEXT-FIG. 1—Male copulatory organs of *Aurila* species. a–c. *A. hataii* (a. MO-1808, Uranouchi; b. MO-1691, Misaki; c. MO-1795, Omi). d–i. *A. ikeyai* n. sp. (d, e. MO-1927; d. right; e. left; f. MO-1639; g. MO-1642; h. MO-1640; i. MO-1689; all Misaki, inclusive of Hayama). Scale: 100 μm; P, pastinum; T, tropis; S, sterinx; Z, zygum; C, costa; DC, Dorsal Cardo; VC, Ventral Cardo.

Kaijyama (1913) assembled 21 podocopid species from Misaki, in which the present *Aurila* species, *subconvexa* and *convexa*, were included. Imanishi (1954) found two species, *Cythere villosa* and *C. convexa*, near Misaki.

Ishizaki reported six *Aurila* species, *hataii, imotoi, miii, munechikai, tosaensis* and *uranouchiensis* from bottom sediments of Uranouchi Bay in 1968, one species *A. miii* from the Nakanoumi Estuary in 1969, three species, *A. miii, A. uranouchiensis* and *A.* cf. *hataii*, from Aomori Bay in 1971, and *A. cymba* from the East China Sea in 1981.

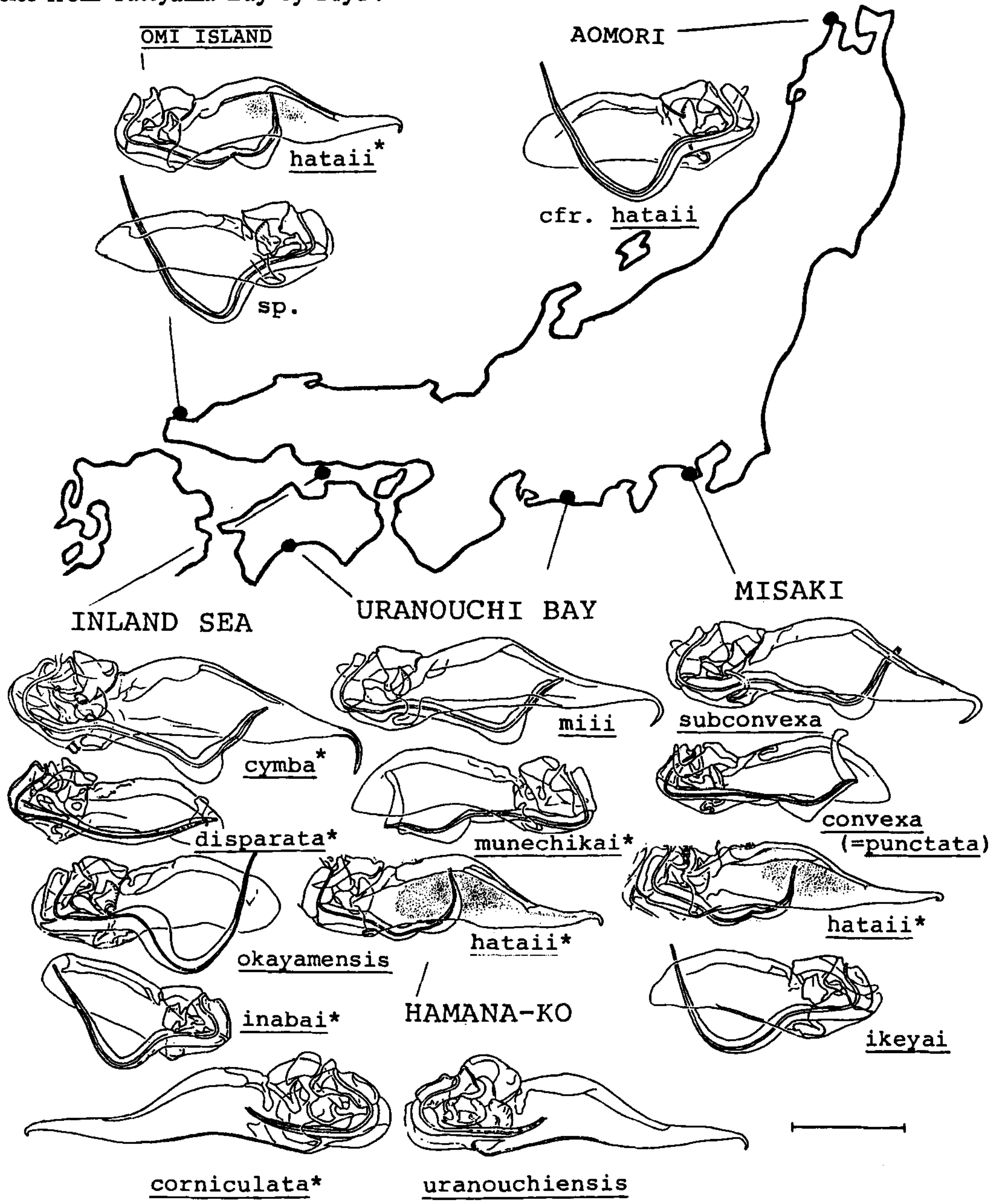
Okubo (1976, 1980) described five *Aurila* species, *inabai, subconvexa, corniculata, disparata* and



TEXT-FIG. 2—Recent *Aurila* species reported from Japan before 1982. Species with an asterisk have been described as new species.

hataii, from the Inland Sea.

In 1982, two *Aurila* species, *hataii* and *uranouchiensis*, from Hamana-ko were listed by Ikeya and Hanai, and six *Aurila* species, *hataii*, *kiritsubo*, *munechikai*, *uranouchiensis* and two uncertain species from Tateyama Bay by Frydl.



TEXT-FIG. 3—Recent *Aurila* species from Japan the author examined. Distal parts of male copulatory organs (scale: 100 μm). Material. Inland Sea (*A. cymba* and *A. inabai*, Okubo, 1980, fig. 7; *A. corniculata*, MO-1917); Uranouchi (*A. miii*, MO-5016; *A. munechikai*, MO-5020; *A. hataii*, MO-1808); Hamana-ko (*A. uranouchiensis*, MO5017); Misaki (*A. subconvexa*, MO-1945; *A. convexa*, MO-1632; *A. hataii*, MO-1640; *A. ikeyai*, MO-1927); Aomori (*A.* cf. *hataii*, MO-5033); Omi (*A. hataii*, MO-1795; *A.* sp., MO-1792). Asterisked species are thought to be valid.

In the above species, Hanai *et al.* (1977) indicated that *C. villosa* was a synonym of *A. hataii*, and that "The pattern of surface ornamentation of *Aurila miii* is identical with that of *A. cymba* illustrated by Brady (1880) in the Challenger report. This species is closely related to *A. uranouchiensis*". Okubo (1980) also pointed out that *A. cymba*, *A. miii* and *A. subconvexa* were conspecific.

I doubted the validity of other species and inspected some *Aurila* species from the type localities, Uranouchi and Misaki, and others. The male copulatory organs of the species are shown in Text-fig. 3. Three species were found from Uranouchi, four from Misaki, one from Hamana-ko, one from Aomori (Tappi) and two from Omi Island, besides five from the Inland Sea.

Species from Uranouchi have proved very worrying. Ishizaki found six species in the sediment samples but I discovered only three species, namely *A. miii*, *A. munechikai* and *A. hataii*.

It has been reported that *A. uranouchiensis* and *A. cymba* (= *A. miii*) occur in very nearly the same places, that is, in the inside of the Uranouchi Bay. The *Aurila* species living around Misaki and Tateyama Bay has been called either *A. uranouchiensis* or *A. cymba*. The two species resemble each other in valve sculpture, as Hanai *et al.* indicated. I could not have found the species that is thought to be *A. uranouchiensis* in Uranouchi Bay and around Misaki, though I have collected *A. cymba* there. Therefore, it may be thought that both *A. uranouchiensis* and *A. cymba* near Misaki are in all probability of the same species. However, Ishizaki has been confident of the separate identity of the species because *A. uranouchiensis* from Uranouchi Bay has a furcate ventral ridge that is not found in *A. cymba* from Hong Kong. Thus, the validity of *A. uranouchiensis* remains unclarified.

A. imotoi resembles *A. cymba* in the shape of valves. However, the former was rather common outside the bay, whereas the latter was common exclusively inside the bay. So *A. imotoi* may be either a good species, or a slightly modified form of *A. cymba* living in the open sea.

A. tosaensis having undeveloped valves is thought to be a juvenile of (some) species. It may be an A–1 juvenile of *A. munechikai*, since their habitats are nearly identical.

There is some doubt as to whether *A. imotoi* and *A. tosaensis* are good species or not. The subject remains unsettled.

A. convexa (= *A. punctata*) reported from Misaki is identical with *A. munechikai* from Uranouchi in the form of the copulatory organ. However, it is highly probable that this *Aurila* species is a species different from European *A. punctata*. Thus the name *munechikai* will be retained as the specific name for Japanese "*punctata*".

The species called *A. hataii* includes at least four different species. The type specimen is the one from Uranouchi, which has a long pigmented plate and a W-shaped ejaculatory duct. The species is also found from Misaki.

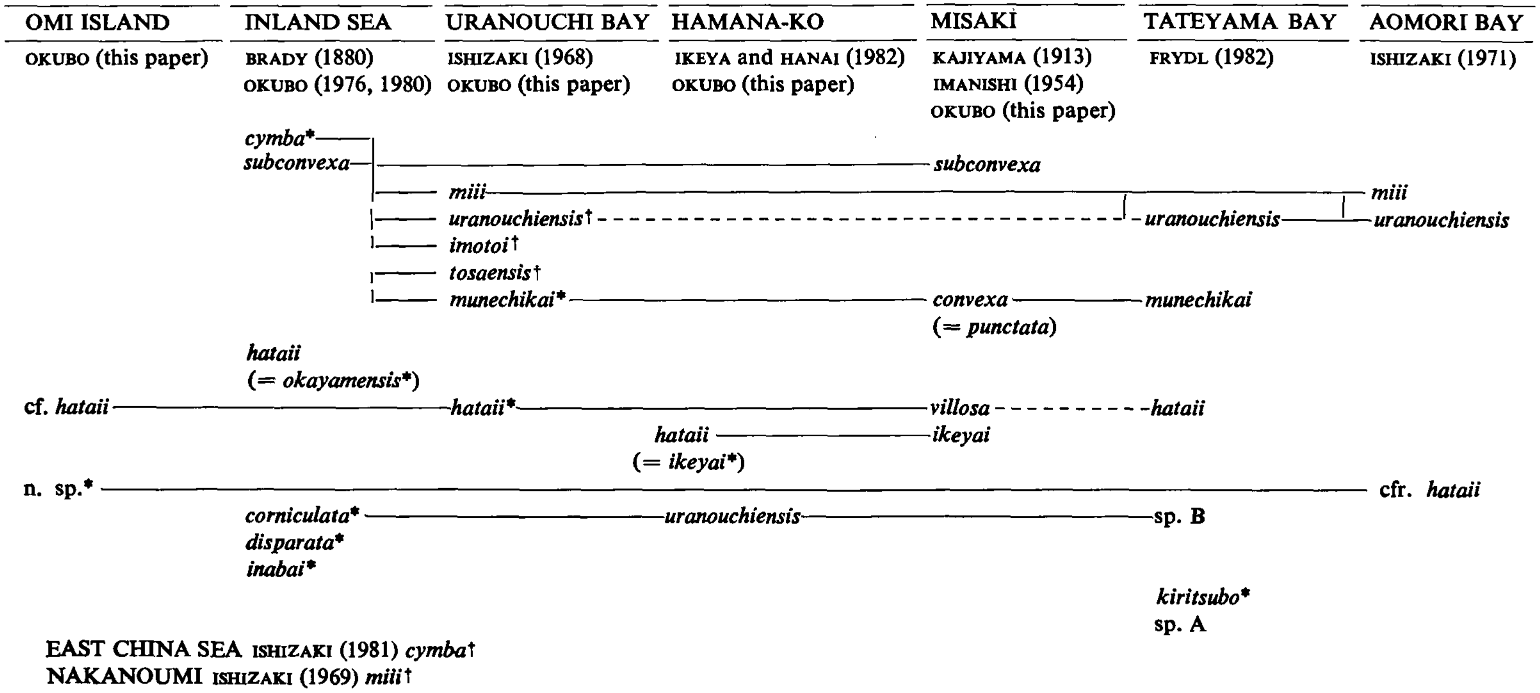
The species from the Inland Sea described as *A. hataii* by Okubo is actually a new species, and is named *A. okayamensis* sp. nov. in this paper.

The species from the Hamana-ko called *A. hataii* by Ikeya and Hanai is not *A. hataii* but another new species. It also occurs from Misaki and is described as *A. ikeyai* sp. nov. in this paper.

The species from Aomori allotted to *A.* cf. *hataii* by Ishizaki is not the true *A. hataii*. This new species, which also comes from Omi Island, is called *A.* sp. in this paper. It will be formally named after the valves have been examined.

The male of *A. corniculata* came from the Inland Sea and the species called *A. uranouchiensis* by Ikeya and Hanai proves to be *A. corniculata*. According to Ikeya, Frydl's *Aurila* sp. B is also identical with this species. There is a faint suspicion that *A. uranouchiensis* from Uranouchi may possibly be the same thing as *A. corniculata* (or less likely *A. disparata*). If so, the name *uranouchiensis* would remain valid.

A. inabai, *A. disparata* and *A. kiritsubo* are thought to be valid taxa. The rest will be clarified, when their males are examined.



TEXT-FIG. 4—Relationships of specific identification among the recent *Aurila* species from Japan.
*Specific names with an astrisk are thought to be valid.
†Specific names with a dagger are thought to be doubtful.

The confusion among the specific names came from identification on the basis of valves alone. If their male copulatory organs had been examined, most of the errors would have been avoided. Even when studying valves from bottom sediments a search should be made for living males nearby. The valves and the copulatory organ are like the two wheels of a cart for the study of Recent ostracods. Furthermore, the valves of living specimens will give us more beautiful SEM photographs.

The relationship of the above species is summarized in Text-fig. 4. And a new checklist of species of the genus *Aurila* recorded from Japan before 1982 is proposed.

DESCRIPTION OF NEW SPECIES

AURILA OKAYAMENSIS sp. nov.

Aurila hataii Ishizaki. OKUBO, 1980, p. 400, Text-figs. 3, 7g–j, 8, 10a–f.

Diagnosis.—Valves sub-rectangular. Heavily sculptured: Postero-ventral ridge breaking at the middle, its anterior half parallel to postero-dorsal ridge. Copulatory organ of generic characteristic: Ejaculatory duct round, with swelling near basal part; holding plates short.

Material.—MO-802, ♂, holotype, Teshima Is., 1977-7-29. MO-923, ♂♀, Wasajima Is., 1976-7-10. MO-938, ♂, A-1; MO-941, ♂; MO-1118, ♀, Ohama, 1977-7-2.

AURIAL IKEYAI sp. nov.

(Text-figs. 1d–i, Text-figs. 5e, f)

Aurila hataii Ishizaki. IKEYA and HANAI, 1982, Tables 2-4.

Diagnosis.—Valves sub-rectangular. Heavily sculptured; Postero-ventral ridge from middle of postero-dorsal ridge (posterior third of valve) to posterior end. Copulatory organ with round, uniform ejaculatory duct and short holding plate.

Material.—MO-1927, ♂, holotype. MO-1642, ♂; MO-1641 a, b, ♂, ♀. Hayama (near Misaki), 1982-7-22.

Locality.—Miura Peninsula and Hamana-ko.

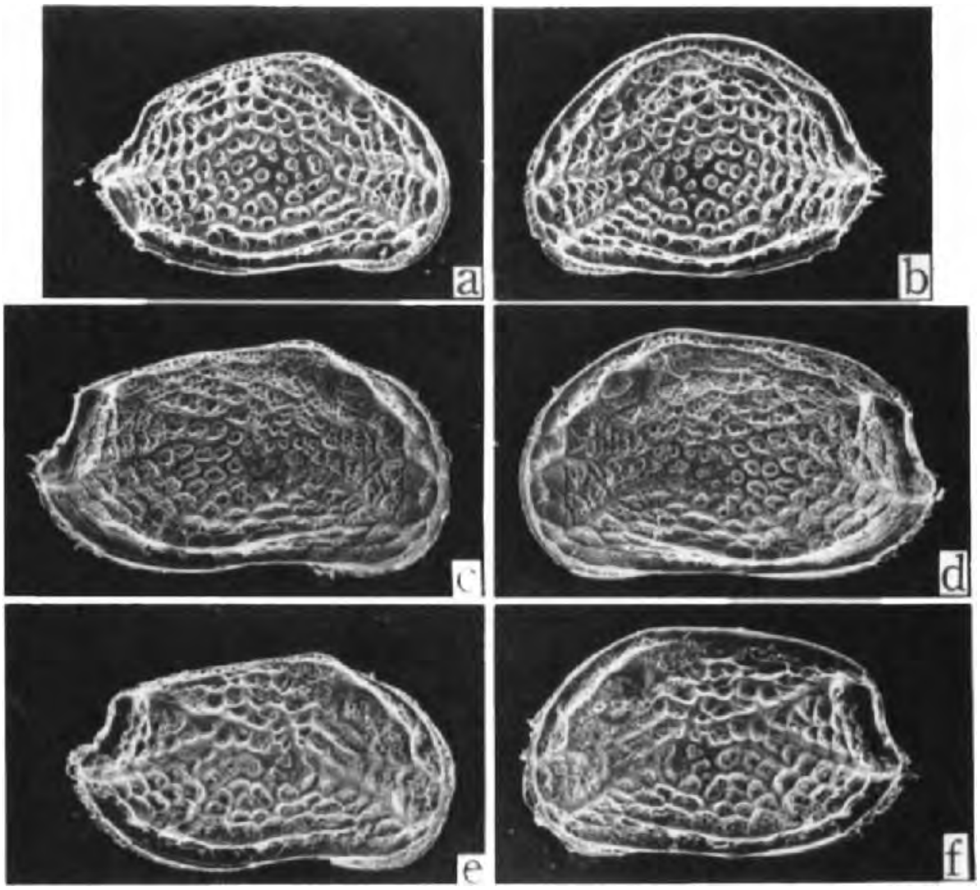
Occurrence.—On algae of rocky shores in intertidal zones.

CHECKLIST OF THE GENUS *Aurila* FROM JAPAN BEFORE 1982

(Synonyms cited without examination are omitted.)

Genus AURILA Pokorný, 1955

1. *Aurila corniculata* Okubo, 1980
    - *Aurila corniculata* Okubo, 1980, p. 399, Text-figs. 10g–j.
    - *Aurila uranouchiensis*: Ikeya and Hanai, 1982, Tables 2–4.
    - *Aurila* sp. B Frydl, 1982, Table 2-1, Pl. 9, figs. 13, 14.
2. *Aurila cymba* (Brady, 1869)
    - *Cythere cymba* Brady, 1880, p. 80, Pl. 20, figs. 5a–f.
    - *Cythereis subconvexa* Kajiyama, 1913 p. 14, Pl. 1, figs. 74, 75.
    - *Aurila miii* Ishizaki, 1968, p. 22, Pl. 2, fig. 9, Pl. 4, figs. 1, 2; Ishizaki, 1969, p. 217, Pl. 25, fig. 13; Ishizaki, 1971, p. 81, Pl. 2, fig. 1.
    - *Aurila subconvexa*: Okubo, 1980, p. 397, Text-figs. 2, 7m, n. 9a–d.
    - *Aurila cymba*: Ishizaki, 1981, Table 2.
    - ? *Aurila uranouchiensis*: Frydl, 1982, Table 2-1.



TEXT-FIG. 5—a, b. *Aurila munechikai* Ishizaki, 1968 (MO-1631, Misaki); c, d. *Aurila hataii* Ishizaki, 1968 (MO-1643, Misaki); e, f. *Aurila ikeyai* n. sp. (MO-1642, Misaki); a, c, e. right valve; b, d, f. left valve.

3. *Aurila disparata* Okubo, 1980
   Aurila disparata Okubo, 1980, p. 402, Text-figs. 4, 7e, f, 9e–j.
4. *Aurila hataii* Ishizaki, 1968
   Cythere villosa Baird, Imanishi, 1954, p. 90, fig. 2.
   Aurila hataii Ishizaki, 1968, p. 20, Pl. 1, figs. 5, 6, Pl. 4, figs. 5, 6; Frydl, 1982, Table 2 - 1.
5. *Aurila imotoi* Ishizaki, 1968
   Aurila imotoi Ishizaki, 1968, p. 21, Pl. 1, figs. 7, 8, Pl. 4, figs. 3, 4.
6. *Aurila inabai* Okubo, 1976
   Aurila inabai Okubo, 1976, p. 34, Text-fig. 1, Pl. 1; Okubo, 1980, p. 401, Text-figs. 7k, 1, 11h–j.
7. *Aurila kiritsubo* Yajima, 1982
   Aurila kiritsubo: Frydl, 1982, Table 2–1.
8. *Aurila munechikai* Ishizaki, 1968
   Cythereis convexa (Baird), Kajiyama, 1913, p. 13, Pl. 1, figs. 72, 73.
   Cythere convexa: Imanishi, 1954, p. 90.
   Aurila punctata (Münster): Hanai *et al.*, 1977, p. 44.
   Aurila munechikai Ishizaki, 1968, p. 23, Pl. 4, figs. 7, 8; Frydl, 1982, Table 2-1.

9. *Aurila tosaensis* Ishizaki, 1968
   Aurila tosaensi Ishizaki, 1968, p. 23, Pl. 4, figs. 16, 17.
10. *Aurila uranouchiensis* Ishizaki, 1968
    Aurila uranouchiensis Ishizaki, 1968, p. 24, Pl. 4, figs. 9, 10; Ishizaki, 1971, p. 82, Pl. 2, figs. 5, 11
11. *Aurila* sp. A Frydl, 1982
    Aurila sp. A Frydl, 1982, Table 2-1, Pl. 9, figs. 10, 11.
12. *Aurila okayamensis* Okubo sp. nov., in this paper
    Aurila hataii: Okubo, 1980, p. 400, Text-fig. 3, 7g–j, 8, 10a–f.
13. *Aurila ikeyai* Okubo sp. nov., in this paper
    Aurila hataii: Ikeya and Hanai, 1982, Tables 2–4.
14. *Aurila* sp. Okubo in this paper
    Aurila cf. *hataii*, Ishizaki, 1971, p. 81, Pl. 2, figs. 2, 3.

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DISCUSSIONS

Adamczak: Did you examine the species of *Aurila* by pattern analysis? If not, do you intend to do this? This would be very important for the studies made by people working with fossil reticulate ostracods.

Okubo: No, but I will give it my consideration.

Keyser: Could you find any relationship between the copulatory tube and shell form?

Okubo: No, I could find little relationship in general, but, closely related species resemble to each other both in the shell and in the copulatory tube.

Function and Significance of Tubules: *Tubulibairdia* vs. *Microcheilinella*

ROBERT F. LUNDIN
Arizona State University, Tempe, U.S.A.

ABSTRACT

Studies of type materials and some especially well-preserved specimens from the Silurian of Gotland and elsewhere lead to the following conclusions.

1) Primary types and topotypes of the type species of *Microcheilinella* are sufficiently altered so as to make studies of shell structure inconclusive.

2) Some Silurian (and Devonian) forms have tubules in their shell wall; other morphologically similar forms have no such features.

3) Tubules open only on the interior surface of the shell. They do not penetrate to the exterior surface of the shell.

4) Although other possibilities exist, tubules most likely housed cells which functioned in a) formation of the cuticle or b) sensing of light.

5) Tubules might represent an early stage in the development of normal pore canals, an interpretation which is potentially compatible with the suggestion that they had a light sensory function.

6) Tubules occur in pre-adult moult stages; they are not restricted to adults.

7) The presence or absence of tubules in these otherwise morphologically similar forms is genetically controlled and therefore tubules are a diagnostic character.

8) *Microcheilinella* and *Tubulibairdia* are distinct genera. Placement of species in these genera should be based upon examination of shell structure.

INTRODUCTION

Geis (1932) established the ostracod genus *Microcheilus* on the basis of materials from the Salem Limestone (Mississippian) of Indiana. *Microcheilus distortus* Geis, 1932 was designated as the type species and the generic name was changed to *Microcheilinella* Geis, 1933 when it was determined that *Microcheilus* Geis, 1932 was a homonym of *Microcheilus* Kittl, 1894, a gastropod.

Swartz (1936) established the genus *Tubulibairdia* (type species *T. tubulifera* Swartz, 1936) on the basis of steinkerns and external moulds from the Shriver Chert (Devonian) of Pennsylvania. Spines on the surfaces of the steinkerns proved the existence of "coarse pores" in the shell of *Tubulibairdia,* an "important distinguishing character" according to Swartz (1936, p. 581).

Since the 1930's numerous sepcies have been assigned to *Microcheilinella* and *Tubulibairdia.* However, often authors have not prepared or illustrated these ostracods in such a way as to verify the presence or absence of the "coarse pores" ("tubules" of various authors), inspite of the fact that these tubules were considered an important diagnostic character of *Tubulibairdia.* The problem is complicated by the fact that *Microcheilinella* is in other ways morphologically similar to *Tubulibairdia.* Because species belonging to *Microcheilinella* and/or *Tubulibairdia* are common elements, even dominant in some cases, of many middle and late Palaeozoic ostracod faunas, a thorough review of these genera is in order.

PREVIOUS INVESTIGATIONS

The primary studies of significance to the *Microcheilinella-Tubulibairdia* problem which I address here are those of Sohn (1960), Berdan and Sohn (1961), Shaver (1961), Zenkova (1969), Gramm (1975, 1977) and Adamczak (1976). Sohn (1960) clearly documented the presence of tubules in the shell wall of *Pachydomella* Ulrich, 1891, *Tubulibairdia* Swartz, 1936 and *Phanassymetria* Roth, 1929. This characteristic of these genera has been reported by many authors for species from North America, Europe and Australia. The widespread occurrence of tubules in the various genera indicated above cannot be denied. This character along with other morphological similarities prompted Berdan and Sohn (1961) to establish the family Pachydomellidae, to include *Pachydomella, Tubulibairdia* and *Phanassymetria* (several genera have since been added; see for example, Berdan, 1971; Bandel and Becker, 1975; Adamczak, 1976). *Microcheilinella* was not originally included in the Pachydomellidae, presumably because the type species does not have tubules. Instead, Shaver (1961) placed *Microcheilinella* in the order Podocopida, suborder and family uncertain. Longitudinal and transverse sections prepared by Shaver (1961), of the type species suggested to him the presence of a calcified inner lamella (duplicature), a feature which had not been previously reported for the genus.

Gramm (1975) used the absence of tubules from *Microcheilinella* as one of the primary reasons (presence of a calcified inner lamella was the other) for considering it to not be a pachydomellid. Instead Gramm erected a new family, the Microcheilinellidae to accommodate the genus. His diagnosis of *Microcheilinella* and motivation for establishing the new family were based primarily on specimens of Carboniferous (Visean) and Middle Triassic age.

Adamczak's (1976) study of *Bythocypris* (*Bairdiocypris*) *clava* Kegel, 1932 inspired him to place the species in *Microcheilinella* inspite of the presence of tubules in the shell wall. Adamczak (1976) concluded that the tubules are an adult feature, that juveniles of the species do not have them, and therefore they are not of significance in distinguishing *Tubulibairdia* from *Microcheilinella.* The latter, being the older generic name, was therefore considered by Adamczak to be a senior synonym of *Tubulibairdia.*

The significance of determining if *Tubulibaridia* is distinct from *Microcheilinella* is emphasized by the fact that dozens of species have been assigned to *Microcheilinella* by European workers (*e.g.* Adamczak, 1976; Feist and Groos-Uffenorde, 1979; Pranskevichius, 1972; and many others). In fact, the Soviet specialists have assigned *Microcheilinella-Tubulibairdia*-like forms almost exclusively to *Microcheilinella.*

PURPOSE

Because of the problems indicated above, this study was undertaken to 1) redescribe and illustrate the carapace morphology of *Microcheilinella distorta,* 2) examine the shell structure of *M. distorta* and other species of the genus, 3) evaluate the form and function of the tubules in *Tubulibairdia* (and related pachydomellids) and 4) discuss the taxonomic significance of the shell structure of *Tubulibairdia.* This will form a background upon which future discussion of the taxonomy of these ostracods can be based.

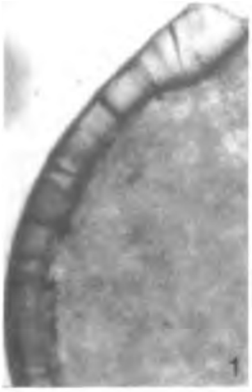
THE TUBULES

Shape.—Although they have not been adequately studied in many species of *Tubulibairdia* and other pachydomellids, it is possible to generalize about the shape of the tubules. In cases where the appearance of the tubules has not been affected by the plane of the thin section or polished surface and where preservation is good, the tubules are cylindrical, or nearly so, from the proximal end to near the distal end where they taper to a point (Pl. 1, fig. 10; Lundin and Scott, 1963, Pl. 180, figs. 4, 6; Zenkova, 1969, fig. 2; Petersen, 1975, Pl. 3, fig. 10; Adamczak, 1976, Pl. 12, fig. 60a). Some tubules seem not to be pointed at their distal end (Sohn, 1960, Pl. 5, fig. 12; Lundin, 1965, Pl. XVI, fig. 1d) and some tubules seem to be bulbous (Adamczak, 1976, Pl. 12, fig. 60a). It is, however, difficult to evaluate from photographs if these latter somewhat unusual shapes result from optical effects or position of the plane of the thin section with respect to the tubules.

Abundance and distribution.—The abundance and distribution of the tubules in pachydomellids is variable. Lundin and Scott (1963) reported them to be scattered throughout the carapace in two species of *Phanassymetria,* but slightly more abundant in the anterior third and ventral half than elsewhere. Berdan (1971) found them to be "evenly distributed in both valves" of *Phanassymetria collilupana* Berdan, 1971. Tubules in various species of *Pachydomella* have been described as "randomly arranged" (Lundin, 1965), "widely and irregularly spaced" (Swain, 1953), and "concentrated in the ventral portion" (Lundin, 1968).

Generally, descriptions and/or illustrations of the tubules for species of *Tubulibairdia* indicate that they are numerous. Furthermore, they are generally reported to be rather evenly distributed throughout the carapace (Pl. 1, figs. 5, 8). However, some authors (e.g., Swartz and Oriel, 1948; Copeland, 1962; Adamczak, 1976) report tubules to be absent from the position of the adductor muscle field for several species of *Tubulibairdia* (in Adamczak, 1976 refer to *Microcheilinella clava*). This also is true for *Tubulibairdia porosa* (originally placed in *Microcheilinella*) from the Soviet Union (Pl. 2, fig. 16) but there is no apparent interruption of the spacing of the tubules in *Tubulibairdia malinowieckaja* (Neckaja, 1966) from the Wenlockian of Gotland (Pl. 2, figs. 13–15). Swartz (1936) reported that tubules are absent from an area bordering the left valve hinge and from near the free edges where marginal overlap of the valves occurs. In *T. accurata,* Zenkova (1969) found tubles throughout the shell wall "except for narrow bands along the hinge", in the "middle of the ventral margin," and "at the posterior end." Furthermore, she reported that tubules are concentrated on the anterior and posterior ends and anterior and posterior parts of the venter of that species. For *T. chaleurensis,* Copeland (1962) reported the absence of tubules from the "marginal edges of the valves" and from the "dorsal lateral surface at the anterior end of the hinge line."

Ontogeny.—The tubules are present in at least some pre-adult instars of some species of *Tubulibairdia* and some other pachydomellid genera. Lundin and Scott (1963) reported tubules in the last four moult stages of *Phanassymetia triserrata* and *P. quadrupla.* Plate 2, figs. 11, 12 show tubules in pre-adult specimens of *T. simplex* and *T.* sp. cf. *T. longula* from the Haragan (Devonian) and Henryhouse (Silurian) formations of Oklahoma. Also, I have seen tubules in pre-adult specimens of *Pachydomella.* Tubules are not restricted to adult pachydomellids. Any claim to that effect should be verified. In any case, I do not consider the ontogenetic stage at which the tubules appear to be significant to the taxonomic issue discussed below. Much generic and suprageneric ostracod taxonomy is based on characters known only in adult specimens. Tubules occur in pre-adults as well as adults.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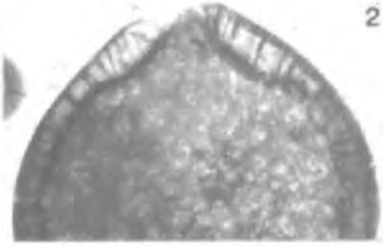
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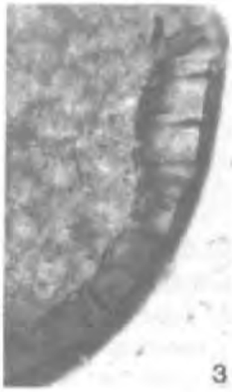
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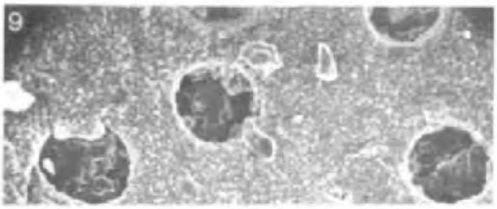
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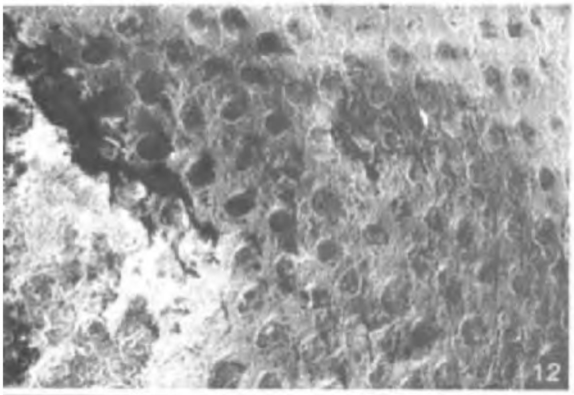
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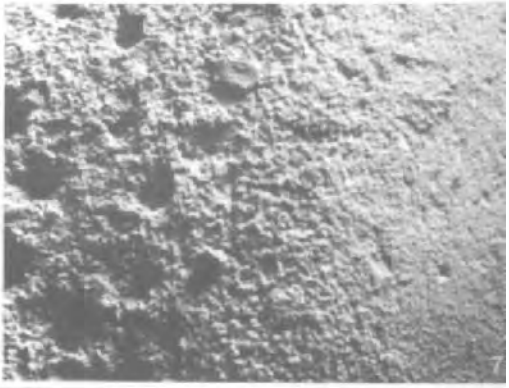
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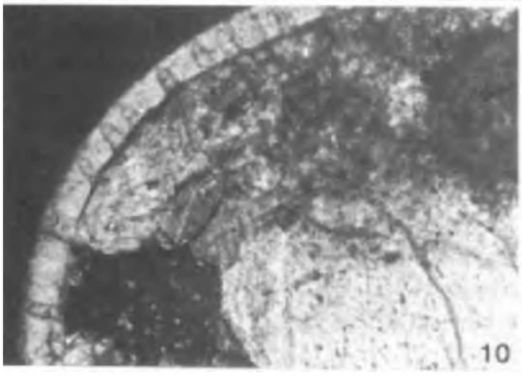
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Extent.—Swartz (1936, p. 581) recognized the extent of the tubules in his original description of *Tubulibairdia tubulifera* when he stated, "Internal molds of both valves bear strong spine-like projections, representing coarse tubular pores which open on the internal surface of the valves, but do not reach the exterior". This characteristic of the tubules (that is, no opening on the exterior surface of the shell) has been reported for *Tubulibairdia* and/or other pachydomellids by numerous authors (see above).

It can be argued that the absence of openings of the tubules on the exterior surface of the shell is due to diagenetic processes which might take place at the sediment-shell surface interface. In order to reasonably speculate about the significance of the tubules, it is necessary to know if they completely penetrated the shell and the exterior openings are obscured because of diagenetic processes, or if the tubules did not completely pierce the cuticle and opened only on the interior surface of the shell. I believe the latter because:

1) The interior openings of the tubules can easily be seen on many single valves from which the interior matrix has been removed (Pl. 1, fig. 5; Adamczak, 1976, Pl. 9, fig. 44; Reynolds, 1978, Pl. 10, fig. 6). Yet no openings of the tubules are present on the exterior surface of the same specimens. On single valves one should expect the same diagenetic processes to act on the interior and exterior surfaces of the valve.

2) Plate 1, figs. 4–10 illustrates *Tubulibairdia malinowieckaja* from the Slite Beds (Wenlockian) of Gotland. Many superbly preserved specimens of this species are known. One specimen (Pl. 1, fig. 6) is abraded on the anterocentral and anterodorsal surface as well as along a narrow strip in the posterior part of the left valve. The tubules are obvious in the strongly abraded area (especially in the anterior part of the valve) but there is no evidence of them on unabraded portions of the shell (Pl. 1, fig. 7). Furthermore, examination of the shell between the abraded and unabraded areas shows no textural change that might suggest diagenetic alteration of the unabraded portions of the shell.

3) Plate 1, fig. 11 shows a *Tubulibairdia* sp. from the Coeymans Ls. (Lower Devonian) of New York. The surface of this species is covered with fossae which are about 12 μm in diameter. The diameter of the tubules in their proximal cylindrical parts is approximately 24 μm. The fine ornament (fossae) is nicely preserved but there is no evidence for openings of the tubules on the exterior surface of the shell (Pl. 1, fig. 12).

In the same regard, Lundin and Scott (1963) reported a very fine fingerprint pattern preserved on the surface of well-preserved specimens of *Phanassymetria triserrata* and *P. quadrupla.* Exterior openings of the tubules have not been seen in these two species.

It has been shown by Okada (1982) and by Bate and Sheppard (1982) that surface ornament of the kind present on the Coeymans Limestone *Tubulibairdia* sp. and on *P. triserrata* and *P. quadrupla* probably is a reflection of epidermal cells of the ostracod. That is, the boundaries of each polygon

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Plate 1—Figs. 1–3. *Newsomites profusus* Lundin and Newton. Views of posterior part of left valve (×86), posterior portion of carapace (×52) and posterior part of right valve (×86) of longitudinal thin section of adult carapace showing sensillum pores, GSA MTC 61. This specimen was incorrectly indicated as an immature specimen in Lundin and Newton (1970, p. 58).

Figs. 4–10. *Tubulibairdia malinowieckaja* (Neckaja). 4, 10. Longitudinal thin section (×29) and enlargement (×78) of posterior part of right valve of adult carapace showing shape and extent of tubules, ASU X-70; 5, 8, 9. Interior view (×36), enlarged oblique interior view (×67) and enlarged interior view (×357) showing tubules opening on interior surface of adult left valve from the Slite Beds (Silurian) at Längars (MS 190), Gotland, Sweden ASU X-71; 6, 7. Left lateral view (×27) and enlarged view (×149) of central part of same showing tubule openings, in the abraded parts of shell, but not on unabraded parts of shell, adult carapace from Längars (MS 190) as above, ASU X-72.

Figs. 11, 12. *Tubulibairdia* sp. Left lateral view (×36), and enlargement (×200) of same, of adult carapace from Coeymans Ls. (Devonian) of New York showing beautifully preserved ornament (fossae) but no tubule openings on exterior surface of shell, USNM 401554, USGS 3114–SD.

on the shell surface represent boundaries of cells in the epidermis which is responsible for formation of the cuticle. If this is correct, and I believe the evidence for it is good, it is practically inconceivable that such ornaments could be preserved while the exterior openings of the tubules are destroyed (obscured) by diagenetic processes.

In summary, I believe the tubules in *Tubulibairdia* and other pachydomellids did not completely pierce the calcified part of the cuticle. Apparently the tubules tapered to a point and "dead ended" within, but very near the outer surface of the procuticle (*sensu* Okada, 1982). If this is not true, that is, if the tubules completely penetrated the cuticle and I am, for some reason unable to detect the exterior openings, the following discussion about the function of the tubules is meaningless.

Function.—I know of no modern ostracods which have tubules like those of *Tubulibairdia* and other pachydomellids. Accordingly, I can only speculate about the function of them. Possible functions of the tubules are 1) to facilitate adhesion of the epidermis to the cuticle, 2) to aid in the formation of the cuticle, and/or 3) to house some sensory apparatus.

That the tubules facilitated adhesion of the epidermis to the cuticle of the outer lamella is possible because if the tubules were occupied by epidermal cells the surface area of contact between the epidermis and the cuticle of the outer lamella would be greatly increased. Although this is a possible function of the tubules, and although there is no direct evdence for or against this possibility, I believe it is not likely to be the primary function of the tubules. Okada (1982) has shown that the epidermis of the modern podocope ostracod *Bicornucythere bisanensis* (Okubo) is anchored to the cuticle by means of intracuticular fibres. Not many studies of this kind have been done, but this suggests that specific structures for connecting the epidermis to the cuticle are present. Accordingly, more than simple adhesion of one layer to the other is involved. It is likely, then, that for connection of the epidermis to the cuticle, the abundance of intracuticular fibres is more significant than surface area. I regard an adhesive function for the tubules as only a slight possibility and if they functioned in this way at all, it was, at best, a secondary function.

The studies of the ultrastructure of the carapace integument (*sensu* Okada, 1982) of ostracods by Jorgensen (1970), Bate and East (1972, 1975,) Rosenfeld (1979, 1982) and Okada (1982, 1983) are important to any discussion of whether or not the tubules of *Tubulibairdia* and other pachydomellids had a function in formation of the cuticle. None of these authors have reported structures morphologically similar to the tubules of *Tubulibairdia* which can be unquestionably associated with cuticle formation. Jorgensen (1970) denied the existence of "pore canals" which Travis (1963) indicated were protoplasmic extensions of the epidermis and were significant to the formation of the cuticle of decapods. Bate and East (1972, 1975) and Okada (1983), however, have identified these kinds of "pore canals" in several species of modern podocope ostracods. These "pore canals" have no openings on the exterior surface of the carapace. In this regard they are like the tubules in question here. On the other hand, these "pore canals" are much smaller in diameter and different in shape, orientation and relationship to each other than the tubules of *Tubulibairdia*. The "pore canals" are about 0.4 μm in diameter and the branching and fusion of them form a network within the cuticle. Features of this kind can hardly be considered analogous to the tubules of *Tubulibairdia* which are simple, straight discreet structures that do not fuse and branch to form a network. Furthermore, the "pore canals" of *Cypridopsis vidua* (see Bate and East, 1972) and *Neonesidea* sp. (see Okada, 1983) are arranged parallel to or obliquely to the cuticle surface whereas the tubules of pachydomellids are invariably essentially normal to the cuticle surface.

Rosenfeld (1979, 1982) has discussed the role of granules, which are present in the epidermis of ostracods, in the formation of the ostracod cuticle. Okada (1982) has shown specifically how the cuticle forms prior to and just following ecdysis. It is possible that the tubules of *Tubulibairdia* and other pachydomellids were occupied by distal extensions of the epidermis which provided the "pore canals" (discussed above) with fluids necessary for maintaining the organic matrix of the procuticle (*sensu* Okada, 1982) or for completion of the recrystallization of the granules after ecdysis. I know of no reports of "pore canals" of the kind discussed by Bate and East (1972, 1975) and Okada (1983) in young fossil material. It is not surprising then that such structures are unknown among the Palaeozoic forms in question here. Still it seems reasonable to suppose that the tubules are some adaptation which facilitated one or more of the processes of cuticle formation indicated by the studies of modern species by Bate and East (1972, 1975), Okada (1982, 1983) and Rosenfeld (1979, 1982), even though these modern species do not have structures significant to cuticle formation that are analogous to tubules. I consider some function in cuticle formation to be a reasonable possibility for the tubules.

A sensory function for the tubules is another reasonable possibility. At first glance the tubules appear to be normal pore canals of the kind which are common in post-Palaeozoic podocope ostracods. The only thing which keeps me from that interpretation is the observation that the tubules do not open to the exterior surface of the cuticle. Accordingly, the tubules could not have functioned in the same way as normal pore canals, the "sensillum pores" of Okada (1983). For the same reason, the tubules could neither have been the ducts of exocrine glands (see Okada, 1983) nor housed any sensory apparatus which required direct contact with the environment to perform its function. Therefore, the most likely sensory function that might have been performed by cells housed in the tubules would be light reception. Keyser (1982) noted that the function of sieve plates and sieve pores is unknown but stated that Müller (1894) suggested they had a light-sensory function. Schallreuter (1983) used this suggestion to interpret that *Klimphores scanensis*, an Ordovician palaeocope species without sieve pores, lived in a darker environment than *K. planus* which has sieve pores. Although sieve pores of *Klimphores* (and for that matter post-Palaeozoic podocopes) are not morphologically like the tubules of pachydomellids, Schallreuter's (1983) observation provides some evidence (meagre though it may be) for the existence of light-sensory appratuses in the lateral surfaces of the cuticle of Palaeozoic ostracods. Tubules could have housed light-sensory apparatuses and performed a light-sensory function just as has been suggested for sieve pores.

Finally, tubules of pachydomellids may represent an early stage in the evolution of normal pore canals (sensillum pores of Okada, 1983). I know of no ostracods older than the pachydomellids which have sensillum pores. If the tubules housed light-sensory apparatuses, it is possible that evolution of these specialized cells produced sensilla which were adaptions for life in poorly illuminated or dark environments. Mechanoreceptors such as the sensilla of ostracods, of course, require direct contact with the environment and therefore such features would require sensillum pores. Gramm's (1977) discovery of Type C (Puri and Dickau, 1969) sieve pores in a Carboniferous species of *Editia* is of interest in this regard because it demonstrates the existence of sensillum pores in a late Palaeozoic ostracod. Also of interest here is the existence of "sensillum pores" (normal pore canals) in the late Silurian *Newsomites profusus* Lundin and Newton, 1970 (see Pl. 1, figs. 1–3 herein). Additional study of normal pore canals, especially in Palaeozoic ostracods is needed to validate or invalidate the hypothesis that tubules are an early stage in the development of sensillum pores.

Taxonomic value.—I consider the tubules of *Tubulibairdia* and other pachydomellids to be a valid taxonomic character. Whichever function of those discussed above (or, for that matter, others), is considered most reasonable, I believe the existence of tubules is genetically controlled. The tubules are a stable morphological character. Tubules are present in a wide variety of species which can be readily categorized into various genera on the basis of other morphological criteria. I conclude, therefore, that *Tubulibairdia* and *Microcheilinella* are distinct and separate genera. Accordingly, species should be placed in these genera only after careful analysis of the shell microstructure. If the shell material of all known specimens of a species is recrystallized or otherwise altered it may not be possible to determine definitely whether the species belongs to *Tubulibairdia* or

Microcheilinella. Although certain other characters such as size and shape can lead to a "best guess", generic designations based only on these characteristics should be queried.

SYSTEMATIC PALAEONTOLOGY

Taxonomy.—I choose not to discuss familial and superfamilial taxonomy at this time because it involves analysis of other characters in addition to the tubules. At the present time I consider the tubules to be of at least generic significance. If one accepts Gramm's (1975) Microcheilinellidae, the diagnosis of that family must be amended for reasons stated below.

Repositories.—Specimens illustrated herein are in the collections of the Department of Geology, Arizona State University (ASU), the U. S. National Museum of Natural History (USNM), the Geological Survey of Alabama (GSA MTC), the U. S. Geological Survey (USGS) and the University of Illinois, Champaign-Urbana (UI).

Subclass OSTRACODA Latreille, 1806

Genus MICROCHEILINELLA Geis, 1933

MICROCHEILINELLA DISTORTA Geis, 1932

(Pl. 2, figs. 1–10, 17, 18, 22)

Microcheilus distortus GEIS, 1932, p. 182, Pl. 25, figs. 15a,b.

Microcheilinella distorta (Geis). SOHN, 1960, Pl. 5, fig. 13; SHAVER, 1961, p. 387, figs. 310A, 3, 310B, 3.

Diagnosis.—*Microcheilinella* with dorsal and ventral borders parallel or nearly so. Small, width greater than height, maximum width distinctly posterior to midlength. Hinge channel weak, bow-shaped projection poorly to moderately deveoped. Anterior and posterior straguloid processes poorly developed or absent. Surface of shell smooth. Tubules and calcified inner lamella not present. Muscle scars unknown. Hinge straight but details of morphology not known.

PLATE 2—Figs. 1–5, 22. *Microcheilinella distorta* (Geis). 1–5. Right lateral, left lateral, dorsal, ventral and posterior views of adult carapace, holotype, UI M366. ×50; 22. Anterior part of right lateral surface of same specimen. ×141.

Figs. 6–10, 17, 18. *Microcheilinella distorta* (Geis). 6–10. Right lateral, dorsal, ventral, left lateral and posterior views of adult carapace. ×50; 17. Longitudinal thin section of same specimen, paratype, UI M367. ×69; 18. Peel of transverse section of adult carapace, anterior view, topotype, USNM 401555 (peel on right end of slide). ×84.

Fig. 11. *Tubulibairdia* sp. cf. *T. longula* (Ulrich and Bassler). Lateral view of pre-adult left valve from Silurian Henryhouse Fm. of Oklahoma, photographed in glycerol to show tubules (tiny white spots), ASU X-63. ×40.

Fig. 12. *Tubulibairdia simplex* (Roth). Lateral view of pre-adult left valve from Haragan Fm. (Devonian) of Oklahoma, photographed in glycerol to show tubules (tiny white spots), ASU X-64. ×62.

Figs. 13–15. *Tubulibairdia malinowieckaja* (Neckaja). Left lateral views of three adult specimens from the Slite Beds (Silurian) at Längars (MS 190), Gotland, Sweden. ×35. Two of these specimens are not available, the third (fig. 14) is ASU X-65.

Fig. 16. *Tubulibairdia porosa* (Pranskevichius). Left lateral view of adult carapace from the Silurian of Lithuania (Krekenava 683.5) showing interruption of tubules at position of adductor muscle field, ASU X-66.

Fig. 19. *Microcheilinella* sp. cf. *M. acuta* Abushik. Transverse thin section of adult carapace, posterior view, from lower Slite Beds (Silurian) at Store Myre (MS 34), Gotland, Sweden, showing well-preserved shell without tubules, ASU X-67. ×60.

Fig. 20. *Microcheilinella* sp. cf. *M. variolaris* Neckaja. Longitudinal thin section of adult carapace, dorsal view, from Lower Visby Beds (Silurian) at Nyhamn (MS 391S), Gotland, Sweden, showing well-preserved shell without tubules, ASU X-68. ×47.

Fig. 21. *Microcheilinella ianica* (Neckaja). Longitudinal thin section of adult carapace, ventral view, from upper Slite Beds (Silurian) at Hide (MS 249), Gotland, Sweden, showing well-preserved shell without tubules, ASU X-69. ×39.


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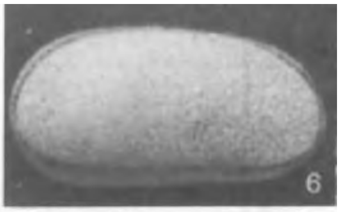
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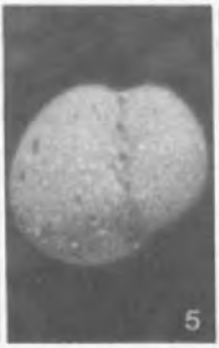
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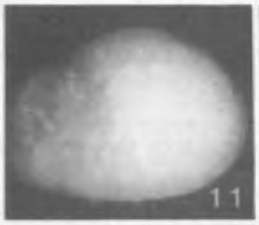
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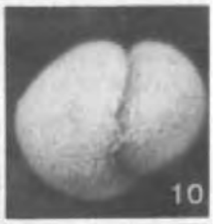
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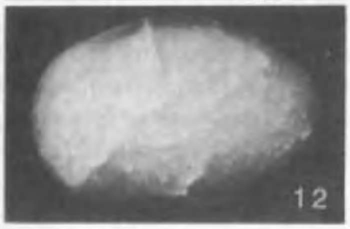
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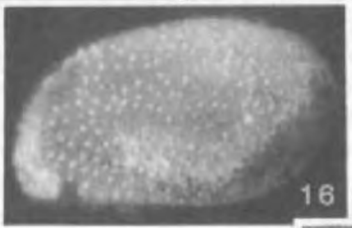
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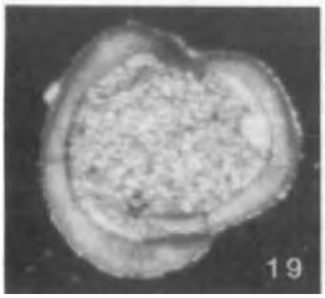
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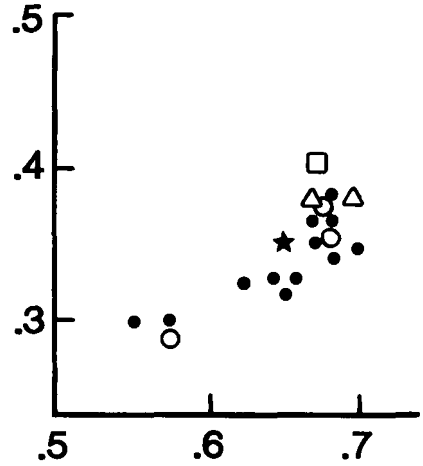

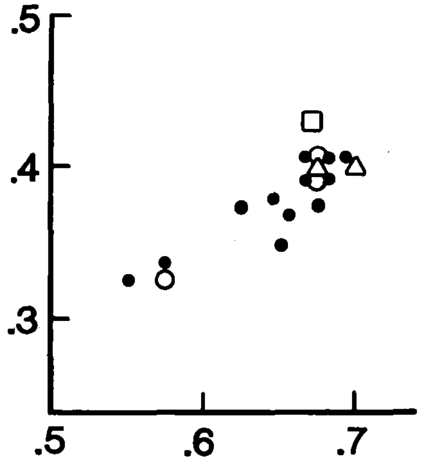

TEXT-FIG. 1—(*left*) Size dispersion (length on abscissa, height on ordinate) of *Microcheilinella distorta*; square, holotype; triangles, paratypes; dots, topotypes (carapaces); star, topotype (left valve); circles, hypotypes (Old Cleveland Quarry, Harrodsburg, Monroe County, Indiana).

TEXT-FIG. 2—(*right*) Size dispersion (length on abscissa, width on ordinate) of *Microcheilinella distorta*; symbols as in fig. 1.

Dimensions.—See Text-figs. 1 and 2. In each of eighteen measured carapaces the width is greater than the height.

Discussion.—The following observations made on primary types, topotypes and other specimens from near the type area are significant to understanding the morphology of *Microcheilinella.*

1) *Microcheilinella distorta* does not have a calcified inner lamella. I have studied Shaver's (1961) thin section and polished surface (one of the original thin sections is lost) and found no evidence of any feature which even resembles a calcified inner lamella. A peel of a transverse cross-section, prepared by I. G. Sohn, shows no indication of a calcified inner lamella (Pl. 2, fig. 18). Finally, a longitudinal thin section of a paratype shows no such feature (Pl. 2, fig. 17).

2) Specimens of *Microcheilinella distorta* show no evidence of tubules or sensillum pores (normal pore canals). In this regard specimens of the type species are not definitive because all specimens known to me are preserved in such a way that microstructure of the shell might have been obscured by diagenetic alteration of the shell. I conclude that *Microcheilinella* does not have tubules or sensillum pores on the basis of well-preserved morphologically similar forms from the Silurian of Gotland, England and the Soviet Union (e.g. Pl. 2, figs. 19–21).

Unless and until differently preserved specimens of *M. distorta* are discovered which prove otherwise, the type species of *Microcheilinella* (and therefore the genus) must be viewed as an ostracod with pachydomellid-like carapace morphology but without tubules, sensillum pores or calcified inner lamellae. Gramm's (1975) diagnosis of the Microcheilinellidae is based on younger species which have calcified inner lamellae and sensillum pores. Whether those species are legitimate members of *Microcheilinella* is open to question.

Material studied.—Twenty-four specimens including the holotype and three paratypes, one of which was thin sectioned and is not included on Text-figs. 1 and 2. All specimens studied are from the type locality (railroad cut at Spergen Hill, Norris, Indiana) or another of Geis' (1932) localities (Old Cleveland Quarry, Harrodsburg, Indiana). Those of Shaver's (1961) specimens which are still available were studied.

Figured specimens.—Pl. 2, figs. 1–5, 22 (holotype); Pl. 2, figs. 6–10, 17 (paratype); Pl. 2, fig. 18 (peel of topotype).

SUMMARY AND CONCLUSIONS

1) *Tubulibairdia* and *Microcheilinella* are morphologically similar. They differ in that the former has tubules in its shell wall and the latter does not. Indeed the type species of *Microcheilinella* shows no evidence of special shell microstructures such as tubules or sensillum pores.

2) The tubules in *Tubulibairdia* and other pachydomellids probably had a sensory function or a function in formation of the cuticle of the ostracode. In any case, tubules open only to the interior of the shell; they do not penetrate to the exterior surface.

3) Tubules occur in pre-adult as well as adult moult stages of various pachydomellid genera including *Tubulibairdia.*

4) Tubules are a stable character within species of *Tubulibairdia* and other pachydomellids. Therefore, I consider them to be diagnostic and taxonomically significant at least at the generic level.

5) *Microcheilinella* and *Tubulibairdia* are distinct and separate genera. Placement of species in these genera should be based upon examination of shell microstructure.

ACKNOWLEDGEMENTS

I wish to express special thanks to I. G. Sohn who so graciously provided specimens and illustrations which were critical to the completion of this study. Other people who contributed materials and/or time which aided this study are Jean Berdan, Linda Visintainer, A. F. Abushik, A. A. Pranskevichius and, most of all, the late Anders Martinsson, who supplied many of the basic collections from Gotland. This study is part of a project supported by the National Science Foundation (Grant No. EAR-8200816).

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DISCUSSION

Keyser: From my work on living ostracods I would guess that the tubules are just big openings for the epidermal sensory cells with a small opening for the seta to get out. I think that these pores are probably obscured by the fossilisation.

Lundin: This is precisely what I have treated in the paper. Several lines of evidence are presented which demonstrate that in *Tubulibairdia* (and, I believe, other pachydomellids) the tubules do not penetrate to the exterior. This, of course, is not to say that this is true for all younger ostracods which have pores. I can, however, say that several species of pachydomellids which I have studied have very fine surface ornament preserved but no evidence for tubule openings on the exterior surface. But I quite agree with you. If my observations on *Tubulibairdia* (and other pachydomellids) are in error, and the tubules completely pierce the cuticle, then it is clear that they are sensillum pores. In any case such a feature is at least of generic level taxonomic value and *Tubulibairdia* and *Microcheilinella* should not be considered synonyms.

Adamczak: It is extremely difficult to recognise juvenile forms in a particular *Microcheilinella* (*Tubulibairdia*) species, because of the "feature-poor" carapace. I have been able to do this, with some confidence, only in one species (*M. clava*). This species shows, in the youngest juvenile form, a few tubules in the ventral part of the carapace only. Their number, however, increase in the following stages.

I think that I can agree with Dr. Keyser that the openings of the tubules may be very indistinct on the carapace surface. I have observed in *M. clava* (*T. clava*) that the tubules may divide dichotomously just below the valve surface and that their openings may be very small.

Lundin: It is true that it is difficult to distinguish juvenile forms of various species of pachydomellids (Lundin and Scott, 1963) but it can be done. The specimens I have illustrated here as juveniles are without question, juveniles and they do have tubules, as you have now found to be true, apparently, in *Tubulibairdia clava*. The point is, juveniles have tubules and therefore the significance of them cannot be discounted on the premise that they occur only in adults.

I shall be pleased when, and if, somebody publishes illustrations which demonstrate that the tubules in Silurian and/or Lower Devonian *Tubulibairdia* (or other pachydomellids) completely pierce the cuticle. That will make it clear that they are sensillum pores. In that case, it is still clear that *Microcheilinella* and *Tubulibairdia* must be distinguished. I judge that the presence (or absence) of sensillum pores is taxonomically significant at least at the generic level.

Kaesler: Did *Tubulibairdia* evolve from *Microcheilinella*? If so, it would be quite interesting to establish the heterochronic relationships between the two. For example, if the earliest species of *Tubulibairdia* have tubules only in the adult but later species have tubules throughout their ontogeny, we would have a good indication of the macroevolutionary origin of a species by paedomorphosis.

Lundin: This is an interesting question which requires more study for an adequate answer. On the basis of present information I believe *Microcheilinella* represents the primitive condition. It ranges from the early Silurian (at the oldest) into the Carboniferous (at the youngest). My own beliefs just now are that *Tubulibairdia* evolved from *Microcheilinella* and that forms like *Newsomites profusus* (from the late Silurian) which has sensillum pores, evolved either from *Tubulibairdia* or directly from *Microcheilinella*. But I really do not have enough information on the ontogeny of the tubules in various species of *Tubulibairdia* to comment further on that problem.

Krstić: Some tubule-like structures of the ostracode shell are known in Recent and Neogene freshwater ostracods. The genera *Stenocypria* and *Ilyodromus* have double punctation of the shell wall (described and figured by Triebel). The bigger are blind pores, the thinner, normal pores. In the extinct genus *Amplocypris* tubule-like structures exist in some species, and not in others. The bulb-like hollows open widely toward the inside, but ends in normal pores towards the outside. The other group of species has thin normal pores. There is not one other difference between these two groups and they are not separated (in different genera/subgenera). They can be found together in the same assemblage.

The Free Margin Contact Structures in Some "Palaeocopid" Ostracods and their Bearing on Classification

MENDEL N. GRAMM
Far East Science Center, Academy of Sciences, Vladivostok, USSR

ABSTRACT

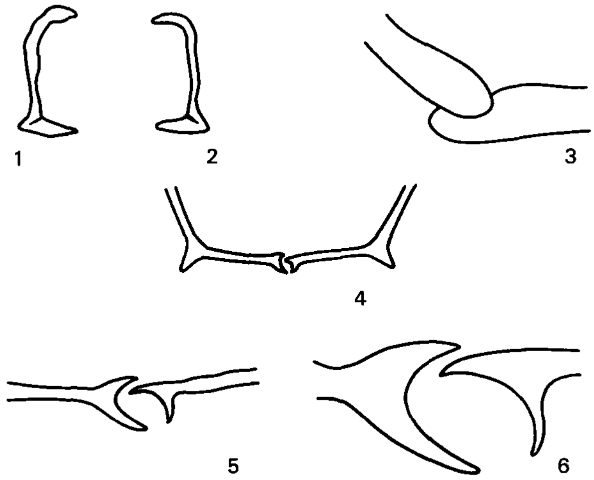
According to the presence of a calcified inner lamella in some of the so-called "palaeocopid" ostracods new taxa are erected: Gerubiellidae n. fam. with the genus *Gerubiella* n. gen. (type species *Buregia krestovnikovi* Polenova), Netzkainidae n. fam. with the genus *Netzkaina* n. gen. (type species *Saccelatia bimarginata* (Netzkaja) and Anfedatiidae n. fam. with the genus *Anfedatia* n. gen. (type species *Přibylites alveolatus* Abushik). These ostracods cannot belong to the Palaeocopia. Their systematic position is unknown.

INTRODUCTION

The difficulties in systematics of some Palaeozoic ostracods, conditionally named here as "palaeocopids," are in no small measure due to the underestimation of the carapaces' internal features (central muscle field, contact structures, hinge) which, in comparison with the external ones, are taken into account to a much lesser degree or completely ignored because they are less accessible for observation (Gramm, 1984b). Owing to this the number of taxonomically important characters is essentially reduced. This situation adversely affects the ascertainment of higher taxa.

In the present study the main attention is concentrated on the construction of the "palaeocopid" ostracod free margin. An opinion is developed that the free margin internal contact structure of these ostracods is of great importance and needs very thorough study. These structures are poorly known because well preserved single valves are needed or if only closed carapaces are available, more sophisticated methods such as preparation of thin- or polished sections are necessary for their investigation. On the basis of the completed studies it is demonstrated that the "palaeocopid" free margin in some cases is formed with the participation of the calcified inner lamella to which great importance is attached.

The question of the presence of the calcified inner lamella in non-podocopid groups of course attracted the attention of researchers. In this respect the work of E. Triebel (1950a) on *Cytherella* and *Ogmoconcha* is of great importance. Here, however, we are dealing with "palaeocopids" only. In the diagnosis of the suborder Palaeocopa Henningsmoen (1953, p. 188) noted: "Apparently no calcareous inner lamella". In the diagnosis of the order Beyrichiida whose volume coincides to a great extent with that of the Palaeocopa (without Kloedenellidae) is indicated: "The calcified inner lamella up to now has not been proved" (Pokorný, 1958, p. 129). Scott (1961b, p. Q110) in his diagnosis of the order Palaeocopida Henningsmoen, 1953 stated quite definitely that "calcare-



TEXT-FIG. 1—Free margin without duplicature, homogenous. Transverse sections of carapaces, valves. 1, 2. homogeneous simple; *Pyxion nitidum* Sarv, left valve, right valve, after Gramm, 1984b, Text-fig. 2 (8, 10). 3–6. homogeneous with contact grooves; 3. *Leperditella prima* Sarv, carapace, ventral part, after Gramm, 1984b, Text-fig. 2 (7); 4–6. *Netzkaina bimarginata* (Netzkaja) (= *Saccelatia bimarginata* Netzkaja), carapace, ventral part, contact of valves. 1–3. Ordovician; 4–6. Upper Silurian. Here and in the next Text-figures all sections in posterior view; without scale.

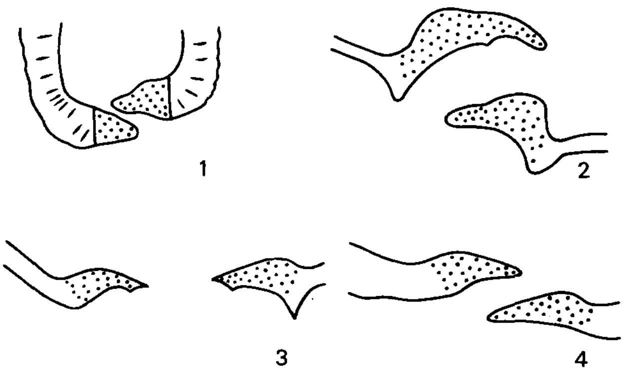
ous inner lamella absent". For a long time the opinion has prevailed that the inner lamella in a form of duplicature is found only in the Podocopina and poorly developed in the Metacopina (Scott, 1961a, p. Q90, table). From the beginning of the sixties, data began to appear on the presence of the duplicature in groups referred to the Palaeocopida (Sohn, 1961, 1969; Adamczak, 1961; Knüpfer, 1968; Schallreuter, 1968). These data have been treated either as evidence for belonging to the Podocopina (Sohn, 1961, 1969), or (if kloedenellid dimorphism is observed) to the Platycopina (Knüpfer, 1968; Schallreuter, 1968).

The author's investigations (Gramm, 1977, 1984b), carried out with the aid of thin sections, have revealed that in cases of calcification of the inner lamella the latter is not concerned with only the formation of the duplicature. In fact essentially different forms of calcification are observed: with formation of the duplicature and without it. The free margin structures arising have independent systematic significance and cannot be assigned to Podocopina or Platycopina.

In the investigated "palaeocopid" ostracods two types of free margin are distinguished, those without duplicature and those with duplicature, each of them with several varieties. In the first type may be discerned:

a) Homogeneous free margin—made of the distal part of the outer lamella; inner lamella absent. This may be a homogeneous simple margin with the opposite margins of valves directly joining each other (Text-figs. 1-1, 1-2) or homogeneous with an uninterrupted contact groove (grooves) (Text-figs. 1-1–1-6). The role of contact structures in these varieties is taken by the outer lamellae.

b) Epibolic (thrown- or placed upon) free margin—formed on both valves by the calcified inner lamella, attached to the outer lamella as a narrow bandlike strip, the *vitta*. There are varieties with symmetrically continued *vittae* (Text-fig. 2-1) and with symmetrical inturned and chute-like curved *vittae* (Text-figs. 2-2–2-4). The role of contact strcutures is played mainly by the *vittae*. Forms with



TEXT-FIG. 2—Free margin without duplicature, epibolic. Transverse sections of carapaces, ventral parts. Vitta is dotted. 1. vitta symmetrical, continued: *Pyxion*? *keilaënsis* Sarv, after Gramm, 1984b, Text-fig. 4 (5). 2–4. *vitta* symmetrical, turned inside: 2. *Gerubiella krestovnikovi* (Polenova) (= *Buregia krestovnikovi* Polenova); 3. *Saccelatia oleskoensis* Netzkaja; 4. *Gravia* sp. 1. Ordovician; 3. Upper Silurian; 2, 4. Upper Devonian.

peculiar calcification and indistinct construction such as *Paraparchites* and *Aparchites* that need further study (Gramm, 1984b) are referred to the type without duplicature.

In the type with duplicature the free margin acquires a bilamellar construction in which the outer and the calcareous inner lamellae join at a more or less acute angle. According to the outlines of the inner lamellae the following are distinguished:

1) Duplicatures with isoplatic (equal in breadth) inner lamella; vestibule absent; observed in forms with symmetrical shells—*Selebratina* and *Coryellina* (Late Devonian-Carboniferous) (Text-figs. 3-5–3-7). The role of internal contact structures is played mainly by the inner lamellae.

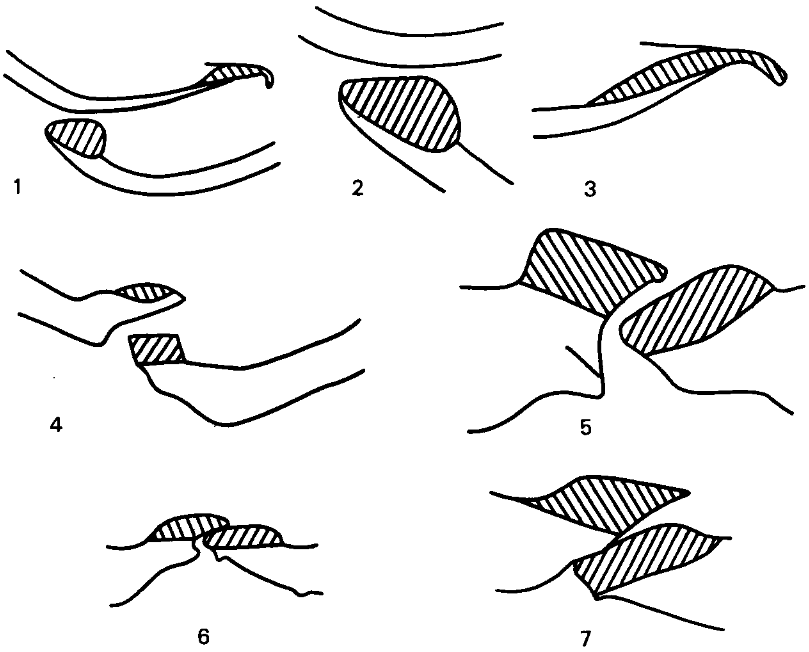
2) Duplicatures with mesoplatic (broad in the middle), lamella; vestibule absent; shells are often asymmetrical. They were first observed in *Geisina* (Sohn, 1961) and *Conodomyra* and *Oejlemyra* (Schallreuter, 1968) and later discribed in *Glyptopleura, Beyrichiopsis* a.o. members of the suborder Parapodocopina (Gramm, 1984b). In the contact both lamellae take part.

3) Duplicature with dilate (broadened) thin, pellicle-like inner lamella; vestibule absent. Observed in the genus *Janischewskya* (Gramm, 1984a).

Morphologically, the above mentioned varieties of the free margin with duplicature differ significantly from one another. They differ also from the situation seen in the free margin of the Podocopina where the inner lamella is mesostenic (narrow in the middle; Gramm, 1984b) being commonly wide in the anteroventral and posteroventral parts where a vestibule may be found, and getting narrower in the region of the oral concavity of the ventral margin.

This short review testifies to a considerable diversity in the structure of the free margin in "palaeocopid" ostracods. Although only partly perceived it shows that the order Palaeocopida in any sense (Osnovy paleontologii, 1960; Treatise on Invertebrate Paleontology, 1961) as well as the order Beyrichiida (Pokorný, 1958) consist of heterogeneous elements. Owing to this the term "palaeocopid(s)" is used here only in a very general sense.

Some examples showing the significance of free margin studies for systematics are given below. The material was studied with the aid of a JSM-U3 and is stored in the Institute of Biology and Pedology, Far East Science Centre, Vladivostok.



TEXT–FIG. 3—Free margin with duplicature. Transverse sections of carapaces, ventral parts. Inner calcified lamella is hatched. 1–3. *Buregia zadonica* Polenova; 4. *Anfedatia alveolata* (Abushik) (= *Příbylites alveolatus* Abushik); 5. *Selebratina curta* Polenova in Rozhdestvenskaja; 6, 7. *Coryellina advena* Schneider et Tkatscheva; 6. after Gramm, 1984b, Text-fig. 7 (6), middle of carapace; 7. in front of the middle. 1–3, 5. Upper Devonian; 4. Upper Silurian; 6, 7. Lower Carboniferous.

METHODS

The study of "palaeocopid" ostracod contact structures was carried out either on closed carapaces by means of thin or polished sections, or on single valves. In the latter the duplicature is usually distinguished during observations in reflected light or on the SEM. The homogeneous and the epibolic free margins, as well as the duplicature, have been investigated in polished sections in reflected and transmitted light and on the SEM. In sections, both in transmitted and in reflected light, the presence of the calcified inner lamella has been recognized by its colour: usually the outer lamella (the wall of the shell) is a pale, often amber colour; the inner lamella is darker coloured, often dark-brown. During studies of sections on the SEM the inner and outer lamellae may be sometimes distinguished by the character of the surface. Obviously the section preparation technique needs to be improved because the boundary between the lamellae has been observed rather rarely.

THE FREE MARGIN OF *Buregia*

During thin section investigations (Gramm, 1984b) it has been established that the construction of the free margins in the species *Buregia bispinosa* Zaspelova in Polenova, 1953 (the type-species of *Buregia*) and *B. zudonica* Polenova, 1953 differ sharply from those in *B. krestovnikovi* Polenova, 1953. It has been accepted that in the former the free margin is epibolic with an assymmetrical *vitta* which is present on the left valve only (?); at the same time it has been noted that "the asymmetrical *vitta* in whole gives rise to doubt" (Gramm, 1984b, p. 31). In *B. krestovnikovi* a symmetrical *vitta* has been revealed as a result of which the conclusion has been drawn that this species cannot be referred to the genus *Buregia* and deserves recognition as an independent genus (*ibid.* p. 10). The diagnosis of this genus—*Gerubiella* n. gen.—is given below.

Investigations in polished sections on the SEM reaffirmed the construction of the free margin in *B. krestovnikovi* (Pl. 1, figs. 7–13; Text-fig. 2-2). Simultaneously it has been revealed that in *B. zadonica* the free margin is not epibolic but with a peculiar duplicature—very narrow with an inner lamella which is thicker on the right valve free margin, and thiner on the left (Pl. 1, figs. 1–6; Text-figs. 3-1–3-3). This has been confirmed by the repeated study of thin sections on a more powerful microscope. The boundary between the inner and outer lamellae is visible.

Transparent shells (I had no single valves) show that the duplicature is of equal width along the left valve free margin. The nature of the curved, outside, distal part of the left valve inner lamella (Text-fig. 3-3) is not clear.

From the given data it follows that the Buregiidae Polenova, 1953 should include the asymmetrical forms *B. bispinosa*, *B. zadonica et al.* only. Polenova (1960) has tentatively assigned the family Buregiidae to the superfamily Kloedenellacea of the suborder Beyrichiida. At present however the systematic position of the Buregiidae is unclear as has already been noted by Shaver (1961). The presence of a duplicature indicates that that Buregiidae does not belong to the Palaeocopida.

The epibolic free margin of *Buregia krestovnikovi* (= *Gerubiella krestovnikovi*) shows that this form also cannot be referred to the Palaeocopida. Its systematic position is unknown.

THE FREE MARGIN OF *Saccelatia*

Gramm, 1984b has shown that the Late Silurian *Saccelatia bimarginata* Netzkaja, 1958 and *S. oleskoensis* Netzkaja 1960 (received from L. K. Gailite, Riga) possess differently built free margins—homogeneous in the case of the first, and epibolic with symmetrical *vittae* in the second. Additional studies on polished sections confirmed the free margin structure of *S. oleskoensis* (Pl. 2, figs. 7–12; Text-fig. 2-3). Simultaneously, it has been found that the homogenous free margin of *S. bimarginata* is not a simple one but has contact grooves on each valve (Pl. 2, figs. 1–6; Text-figs. 1-4–1-6).

Abushik (1971), due to the presence of a marginal ridge (velate structure) transferred both species to the genus *Přibylites* Pokorný, 1950. At the same time, she has described the species *Přibylites alveolatus* Abushik, 1971 with a ridge-like projection (marginal ridge) from the Upper Silurian of Podolia. In a transverse thin section (material kindly sent to me by A. F. Abushik) the inequivalve nature of the carapace and the presence of a duplicature were established; the right valve inner lamella is thicker and rectangular, the left—lenticular. In closed valves the right valve inner lamella is in contact with the left valve outer lamella (Pl. 2, figs. 13–15). It is believed that the width of the lamella along the free margin is uniform.

All three forms possess different free margins and therefore belong to different and unrelated genera. Unfortunately the free margin structure of the type species of *Saccelatia* Kay, 1940 (*S. arrecta* (Ulrich, 1894) and *Přibylites* (*P. moravicus* Pokorný, 1950) is still unknown. In the light of the data obtained the important thing, of course, is not the question of which genera the above-mentioned forms, should be assigned to, but the fact that the sharp differences in the free margin contact structures do not allow them to be assigned to one and the same genus. The strongly flattened ventral part suggests that *S. bimarginata* does not belong to the genus *Saccelatia* and should be considered as a separate genus. The diagnosis of this genus, *Netzkaina* n. gen., is given below. It may be assumed, although with a certain amount of doubt, that the homogeneous free margin allows it to be considered a member of Palaeocopida. Until data on the free margin of the type species of *Saccelatia* appears, *S. oleskoensis* can be left in this genus. *Přibylites alveolatus* is significantly inequivalve and because of this cannot belong to the genus *Přibylites*. Based on this species an independent genus *Anfedatia* n. gen. is erected (see below). The participation of the inner lamella in the free margin structure shows that the two forms cannot belong to the Palaeocopida.

FREE MARGIN OF *Selebratina*, *Coryellina* AND *Gravia*

In 1952 Polenova created the subfamily Graviinae. Later (Polenova, 1960) it was promoted to the rank of family in which were included the genera *Gravia* Polenova, 1952, *Selebratina* Polenova, 1952, *Coryellina* Bradifield, and others.

The contact structures of *Selebratina* and *Coryellina* have been described by Gramm, (1984b). They represent a duplicature with an isoplatic lamella. Here additional data are given that confirm the validity of the duplicature. The inner lamella is well seen on separate valves of *Selebratina* aff. *S. spinosa* Rozhdestvenskaja, 1959 from the Upper Devonian of the Novgorod region (Pl. 3, figs. 1–3), *S.* aff. *S. legibilis* Polenova, 1953 from the same deposits of the Vologda region (Pl. 3, figs. 4, 5) and *S.* ex gr. *S. variolata* Zanina, 1956 from the Visean of the Novgorod region (Pl. 3, figs. 6, 7) (material received from G. I. Egorov). All valves belong to heteromorphs as indicated by the tubercles on the posterior end. On the left valve of *S.* ex gr. *S. variolata* the inner lamella rises above the outer lamella (Pl. 1, fig. 14). On the SEM-micrograph of a polished section of *S. curta* Polenova in Rozhdestvenskaja 1959 the duplicature is well seen (Pl. 3, figs. 11, 12; Text-fig. 3-5) (material received from A. A. Rozhdestvenskaja).

Separate valves of *Coryellina* were not available. Photographs are given of thin and polished sections of carapaces of *C. advena* Schneider et Tkatscheva, 1972 from the Tournaisian (Pl. 3, figs. 8–10) (material received from M. N. Noskova). On the sections of *C. advena* and *S. curta* the inner lamella is distinctly visible. In reflected light it is distinguished from the outer lamella by its darker colour. On SEM-micrographs both lamellae differ in the surface structure, bubbled and smooth in the case of the inner lamella and fine-grained in the outer lamella (Pl. 3, figs. 10, 12). These facts prove the real existence of the inner lamella in *Selebratina* and *Coryellina* and do not allow one to speak of a "thickened part of the free margin" in Adamczak's sense (Adamczak, 1968, p. 48) or an infold in Kornicker's sense (Kornicker, 1969). There are two different layers.

Representatives of *Gravia* were also investigated (Gramm, 1984b). An epibolic free margin with a symmetrical *vitta* has been found in them. Here SEM-micrographs are given of a transverse

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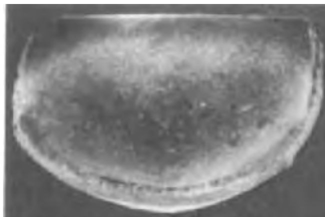
Plate 1—Most of the photographs were prepared from polished sections with the aid of SEM. Special indications are made in cases of using transmitted light. All sections are transverse, given in posterior view. L: length of carapace or valve, μm.

Figs. 1–6. *Buregia zadonica* Polenova. 1. Carapace left lateral view, 1147/69–3, L = 1130. ×37; 2–6. Carapace, 1147/69–4, L = 1125, transverse section. 2. ×66; 3. Ventral part. ×213; 4. Right valve duplicature. ×530; 5. Left valve duplicature. ×490; 6. The same, nearer to the middle. ×540. Novgorod region, Upper Devonian, Lower Frasnian.

Figs. 7–13. *Gerubiella krestovnikovi* (Polenova) (= *Buregia krestovnikovi* Polenova). 7–9. Right valve, 1147/10–1, L = 1400. 7. External view. ×26; 8. Internal view; vitta and hinge are seen; the adductor muscle scar is slightly observed. ×36; 9. Posterior part of ventral margin; vitta with list is seen. ×130; 10, 11. Carapace, 1147/80–1, L = 1500, transverse section. 10. ×43; 11. Ventral part, vittae are seen. ×350; 12. Carapace, 1147/80–7, transverse section; vittae. ×300; 13. Carapace, 1147/80–8, transverse section; left valve vitta. ×300. Novgorod region, Upper Devonian, Lower Frasnian.

Fig. 14. *Selebratina* ex gr. *S. variolata* Zanina. Left valve internal view, 1147/40, L > 550. Along the free margin on proximal side the inner lamella runs. ×70. Novgorod region, Lower Carboniferous, Visean.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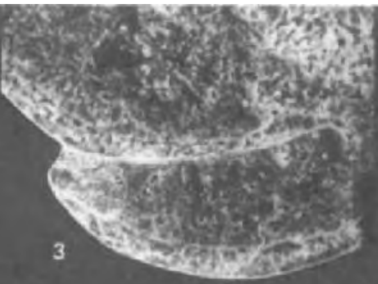
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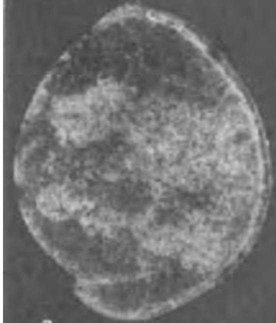
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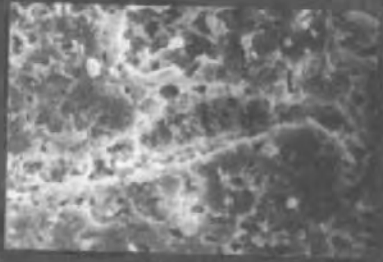
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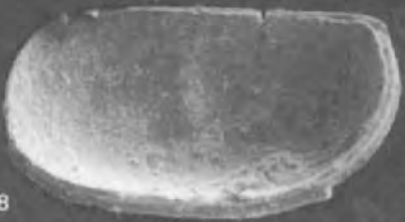
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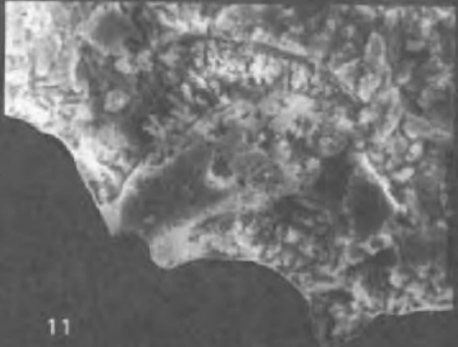
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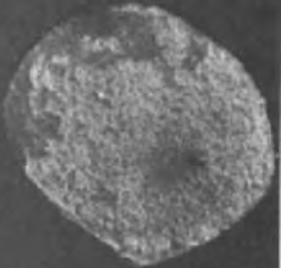
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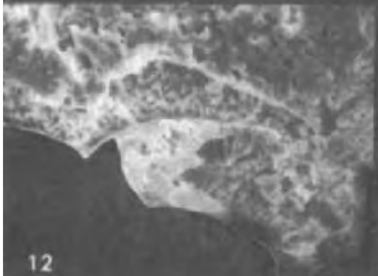
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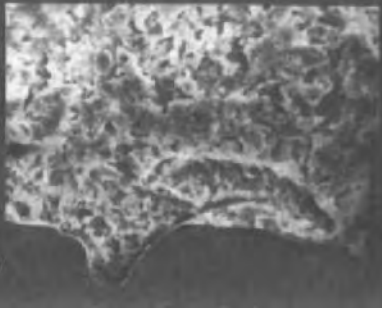
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polished section of *Gravia* sp. from Upper Devonian (Pl. 3, figs. 14, 15) (material received from N. A. Fokin), on which the *vittae* are seen on both valves (Text-fig. 2–4).

The presence of the free margin with duplicature in *Selebratina* and *Coryellina* and epibolic in *Gravia* shows that we have two essentially different Ostracoda groups that cannot be placed in the same family (Gramm, 1979). Because of this *Selebratina* and *Coryellina* were separated from the Graviidae and the family Selebratinidae has been erected (Gramm, 1984b). The position of the latter is discussed below.

THE SYSTEMATIC POSITION OF THE SELEBRATINIDAE

The genera *Selebratina* and *Coryellina* and their systematic position were a point at issue in many works (Bradfield, 1935; Polenova, 1952, 1953, 1960, 1982; Rozhdestvenskaja, 1959, 1966, 1972; Tschizhova, 1960; Levinson *et al.*, 1961; Sohn, 1962; Adamczak, 1968; Becker, 1970; Gründel, 1977; Melnikova, 1979; Wang Shang-qi, 1982; Adamczak and Becker, 1983). Apart or together they were assigned to Primitiidae, Aparchitacea, Graviidae, Kloedenellidae, Leperditellidae. Rozhdestvenskaja (1959) and Tschizhova (1960) indicated a vertical row of three little knobs on the posterior. It should be noted, that due to these dimorphic features Sohn (1962) tentatively placed *Coryellina* (and *Selebratina*) in the Primitiopsidae Swartz, 1936. Adamczak (1968) introduced the concept of perimarginal structures in which he placed the three tubercles (of *Coryellina*) already mentioned. Rozhdestvenskaja (1966) objected to assignment of both genera to the Primitiopsidae. After 1970 the idea became prevalent that *Selebratina* and *Coryellina*, as a part of the Graviidae, belonged to the Primitiopsacea.

In a short report Gramm (1979) has shown that the calcified inner lamella takes part in the free margin structure of *Gravia* (in a form of *vitta*) and in *Selebratina* and *Coryellina* (as a duplicature). Later on the family Selebratinidae was established (Gramm, 1984b). With that was noted "the striking resemblance of *Selebratina* and *Coryellina* to *Gravia* that is expressed by similar outlines, by the presence in them of lateral spines and such dimorphic features as vertical rows of tubercles on the posterior end." (Gramm, 1984b, p. 43). It has been mentioned also that this similarity may be either an astonishing example of convergence or, in contrast, evidence that *Selebratina* has descended from *Gravia* (*ibid.*, p. 43). In the latter case it has been assumed that the duplicature of *Selebratina* may have originated from the *vitta* of *Gravia* (*ibid.*, p. 47). Now, however, it is preferable to consider the epibolic free margin and the free margin with duplicature as independent structures. The above-mentioned similarity of external morphology of *Selebratina* and *Gravia* needs an explanation that excludes relationship. Most likely the question may be one of homoeomorphy.

Of paramount importance is the question of relationship with the Primitiopsidae. Observations

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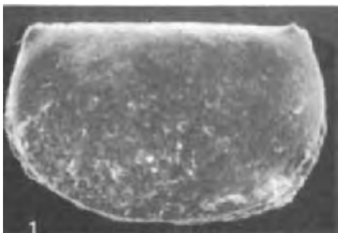
PLATE 2—Most of the photographs were prepared from polished sections with the aid of SEM. Special indications are made in cases of using transmitted light. All sections are transverse, given in posterior view. L: length of carapace or valve, μm.

Figs. 1–6. *Netzkaina bimarginata* (Netzkaja) (= *Saccelatia bimarginata Netzkaja*). 1. Carapace right lateral view, 1134/29–2, L = 1075, ×39; 3. Carapace, 1134/29–1, L = 1075, transverse section. ×54; 2, 4–6. Carapace, 1134/30–3, L = 1100; 2. Ventral view. ×40; 4–6. Transverse section, ventral part; 4. ×132; 5, 6. Contact grooves on the free margin of each valve. ×350, ×900. Lithuanian SSR, Upper Silurian, Ludlovian stage.

Figs. 7–12. *Saccelatia oleskoensis* Netzkaja. 7. Carapace left view, 1134/32–3, L = 950. ×39; 8. Carapace ventral view, 1134/33–4, L = 875. ×39; 9–12. Carapace, 1134/31–1, L = 875, transverse section; 9. ×62; 10. Ventral part, ×198; 11. Left valve vitta. ×470; 12. Right valve vitta. ×470. Lithuanian SSR, Upper Silurian, Ludlovian stage.

Figs. 13–15. *Anfedatia alveolata* (Abushik) (= *Přibylites alveolatus* Abushik). 13–15. Carapace, 1118/19–2, L = 600; 13. Lateral left view, ×50; 14, 15. Transverse section, transmitted light; 14. ×93; 15. Ventral part; duplicature is seen. ×445. Podolia, Upper Silurian, Ludlovian stage, Malinovtsy horizon.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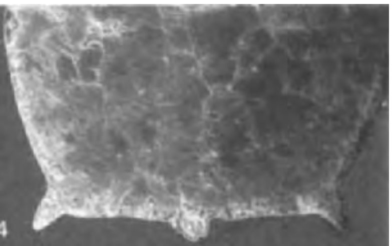
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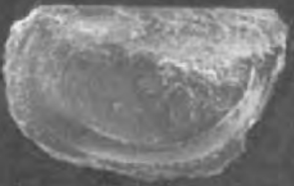
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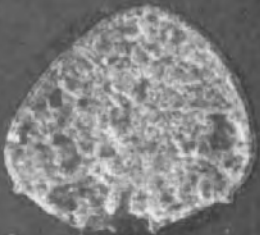
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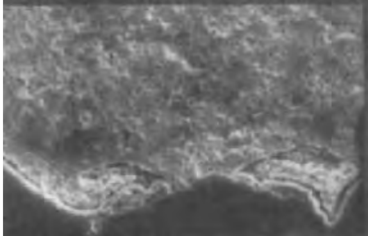
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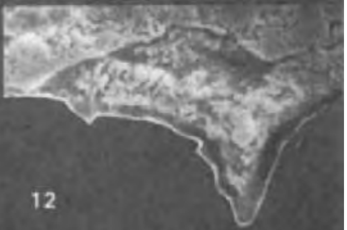
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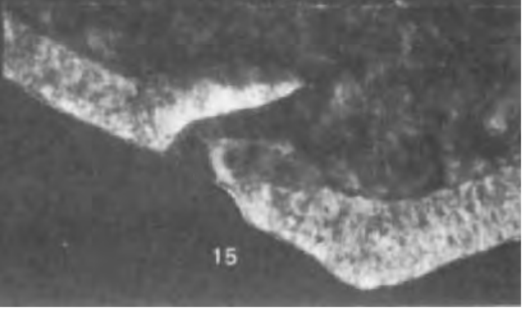
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on sections of *Primitiopsis planifrons* Jones, 1887 (received from Vl. Pokorný), *Amygdalella subclusa* Martinsson, 1956 and *Polenovula solida* Gailite, 1966 (received from A. F. Abushik, L. K. Gailite and N. V. Sidaravitchene) have not revealed on the free margins of these forms a calcified inner lamella either in a form of a *vitta* or as a duplicature. The presence of a *vitta* in *Gravia* and of a duplicature in *Selebratina—Coryellina* does not allow their amalgamation with the Primitiopsidae.

From the above it follows that at present the systematic position of the Selebratinidae is not clear. The systematic position of *Gravia* is also not clear.

CONCLUSIONS

E. Triebel has shown convincingly that in ostracods the role of "adaptive convergences" is considerable, (Triebel, 1941, p. 366) similar external features being found in different genera and families. Of great importance is his idea that if "the ties of relationship are expressed also in taxonomical grouping then preference cannot be given to less valuable but easily recognised characters at the expense of those that have a fundamental significance although they are harder to observe (*ibid.*, p. 372). Undoubtedly, under the latter, Triebel implied the internal features. On the genera *Paracytheretta* (Triebel, 1941, p. 374), *Cnestocythere* and *Schizocythere* (Triebel, 1950b) he demonstrated the significance of the inner lamella and of the hinge (correspondingly) for revealing cases of homoeomorphy. These views were backed up by Pokorný who wrote concerning the Palaeozoic ostracods: "The diversity of free margin and hinge structures gives the palaeontologist a very suitable tool for a radical improvement of the existing system of the Palaeozoic ostracords, which is based largely on the general form and sculpture. Both these features, however, are largely convergent and the conclusions made on their basis must be neccesarilly controlled on another basis" (Pokorný, 1959, p. 339). In other words Pokorný admits that the external features must be controlled by the internal.

In several examples I have demonstrated that notwithstanding the similarity of external characters a significant lack of coincidence of free margin contact structures is observed: 1. In spite of a certain resemblance of general form (straight hinge margin, convex ventral margin) and spines

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PLATE 3—Most of the photographs were prepared from polished sections with the aid of SEM. Special indications are made in cases of using transmitted light. All sections are transverse, given in posterior view. L: length of carapace or valve, μm.

Figs. 1–3. *Selebratina* aff. *S. spinosa* Rozhdestvenskaja. 1–3. Left valve. 1147/31-1, L = 775; 1. External view. ×38; 2, 3. Internal view; the inner lamella is seen; 2. ×45; 3. ×115. Novgorod region, Upper Devonian, Lower Frasnian.

Figs. 4, 5. *Selebratina* ex gr. *S. legibilis* Polenova. 4, 5. Right valve (broken longitudinally), 1147/42-1, L = 775; 4. External view. ×37; 5. Ventral part internal view; the inner lamella is seen. ×66. Vologda region, Upper Devonian, Lower Frasnian.

Figs. 6, 7. *Selebratina* ex gr. *S. variolata* Zanina. 6, 7. Left valve (damaged anteriorly), 1147/40, L = 550; 6. External view. ×60; 7. Internal view; the inner lamella is seen. ×64. Novgorod region, Lower Carboniferous, Visean.

Figs. 8–10. *Coryellina advena* Schneider et Tkatscheva. 8. Carapace left lateral view, 1132/5-3, L = 700. ×47; 9. Carapace, 1132/5-4, L = 700, transverse section, transmitted light; inner lamellae in contact. ×104; 10. Carapace, 1132/5-2, L = 725, transverse section, ventral part; on the left valve the limit between the inner and outer lamellae is better seen. ×490. Komi Autonomous Republic, Lower Carboniferous, Tournaisian.

Figs. 11, 12. *Selebratina curta* Polenova in Rozhdestvenskaja. 11. Carapace left lateral view, 1139/1-5, L = 675. ×41; 12. Carapace, 1139/1-3, L = 630, transverse section, ventral part; the inner lamella is well distinguished on both valves. ×350. Bashkiria Autonomous Republic, Middle Devonian, Givetian.

Figs. 13–15. *Gravia* sp. 13. Carapace left lateral view, 1128/54-3, L = 800. ×37; 14, 15. Carapace, 1128/55-2, L = 825, transverse section; 14. ×69. 15. Ventral part; vittae are seen. ×400. Komi Autonomous Republic, Upper Devonian, Lower Frasnian, Sargajev horizon.


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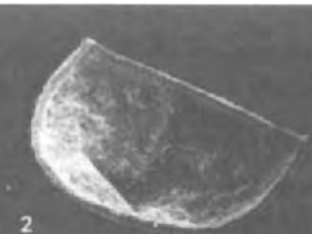
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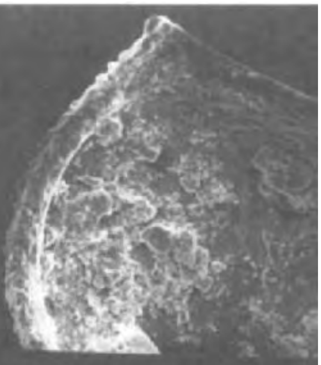
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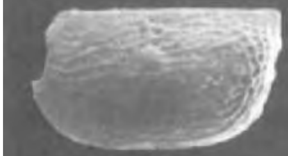
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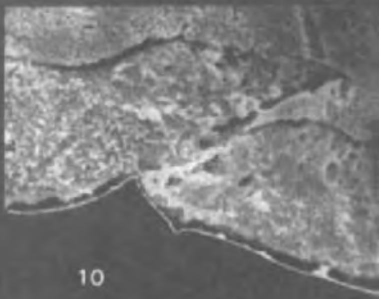
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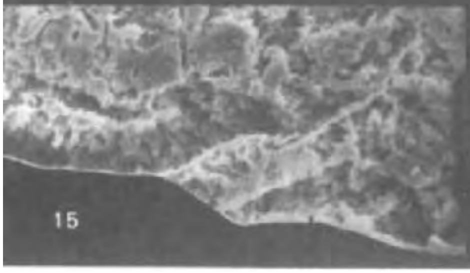
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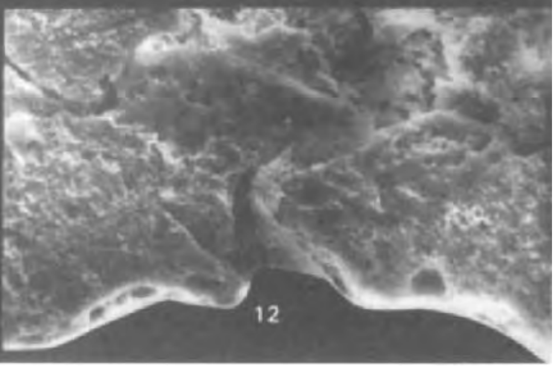
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on antero-ventral and postero-ventral parts in *Buregia zadonica* and *B. krestovnikovi* the free margin in the first species has a duplicature and in the second is epibolic. 2. The presence in *Saccelatia bimarginata, S. oleskoensis* and *Přibylites alveolatus* of a ridge-like projection or a marginal (velate) ridge suggests the genus *Přibylites*, but the first species has a homogeneous free margin, the second an epibolic and the third has a duplicature. 3. There are similar spines in the ventral half and similar dimorphic structures in the form of perimarginal tubercles on the posterior end in *Gravia, Selebratina* and *Coryellina*, but the first genus possesses an epibolic free margin and the other two have a free margin with duplicature with an isoplatic inner lamella.

Great importance is attached to these facts. In accordance with the afore-mentioned views of Triebel and Pokorný I believe that in course of classification of the listed "palaeocopid" ostracods preference should be given to the internal characters but not to the external ones. The study of internal contact structures shows that in the examples given we are dealing with homoeomorphs, *i.e.* outwardly similar forms that possess different inner structure (Afanasieva, 1977); they do not belong to the same genera and certainly have a different family (or even higher) status. From this it follows that terminal and lateral spines, ridge-like projections or marginal (velate) ridges and perimarginal dimorphic structures are convergent formations (features) the use of which in classification needs great care. Therefore, purely on the grounds of internal contact structures the new genera *Netzkaina* n. gen., *Gerubiella* n. gen. and *Anfedatia* n. gen. are distinguished, and the independence of Graviidae and Selebratinidae is recognized.

Because of the investigation of inner contact structures the meaning of the domiciliar dimorphism is better comprehended; its presence in *Buregia* s. s. and in *Gerubiella* n. gen., which possess different patterns of free margin, shows that this type of dimorphism occurs in unrelated groups and therefore cannot rank highly as a systematic criterion. At present the data obtained are not numerous. A wide examination of "palaeocopid" ostracods is needed for the purpose of revealing the different types and varieties of free margin and clearing up the extent to which the calcified inner lamella takes part in it. Of great importance also is the need to comprehend the interrelationship between the external features and the margin contact structures of "palaeocopids".

It is believed that studies of the free margin internal structures together with investigations of other internal structures of "palaeocopids" such as the central muscle field, and hinge should favour a better understanding of the history and evolution of the whole Class Ostracoda with the elucidation of the phylogenetic relationships of the different groups.

SYSTEMATIC PART

Incerti Ordinis et subordinis

Family NETZKAINIDAE n. fam.

Type genus.—*Netzkaina* n. gen. Upper Silurian, Ludlovian stage. Estonian SSR.

Diagnosis.—Carapace equivalved; free margin homogeneous with a groove on each valve. Laterally truncate-oval. Dorsally boat-shaped, greatest width behind the middle. Dorsal margin straight, ventral margin convex. Both ends broadly rounded, the anterior slightly higher. Ventral part flattened with a marginal ridge along the bend. Surface smooth. Central muscle field and hinge unknown.

Assigned genera.—The type genus.

Remarks.—The systematic position of the new family is unknown. By the presence of a homogeneous free margin with a groove the family differs strongly from the Graviidae which possesses an epibolic free margin.

Upper Silurian.

Genus NETZKAINA n. gen.

Derivation of name.—In honour of Anna Iossifovna Netzkaja—the distinguished investigator of Ordovician-Silurian ostracods.

Type species.—*Saccelatia bimarginata* Netzkaja, 1958. Netzkaja, 1958, p. 246, Pl. 2, fig. 9. Upper Silurian, Ludlovian stage, Kaugatma strata. Estonian SSR, Esel.

Diagnosis.—As for the family.

Assigned species.—The type species only.

Remarks.—The setting up of the new genus and its separation from the genus *Saccelatia* is based on the homogeneous free margin and flattened ventral part. It is accepted (until data about the free margin of *S. arrecta*, the type species of *Saccelatia*, is available that for *Saccelatia* the epibolic free margin is characteristic (*S. oleskoensis*). Gramm, (1984b) has shown that *S. bimarginata* (= *Netzkaina bimarginata*) has a simple homogeneous free margin; new observations have revealed the presence of grooves.

Occurrence.—Upper Silurian; Estonia and Podolia.

Incerti ordinis and subordinis
Family GERUBIELLIDAE n. fam.

Type genus.—*Gerubiella* n. gen. Upper Devonian, Frasnian. Voronezh region.

Diagnosis.—Carapace with epibolic free margin and symmetrical *vitta*. Carapaces elongate-ovate, nearly equivalved, the right valve slightly overlaps. Both ends rounded with an anteroventral and posteroventral spine. Surface punctate or reticulate. Domiciliar dimorphism present.

Assigned genera.—The type genus.

Remarks.—The systematic position of the new family is uncertain. The epibolic free margin of *Gerubiella* n. gen. with its asymmetrical *vitta* differs markedly from the asymmetrical free margin of *Bureiga* with a peculiar duplicature. Domiciliar dimorphism observed in Gerubielleidae n. fam. cannot validate assignment to the Kloedenellacea as this type of dimorphism is present in different unrelated groups.

Middle and Upper Devonian.

Genus GERUBIELLA n. gen.

Derivation of name.—anagram from *Buregia* + *ella.*

Type species.—*Buregia krestovnikovi* Polenova, 1953. Polenova, 1953, p. 63, Pl. 7, figs. 1–3. Upper Devonian, Frasnian, Voronezh region.

Diagnosis.—As for the family.

Assigned species.—In addition to the type species, *Buregia magnifica* Rozhdestvenskaja, 1972 from the Lower Famennian of Bashkiria and *B. groosae* Zbikowska, 1983 from the Upper Givetian of Poland and BRD.

Remarks.—In *G. krestovnikovi*, on the external side of the *vitta* there is a list (Pl. 1, figs. 9, 11); the adductor muscle scar is some distance in front of the middle (Pl. 1, figs. 7, 8) and represents an irregular crowding of up to 25 tuberculate stigmata; the hinge-margin of the right valve bears a narrow groove that widens slightly in its posterior third (Pl. 1, fig. 8).

Occurrence.—Middle and Upper Devonian; European part of RSFSR, Poland and BRD.

Incerti ordinis et subordinis
Family ANFEDATIIDAE n. fam.

Type genus.—*Anfedatia* n. gen. Upper Silurian, Ludlovian stage, Malinovtsy horizon. Podolia.

Diagnosis.—Carapace with duplicature on free margin; from subtriangular to semicircular in outline; dorsal margin straight, ventral margin convex. Right valve larger than the left. A ridge-like projection or a poorly developed ridge runs along the ventral and posterior margins. Surface sparsely punctate. Central muscle field and hinge unknown.

Assigned genera.—The type genus.

Remarks.—The systematic position of the family is uncertain. In the presence of a duplicature the family differs markedly from the Graviidae which possesses an epibolic free margin and to which the type species of the type genus was originally assigned (Abushik, 1971). The participation of the inner lamella in the free margin structure does not allow assignment to the Primitiopsacea.

Upper Silurian.

Genus ANFEDATIA n. gen.

Derivation of name.—The name is compiled from the initial syllables of the name and patronymic of Anna Fedosovna Abushik—the distinguished researcher on Silurian-Devonian ostracods.

Type species.—*Přibylites alveolatus* Abushik, 1971. Abushik, 1971, p. 52, Pl. 22, figs. 5, 6. Upper Silurian, Ludlovian stage, Malinovtsy horizon, lower part. Podolia, the Dniester.

Diagnosis.—As for the family.

Assigned species.—The type species.

Remarks.—The new genus cannot belong to the genus *Přibylites* because of its significantly inequivalve nature (Pl. 2, figs. 14, 15) and the presence of a duplicature which is most likely absent in *Přibylites.* Data on the free margin structure in the type species of *Přibylites, P. moravicus* Pokorný, 1950 are badly needed.

Occurrence.—Upper Silurian, Ludlovian. Podolia.

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III

Morphology and Morphogenesis

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The Origin of the "*Xestoleberis*-spot"

DIETMAR KEYSER
Zoologisches Institut und Museum, Hamburg, F.R. Germany

ABSTRACT

The *Xestoleberis*-spot of *Xestoleberis aurantia* is studied in detail. The main feature of the spot is an irregularity in the inner part of the calcified exocuticle. Apart from that it is just a place where two muscle scars are present. The question of whether the varying size of the spinning gland lying in between these muscles is the cause of noncalcification in the *Xestoleberis*-spot is discussed.

INTRODUCTION

Among the podocopid ostracods, the family Xestoleberididae stands apart from the other families. This family sprang up, as many others did, in Cretaceous times (Deroo, 1966; Van Veen, 1936). Since then it has not changed much in character. Nothing is known about its ancestry and its relationship to other families.

It is characterised by a smooth, highly arched shell which is pointed anteriorly and flattened ventrally. A diagnostic feature of the whole group is the so-called "*Xestoleberis*-spot" (or "nierenförmiger Fleck"). This spot is a conspicuous irregularity visible on the inner surface of the detached valve. G.W. Müller in 1884 was the first to notice this structure and believed that this feature was a remnant of a "valve-gland". However in 1894 he recanted this and mentioned only that this structure belonged to the inner chitin layer of the calcified lamella of the shell (G.W. Müller, 1894, p. 93). Wagner (1957) mentioned this spot in his thesis as antennal muscle scars, although with a question mark. An outstanding photograph of this spot was presented by Triebel (1958, Pl. 2, fig. 9) but without explanation. McKenzie (1972) referred to it as "eye-scar", an explanation which is found more often in the younger literature. Bonaduce *et al.* (1980) figured the spot on the outside of *Ornatoleberis,* where it appears on a pitted surface as a smooth area, comparable to the region of the eye.

The only conclusion that can be drawn from all these works is that nothing is known about the morphology, origin and function of this peculiar structure. The present study was undertaken to gather more information on this structure and to solve the problem of the function of the "*Xestoleberis*-spot."

MATERIAL AND METHODS

The material for this study was mainly *Xestoleberis aurantia* (Baird, 1838) collected in the Baltic

Sea. About fifty specimens were available for light microscope, transmission electron microscope and scanning electron microscope studies. The specimens were collected with a handnet, 180 μm mesh, in the phytal zone at a depth of between 1 and 8 metres. They were picked out individually under a stereo-microscope using a pipette. The animals were kept alive in a small bowl at 15 °C with 14 hours of light, a weekly change of water and no extra food.

Several live animals were observed under the stereo-microscope. Afterwards they were fixed in 70 % ethyl alcohol, dissected and embedded in polyvinyl-lactophenol stained with Orange-G. Some were heated in KOH prior to dissection and were then embedded. Others were put in clove oil for a fortnight to make them translucent and then examined under the microscope. Specimens used for sectioning and examination under the light microscope (LM) and in the TEM were treated in the same manner. They were initially fixed in 2.5 % glutardialdehyde in 0.05 mol phosphate-buffer and 5 % sucrose and then washed in buffer with sucrose three times. Postfixed with 2 % OsO_4 in the same buffer, they were then washed three times in buffer, decalcified in EDTA and dehydrated in graded acetone, before being embedded in Spurr's resin (Spurr, 1969). Semi-thin and ultra-thin sections were cut with a Reichert Om/U II Ultramicrotom. Semi-thin sections were stained with Toluidinblue and Pyronin after Holstein and Wulfhenkel (1971), ultra-thin sections with uranylacetate (Stemper and Ward, 1964) and leadcitrate (Reynolds, 1963). Photographs were taken with a Leitz Dialux for light microscope and a Zeiss EM 9 for TEM.

Specimens for the SEM were fixed in 2 % glutardialdehyde in phosphate-buffer, dehydrated in acetone and critical-point dried with CO_2 in a Balzers CPT. They were sputtered in a GEA-004 S manufactured in Graz, Austria, and viewed under an SEM Cambridge S-4. These dried specimens were broken up with fine needles to allow the inner structure to be seen.

RESULTS

Xestoleberis auraniia (Baird, 1838) is an ostracod of 500 μm length. The shell is roughly round when seen end on and triangular from the side. In dorsal view it is slightly egg-shaped with a pointed anterior (Pl. 1, fig. 1). The ventral part is flattened. The surface of the valves is smooth with several simple or sieve type pore canals. The fused zone is broad. The calcified inner lamella is especially broad in the anterior part thus forming a pronounced vestibule (Pl. 1, fig. 5). The hinge is merodont. The central muscle field consists of four vertically arranged scars and a V-shaped frontal scar. Behind the eye region is a typical reniform spot, which is diagnostic for all Xestoleberididae, the so-called "*Xestoleberis*-spot" (Pl. 1, figs. 4–8).

The nauplius-eye of *Xestoleberis aurantia* is divided into three parts. Two are laterally coalesced with the valves, just in front of the frontal end of the hinge. The third eye is found at the top of the forehead on the same level as both lateral eyes (Pl. 1, fig. 3). The "*Xestoleberis*-spot" is situated behind the lateral eyes. It is always separated from the eye-scar. From the outside no imprint is visible in this area on the surface. In transmitted light an elongated inclusion, bordered by several bubble-like structures (Pl. 1, fig. 4, s.a. Triebel, 1958) is visible.

In single detached valves the inner view reveals mostly a slitlike, elongated and elevated struc-

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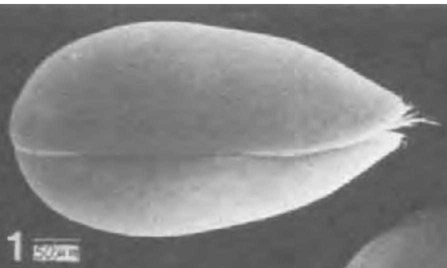
PLATE 1—*Xestoleberis aurantia* (Baird, 1838)

Fig. 1. Dorsal view. Fig. 2. Lateral view of the complete male animal with removed right valve. Fig. 3. Frontal view. Fig. 4. Light microscopic view of the animal, showing the "*Xestoleberis*-spot". Fig. 5. Interior view of the left valve, showing the "*Xestoleberis*-spot" with two slits. Fig. 6. "*Xestoleberis*-spot" with two muscle scars. Fig. 7. "*Xestoleberis*-spot" with two slits. Fig. 8. "*Xestoleberis*-spot" with one big slit. Fig. 9. Transverse fracture through the "*Xestoleberis*-spot" showing the main and two side vesicles within the calcified outer layer of the cuticle. Fig. 10. The same area as in Fig. 9 only in a TEM section.



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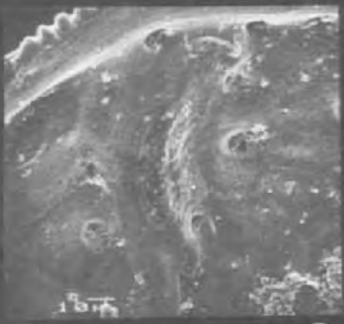

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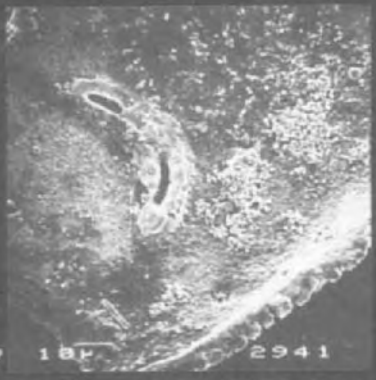

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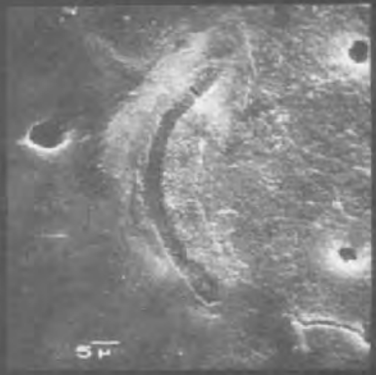

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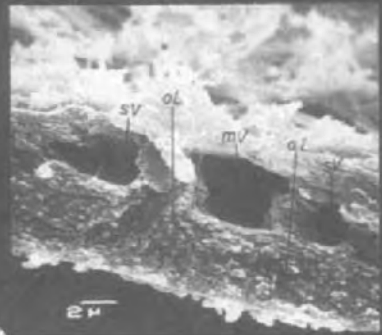

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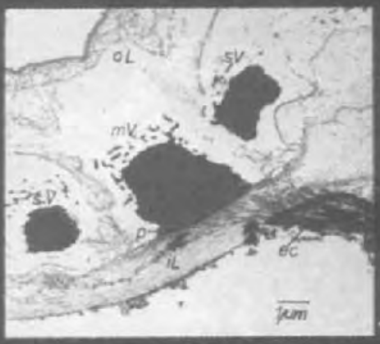

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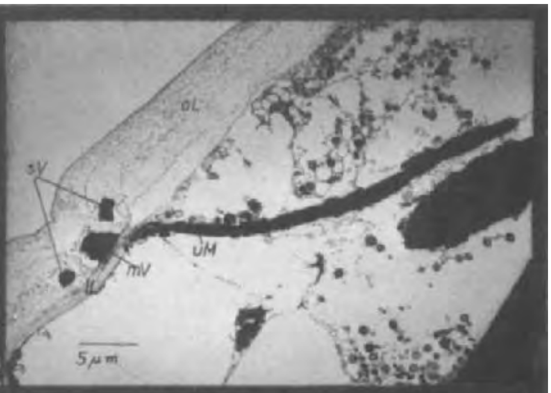
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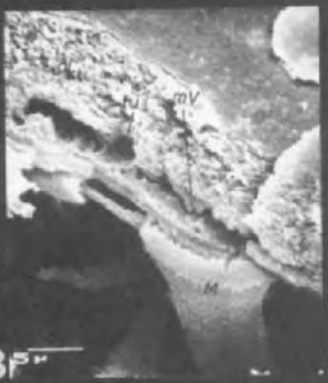
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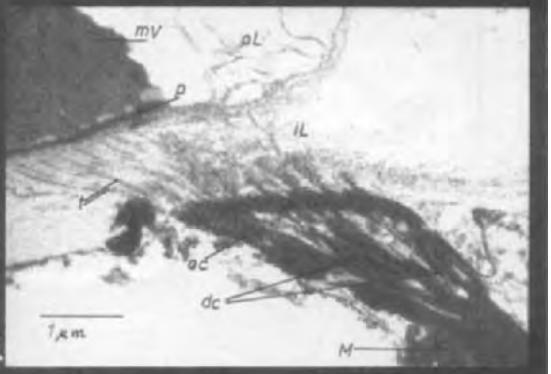
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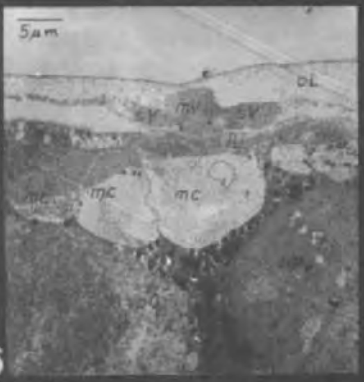
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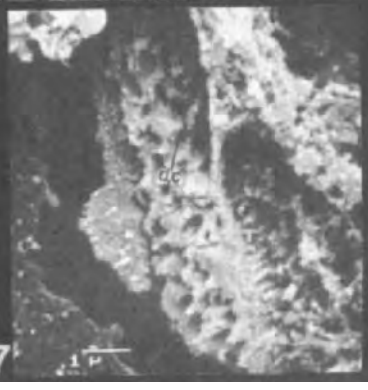
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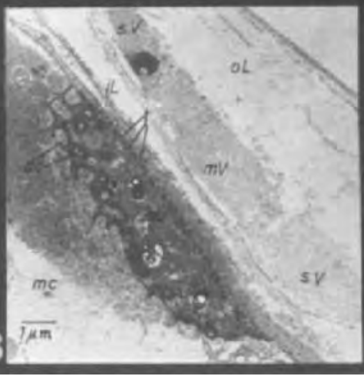
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ture behind the eye-scar (Pl. 1, fig. 5). This slit begins slightly beneath the anterior part of the hinge and runs, slightly arched anteriorly, in a vertical direction to about the middle part of the valve. The slit is mostly surrounded by an elevated rim and opens into the shell (Pl. 1, fig. 8). In some instances this slit is divided into two vertically running clefts separated by a solid ridge (Pl. 1, fig. 7). Only in very rare cases is a specimen found without this torn area. The region is then elevated and shows a muscle scar at both the upper and lower ends of the arch (Pl. 1, fig. 6). These scars are located at the front edge of the elevated area. The muscle scars each measure 20 μm by 4 μm with the gap between them (7 μm) bringing the length of the whole elevated structure to about 50 μm. The breadth varies from about 10 μm to 15 μm. In fractured shells this area shows up as vesicles underlying the "*Xestoleberis*-spot" (Pl. 1, fig. 9), with a main vesicle running beneath the whole spot, flanked by smaller and shorter ones connected to the main one by small tubes (Pl. 1, fig. 10; Pl. 2, figs. 6 and 8). These lateral vesicles correspond to the bubble-like structures seen in transmitted light in the living animal. The vesicles are separated from the surface of the shell and from each other by the normal calcified cuticle which is then arranged in such a manner as to withstand tractive forces from the side of the inner cuticular layer (Pl. 1, fig. 10; Pl. 2, fig. 2). While the calcified cuticular layer shows only a few chitinous fibrils often oriented in various directions, the inner cuticular layer is mainly composed of chitinous fibrils running parallel to the extension of the shell. This can best be seen in TEM sections (Pl. 1, fig. 10).

The vesicles are filled with a homogenous substance which differs in appearance (in SEM and TEM micrographs) from the other material present (Pl. 2, fig. 3). However one thing is striking. Material of the above type is often encountered in TEM sections when it lies as filiform droplets in the middle of the calcified layer of the shell without there being any connection to the "*Xestoleberis*-spot" (Pl. 2, fig. 2). It stains in the same manner as the other chitnous substances present.

At the junction of the main vesicle and the inner cuticular layer is an electron-dense plate of 0.1 μm thickness within the inner cuticular layer (Pl. 1, fig. 10; Pl. 2, fig. 4). The material of the main vesicle adheres to the plate by means of several protrusions which have "footholds" on the plate (Pl. 1, fig. 10; Pl. 2, fig. 2). In the vicinity of the "*Xestoleberis*-spot" the inner cuticular layer is very well defined and here about 1 μm thick. No electron-dense plate is developed between the small bubble-like vesicles at the margin of the main vesicle and the inner chitinous layer (Pl. 1, fig. 10).

From the electron-dense plate, at right angles to the inner cuticular layer, tendon-like filament-bundles penetrate this layer to the underlying epidermal cell. This is itself connected to the above bundles on the one hand and to a muscle through strong clefts and desmosomal adhering plaques on the other (Pl. 2, fig. 4).

Four strong muscles are connected to the "*Xestoleberis*-spot". They are separated into an upper and three lower ones. The upper one runs from the forehead of the animal from just above and median of the base of the antennule beneath the median eye tubercle. The other three muscles adhere at the protopodite of the antenna, the lowermost running to the base of the spinning bristle. The

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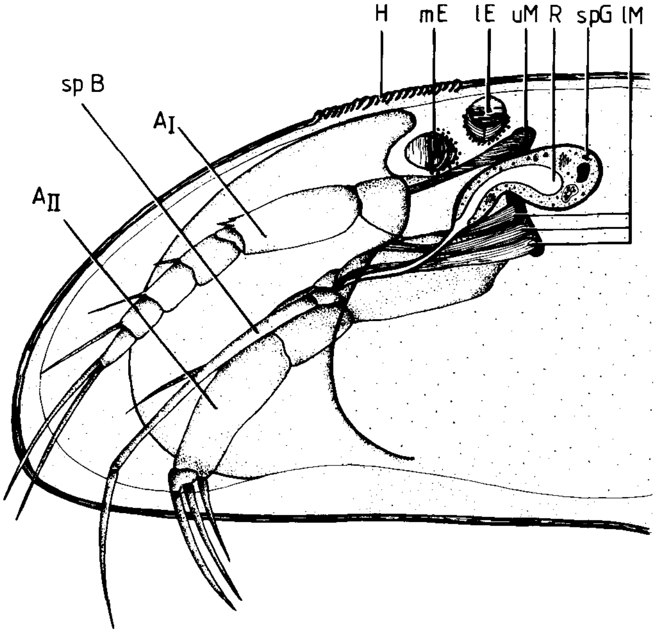
PLATE 2—*Xestoleberis aurantia* (Baird, 1838)

Fig. 1. Fracture of the "*Xestoleberis*-spot" showing the vesicles and the impression of the spot on the inner surface of the shell. Fig. 2. TEM section, showing vesicles in the shell and the adjoining upper muscle. Fig. 3. Fracture of the main vesicle showing the adhering muscle, the homogenous substance and a connecting tunnel entrance to the side-vesicles. Fig. 4. A section showing the inner chitinous layer with the incorporated plate. On top of it the vesicular substance with its footholds. Below the epidermal cell with the big clefts connecting itself to the muscle. Note the tendon-like fibre-bundles connecting the epidermal cell to the plate. Fig. 5. SEM-photograph of the tendon-like projections left over by removing the epidermal cell from the chitinous layer. Fig. 6. "*Xestoleberis*-spot" with the three lower muscle cells, the spinning gland and the hepatopancreas (liver). Fig. 7. SEM-photograph of the desmosomal clefts in the epidermal cell where it connects to the muscle. Fig. 8. A TEM-section showing the desmosomal clefts as well as the tendon-like fibre-bundles distributing the pull of the muscle to the main vesicle in the cuticle.



TEXT-FIG. 1—Schematic drawing of the internal organisation of the functionally important parts related to the "*Xestoleberis*-spot".

muscle scars which are sometimes visible in an inner view of the "*Xestoleberis*-spot" are the adhesion points of the upper and all three lower muscles (Text-fig. 1). Between the space of the upper and lower muscles lies the spinning gland with its reservoir. In the posterior part it is linked to the hepatopancreas (Pl. 2, fig. 6).

The upper muscle meets a second one which connects to the shell more dorsally than the "*Xestoleberis*-spot". Both lie in the vicinity of the lateral eye and run ventrally of the lateral eye nerve to the frontal part of the head. The lower muscle follows more or less the path of the excretion tube of the spinning gland. A characteristic feature of the muscle cells is a swelling of their base at the shell. The reason for the swelling is not yet understood since one part of the cytoplasma does not have any inclusions and stains very light, and another part of the cell opposite the muscle fibres appears normal with dense cytoplasma (Pl. 2, fig. 6).

A connection to the eye is not visible. There is also no hint in the morphologic structure of an underlying gland. The area does not show any special nervous connections. The only specialized region in the "*Xestoleberis*-spot" is the three arched vault in the non-living material of the calcified lamella in the shell.

DISCUSSION

Since 1884, when Müller (p. 14) first mentioned the "*Xestoleberis*-spot", not many investigations have dealt with this feature. Müller (1894) himself noticed the systematic value of the spot when he used it in his generic diagnosis. He also noticed this spot in the genus *Microxestoleberis*. Most of the later authors did not mention this diagnostic feature for the genus (Sars, 1928; Klie, 1938). However this changed when Triebel (1958) recognized that the spot was a diagnostic feature for the whole family. Since then most studies include the "*Xestoleberis*-spot" in the systematic description, sometimes as an "eye-scar" (McKenzie, 1972, 1977), sometimes as a crescentic spot (Bate *et al.*, 1981) or just as "*Xestoleberis*-spot" (Athersuch, 1977).

Many hypotheses have been put forward in explanation and rejected. Müller (1884) thought it was a remnant of the shell-gland. He rejected this however in 1894. Wagner (1957) thought it represented antennal muscle scars, a suggestion that has not been accepted by anyone. Whittaker (1972) believed that he had seen a connection between the eye and the '*Xestoleberis*-spot" on the shell and suggested a sensory function connected with vision. This has also not been verified (Athersuch, 1977).

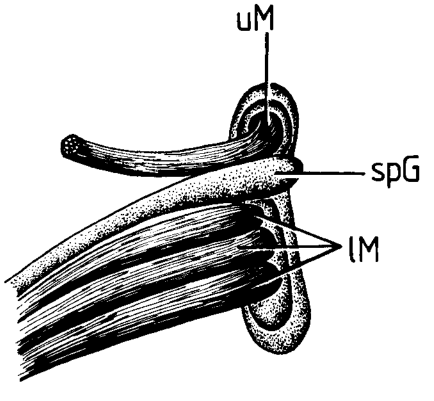
The structure itself has already been observed by Müller (1894), and Athersuch (1977) also studied this area. It is a slit between the upper and lower part of the calcified lamella. Müller simply called it an irregularity in the inner chitinous layer. These observations have been verified in the present study. However, in living animals, the observed slit is always filled with material (Pl. 2, fig. 3). The observation of Wagner (1957) that it is connected with the antennal muscles, was also correct. In most instances though, as already mentioned, these muscles are torn off the carapace and the thin inner chitinous layer tears with it so that the underlying slit of the main vesicle (Pl. 1, fig. 8) is opened up. At times the whole channel is opened, but sometimes only the point at which the muscles adhere is (Pl. 1, fig. 7). In one instance, therefore, only one big slit can be seen (Bate *et al.*, 1981) and in another, two smaller slits (Athersuch, 1977). Only very rarely are the muscles removed so gently that the muscle scars are visible (Pl. 1, fig. 6).

It is remarkable that no one believed the theory of Wagner (1957) that this was a place where muscles connect to the shell. Triebel (1958) refers to Wagner, but rejects the latter's ideas because other muscle scars do not possess such a structure as the "*Xestoleberis*-spot". The results of the present study show that in this place a group of muscles are fastened to the shell (Pl. 2, figs. 2, 3, 6, 8). These muscles are present also in other ostracods, such as *Cypridopsis vidua* (Smith, 1965) for instance, but they are grouped in another way due to the different shape of the shell. Due to their function of retraction of the complete forehead together with the antennule and antenna, these muscles are comparatively strong. As a result of the shape of the carapace, which is elongated and pointed in the species studied, the animal has to extend its front limbs more than those in other families in order to work them properly (Pl. 1, fig. 2).

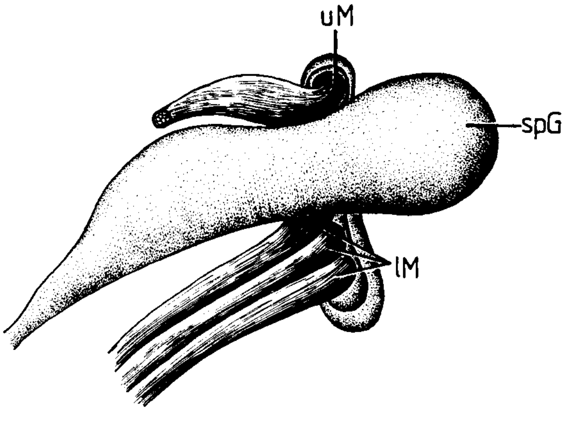
A further important factor is that one of the lower muscles controls the efflux of the spinning secretion (H. Müller, 1980). If one considers that this animal depends up to about 90% on the spinning threads it produces for its movements, it can be understood why the spinning gland is very strongly developed. The statement by Zenker (1854) that the spinning gland lies between the muscles of the antennae was verified. The pull exerted by the muscles is transferred by way of an epidermal cell and by tendon-like filament bundles on to the plate in the chitinous layer of the calcified shell and then over the footholds into the homogenous substance of the "*Xestoleberis*-spot" (Pl. 2, figs. 2, 4). This is a relatively clear way of muscle function. However, the question posed by Triebel (1958) remains: Why do other muscles not develop such a structure? What is so special at this adhesion point, and especially in this family?

Members of this family differ from other families in two ways. Firstly, in the shape of the shell, which is pointed at the front and so requires the presence of strong retracting muscles. Secondly, in the greatly developed usage of the spinning gland which lies just in the middle of the muscles. Both are here taken into consideration, as both these facts could provide the answer to the question, since no other specialised structures could be found.

If it is realized that the activity of the spinning gland is very high (H. Müller, 1980), it means that the secretion has either to be stored away in the reservoir of the cell or be constantly used for the secretion of the spinning thread. In a closed shell, a constant secretion is unlikely, so the reservoir



TEXT-FIG. 2—Muscle direction with empty reservoir of spinning gland.



TEXT-FIG. 3—Muscle direction with filled reservoir of spinning gland.

of the spinning gland has to change constantly its volume. If the muscles contract when the reservoir is empty, the force of the muscles is applied at right angles to the shell (Text-fig. 2). If the reservoir is filled, the muscles have to strain around this swollen, ball-like structure (Text-fig. 3). This means a different direction of pull at the shell. Such constant change in the direction of pull at the muscle scar must account for the development of the "*Xestoleberis*-spot". Two facts therefore explain the reason for this spot. Firstly, the scars must sit on the shell in such a way that it is flexible. This is achieved by the morphological structure found. Secondly, during calcification after moulting, it is not possible to develop calcite in this area because of continuous changing stress. The vesicles, therefore, contain only the matrix of the calcified layer of the cuticle. Such an explanation would also account for it having the same staining quality as is found in the other chitinous parts of the shell.

Several questions must follow such an explanation. With a spinning gland developed in many Cytheracea (Hartmann, 1966), why is such a spot only developed in the Xestoleberididae? The answer must lie in the different internal organisation and body shape of the animals. For example, in *Hirschmannia* the corresponding muscles are very small, in *Semicytherura* they lie in front of the gland, in *Hemicythere* the gland is not so strong and in *Paradoxostoma* there are no muscles in the vicinity.

A further question must be: Why are the spots so different that their shape can sometimes be characteristic for a species (Hartmann pers. comm.)? It appears that the outline of the carapace in connection with the position of the spinning gland can account for these differences. In short, high specimens the spot is often more prominant than in longer, more depressed forms. (Hartmann, 1978, 1979, 1980, 1981; Athersuch, 1976). Several other questions still remain to be solved. For example: what is the development in larval animals? why do the muscle cells have such swollen bases? and several others.

SUMMARY

The "*Xestoleberis*-spot" of *Xestoleberis aurantia* (Baird, 1838) was investigated. The main feature of the spot is an irregularity in the calcified layer of the shell. The spot consists of a main vesicle with several bubble-like extensions within in the calcified matrix of the cuticle. These structures are filled with a homogenous substance which has the same staining qualities as the other chitinous substan-

ces of the calcified shell. Between these vesicles in the calcified layer and the epidermal cells is a distinct inner chitinous layer. It is stabilized at the border to the main channel in a plate which connects tendon-like fibre-bundles from the epidermal cell with small foot-like extensions from the homogenous substance.

Four muscles are connected to the "*Xestoleberis*-spot", one upper and three lower ones. The upper one connects the shell with the forehead medially from the first antenna. The lower muscles run to the prodopodite of the second antenna. Enclosed by the muscles is the spinning gland.

The different degree of filling of the reservoir of the spinning gland alters the direction of the pulling force of the muscles. This is thought to be the reason for the flexible nature of the "*Xestoleberis*-spot".

The different size of the spot in different species is due to the difference in the shape of the body and also to the position of spinning gland.

ACKNOWLEDGEMENTS

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ABBREVIATIONS

A_I = antennule
A_{II} = antenna
dc = desmosomal cleft
ec = epidermal cell
H = hinge
HP = hepatopancreas (liver)
iL = inner chitinous layer of the cuticle
lE = lateral eye
lM = lower muscles
mc = muscle cell
mE = median eye
mV = main vesicle
oL = outer calcified layer of the cuticle
P = plate in the inner chitinous layer
R = reservoir of the spinning gland
spB = spinning bristle
spG = spinning gland
sV = side vesicle
t = tendon-like filament bundles
tu = tunnel from main vesicle to side vesicle
uM = upper muscle
Xsp = *Xestoleberis*-spot

DISCUSSION

Kaesler: How variable is the size of the spinning gland?

Keyser: It varies from 35–40 µm in diameter when it is full, down to 5 µm in diameter when it is empty.

Schweitzer: Did you use critical-point drying techniques to mount your SEM specimens?

Keyser: Yes. I did; you will find the methods used in the written paper.

Geometrical Optics of Some Ostracod Eyes

JOHN H. MYERS AND MERVIN KONTROVITZ
Northeast Louisiana University, Monroe, U.S.A.

ABSTRACT

Vision in some ostracods involves a lens (eyespot) of fixed focal length and a tapetal layer. Simply, the eyespot can be considered as a thin converging lens in front of a reflecting spherical segment. To provide a final formed image (real), the eyespot must provide an intermediate image that is proximal to the curved tapetal layer.

The cardinal points of the ostracod's lens-mirror combination can be calculated from the general thick-lens formulas of Jenkins and White (1976). The focal lengths of the eyespot and reflecting layer are substituted, respectively, in place of those for the distal and proximal thick-lens surface. The tapetal layer alone would form a real inverted image, but the addition of the eyespot displaces the image toward the reflecting layer. The shorter the focal length of the eyespot, the closer will be the final image to the reflecting surface and the larger and dimmer will be the final image.

The shortest possible focal length of the eyespot is R, given for an eyespot focal length of the same value. If the focal length of the eyespot is increased, the system focal length would decrease rapidly and approach the value, $R/2$, the focal length of the tapetal layer alone. Because the focal length of the system is within the limits $R/2 \leq f_s \leq R$, the image size can vary by a factor of two.

The illuminance or brightness of the final image with an extended light source has an *f* number or relative aperature of from 0.50 to 0.25, where there is a hemispherical tapetum. The larger value represents the strongest possible converging lens, and the smaller value represents no lens at all. Thus, regardless of the focal length of the eyspot, ostracod eyes seem to be well adapted for efficient viewing of dim extended sources. Ostracod eyes have *f*-values that are among the smallest known for those organisms with eyes.

INTRODUCTION

A common aspect of function in animals is the economical use of energy and materials (Rashevsky, 1961). It implies that ostracods would not develop ocular structures that are useless, but rather they must represent adaptations to the light conditions that prevail in the organism's environment. Further, Lythgoe (1979) wrote that ". . . the laws of physics that govern the behavior of light encompass every aspect of vision; every animal has to function within the same set of rules . . . " Thus, the nature of the ocular structures should be indicative of the usual light conditions. In turn, the structures may be useful in reconstructing some environmental conditions that controlled light in ancient environments (Benson, 1975, 1976).

In this study we examine the geometrical optics of some ostracods that live in the euphotic or disphotic zones of the ocean (Ager, 1963). First we present a model for the limits of vision possible for ostracods with eyespots and tapeta. Then data from actual specimens are compared to the model (Kontrovitz and Myers, 1984; Kontrovitz, in press; Andersson and Nilsson, 1981; Land, 1978, 1981).

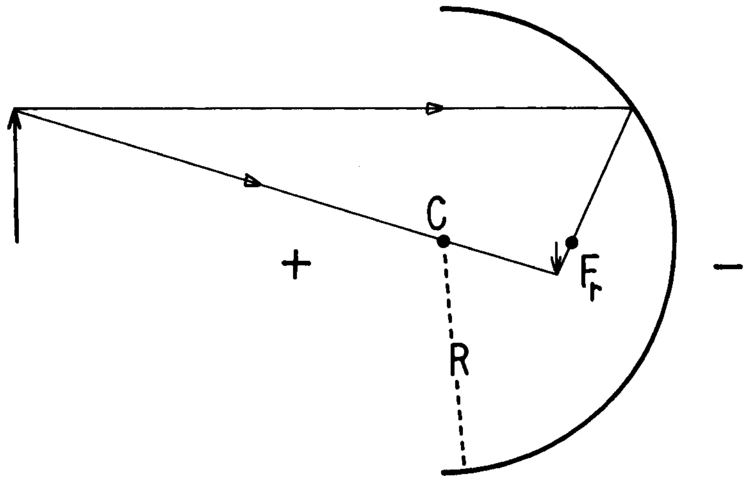
In regard to vision, it must be considered that light intensities diminish rapidly with water depth. In clear oceanic waters, light intensities are reduced by one-half for every 15 m, while in coastal waters, on an average, light is reduced by one-half for every 1.5 m. Downwelling sunlight may be reduced to 1 % at depths of 100 m, even in the clearest water (Clarke and Denton, 1962). It follows that most of the ocean is either dimly lighted or dark, and benthonic and deep-water pelagic forms must adapt to these conditions.

Two evolutionary adaptations are useful in dim light, namely a large aperture and/or a small *f*-value. A large aperture is useful for sensing bright points of light against a dark background. Examples include seeing stars at night and bursts of bioluminescence in an otherwise dark ocean. A small *f*-value is useful for vision in a dim extended light source as with downwelling sunlight in the ocean (Lythgoe, 1979).

METHODS

As a simple model for investigating the ostracod optical system, consider a thin converging lens (eyespot) in front of a reflecting hemispherical segment (tapetum) that resembles a spherical mirror (see Text-fig. 1). In such a system, the lens will form an intermediate image that serves as the object for the mirror. Then, the mirror will form the final image of the system. Note that in this study, all optics terms are from Jenkins and White (1976): capital letters such as "*F*" are used for positions and small letters such as "*f*" are used for distances.

For more detail, consider the spherical mirror equation for the concave reflecting surface alone:



TEXT-FIG. 1—Representation of tapetum (curved surface) and important features. Letter C is centre of curvature; F_r is focal point; R and dashed line depict radius of curvature. Large arrow is object; small inverted arrow is image. Lines with open arrow heads are ray paths. Note sign convention wherein positive (+) is distal to surface vertex, and negative (−) is proximal.

$$\frac{1}{s}+\frac{1}{s'}=\frac{1}{f_r}=\frac{2}{R} \tag{1}$$

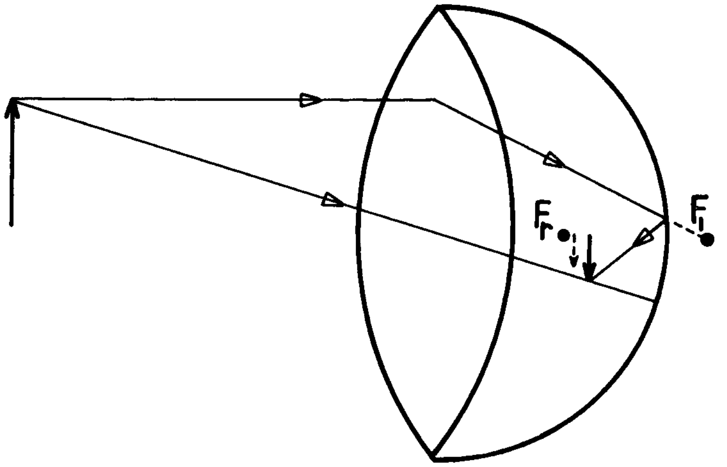
where s is the object distance, s' is the image distance, R is the absolute value of the radius of curvature of the concave mirror and f_r is the focal length of the mirror or reflecting layer. The usual negative sign on R has been incorporated in the equation for simplicity. Focal lengths as well as image and object distances are positive when the corresponding points are distal to the vertex of the mirror (Jenkins and White, 1976).

Solving for the position of the mirror's object (s) in terms of the final image (s') position gives:

$$s=\frac{Rs'}{2s'-R} \tag{2}$$

For the final image to be focused on the sensing cells within the eye cup, distal to the vertex of the reflecting layer, s' must be positive. Also, the value of s' must be less than $R/2$, otherwise a diverging eyespot or having objects closer than an eyespot focal length would be required. Therefore, the denominator of equation 2 is negative so s itself is negative. This means that if a lens (eyespot) is imposed in front of the mirror, any image formed by that lens must be proximal to the vertex of the tapetum. The sign will be negative for the image presented by the lens. If the lens formed an image distal to the tapetum surface (+), the final image formed by the eyespot-tapetum system would be either virtual or distal beyond the lens, and useless for vision.

Image formation for the lens-mirror system is investigated easily by considering the principle rays used in geometrical optics. Text-figure I shows real inverted images would be formed by the reflecting layer alone. These would be located at one focal length (f_r) or farther from the mirror. Text-figure 2 illustrates how a lens would change the images; they would form one focal length or less from the mirror. Therefore, the effect of the lens is to shift the image toward the proximal portion of the tapetum in the eyecup.



TEXT-FIG. 2—Representation of tapetum and eyespot, latter as a biconvex lens. F_r is focal point of tapetum; F_l is focal point of eyespot. Solid lines with open arrow heads are ray paths; dashed line is projected ray path. Large and small solid arrows are object and image, respectively. Small dashed arrow represents an image that would result if eyespot had a longer focal length. Note that eyespot causes image to form closer to tapetum as compared to Text-fig. 1 (without eyespot).

The shorter the focal length of the lens the more the final image will be displaced toward the tapetum and the larger it will be. Images would also be less bright as they are enlarged.

The cardinal points of the eyespot-tapetum combination can be calculated from the general thick-lens formulas (Jenkins and White, 1976). The focal lengths of the eyespot and tapetum must be substituted in place of those for the two refracting surfaces associated with a thick-lens. Observing the sign conventions for lenses and mirrors, the focal length of the system is given by:

$$f_s = \frac{f_r f_l}{f_1 + f_1 - R} \tag{3}$$

where f_s = the focal length of the system, f_r = focal length of tapetum, R is the radius of curvature of the tapetum, which also equals the separation of the lens centre and tapetal vertex, and f_1 = focal length of the eyespot.

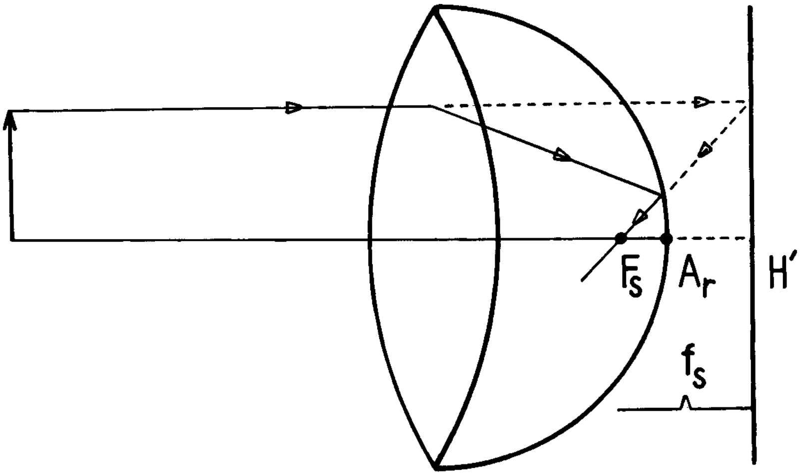
The focal length of the system (f_s) is not measured from the vertex of the tapetum, but rather from the secondary principle plane, H'. The principle plane allows for a simplified description of the function of the system; its location is given by:

$$\overline{A_r H'} = \frac{f_r R}{f_1 + f_r - R} \tag{4}$$

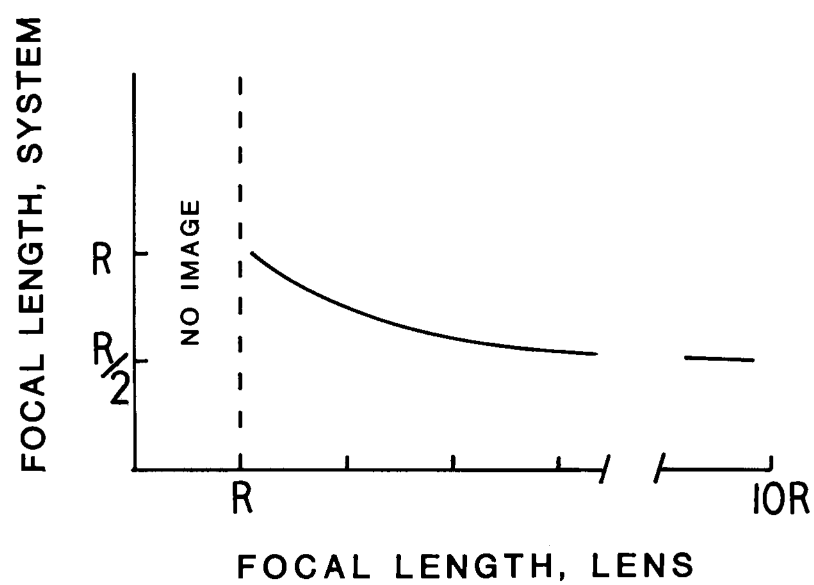
where $\overline{A_r H'}$ is the distance from the vertex (A_r) to the principle plane (H'); it is not the product of A_r and H'. Other terms are defined above and the relationships are shown in Text-fig. 3.

The longest possible focal length of the system is R, given for a lens focal length of the same value. As the focal length of the lens is increased, the system focal length decreases rapidly and asymptotically approaching the value $R/2$, the focal length of the tapetum alone (Text-fig. 4).

The brightness of the final image formed with an extended light source can be determined by the f-value or relative aperture as:



TEXT-FIG. 3—Thick-lens analogy to eyespot-tapetum system. A_r is vertex of tapetum; F_s is the focal point of the system; f_s is the focal length of the system; H' is secondary principle plane, from which f_s is measured. Solid lines with open arrow heads are ray path; dashed lines are projected ray paths. See equation 4 in text.



TEXT-FIG. 4—The effect of the focal length of the eyespot on the focal length of the eyespot-tapetum system. R equals the radius of curvature of the tapetum. The longer the focal length of the eyespot the shorter will be the system focal length.

$$f\text{ value} = \frac{f_s}{D} \tag{5}$$

where f_s is the focal length of the eyspot-tapetum system, and D is the eyespot (aperture) diameter.

RESULTS AND DISCUSSION

The model given describes the limits that could be achieved by an ostracod with eyespots and tapeta. We include data from actual specimens to demonstrate the application to specimens.

If objects imaged by the eyespot-tapetum system are more than several times R distant, as would seem likely, the final image would be formed close to the principle focus of the system (F_s). The final image size will be approximately proportional to the system focal length (f_s). Because the system focal length is within the limits $R/2 \leq f_s \leq R$, the images can vary in size by a factor of two. If the eyespot has a long focal length the image will be smaller and formed well within the eyecup near the focal point of the tapetum (F_r). If the focal length of the eyespot is short, a larger image will be formed closer to the tapetum. It must be remembered that the system focal length is measured from the secondary principle plane.

If the tapetum is hemispherical, the aperture will be equal to $2R$ and the *f*-value limited to the range of 0.50 to 0.25. The former corresponds to the strongest converging eyespot and the latter to an eyespot without any power to converge light. Note that as in any other optical system, the *f*-value does not depend upon the absolute size of the system but rather upon the shape and proportions.

The *f* value depends upon the relative spacing between the eyespot and tapetum, because the aperture is smaller for a closer spacing; however, the effect is not great for similarly shaped segments. For example, if the spacing from eyespot to tapetum is reduced from R to one-half R, the

TABLE 1.
THE *f*-VALUE OF EYES OF VARIOUS ORGANISMS INCLUDING OSTRACODS. AFTER LYTHGOE (1979) EXCEPT AS INDICATED.

Organism	*f*-value	Comments; references
Man	3.30	
Bee	2.40	species not given
Tawny owl	1.30	*Strix aluco*
Fish	1.25	species not given; Land, 1978
Domestic cat	0.90	
Net casting spider	0.58	*Dinopis subrufus*
Ostracode eye model, herein	0.50–0.25	hemispherical tapeta
	0.70–0.30	Spherical segment, more shallow than hemisphere
Ostracods		
Echinocythereis margaritifera (Brady)	0.40	Kontrovitz and Myers, 1984
Notodromas monachus (O. F. Müller)	0.27	Andersson and Nilsson, 1981
Gigantocypris muelleri Skogsberg	0.30	Land, 1978, 1981

aperture is reduced to 87% of its former size. The resulting *f*-value range, now 0.70 to 0.30, is not appreciably different from that for a hemispherical tapetum.

In *Echinocythereis margaritifera* the eyespot is astigmatic, but concentrates most light at about 40 microns, proximal to its inner surface (Kontrovitz and Myers, 1984). The *f*-value is about 0.40, near the upper part of the range of the model given for a hemispheral tapetum. In *Notodromas monachus,* there is a nearly hemispherical tapetum in each lateral eyecup and an eyespot with a broadly curved distal surface and a more convex proximal surface (Andersson and Nilsson, 1981). This shallow fresh water form has an *f*-value of 0.27, which is very close to the smallest value in our model. Land (1978, 1981) showed that the pelagic species *Gigantocypris muelleri* has somewhat parabolic tapetal layers, but eyespots that seem to have little refractive power. The *f*-number is 0.30, very useful at great depths (1000 m) where the form was collected.

Thus, it appears that ostracods are very well adapted for dimly lighted environments (Table 1). Indeed, they are among those organisms with the smallest known *f*-values.

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DISCUSSION

Keyser: Do you believe you have an eye with an indentation or a division of three parts in just one eye-cup? One of your SEM internal moulds shows three projections on top of the "eye-stalk".

Kontrovitz: The undulations in the moulds represent the lobes of each eye cup. There may be two or three lobes per cup in our specimens. The tapetum would be proximal to those lobes and still form a nearly hemispherical reflecting layer.

Keyser: Are you talking about the nauplius eye or the compound eye? You mentioned *Gigantocypris*.

Kontrovitz: Even in *Gigantocypris* there is a well developed tapetum which functions with a cuticle that causes no refraction, as described by Land (1978, 1981). Most of our work has been with the lateral cup of the nauplius eye; we included *Gigantocypris to* show that it, too, has a very small *f*-number. This seems to be the usual condition, regardless of the water depth at which an ostracod may live.

Keyser: Do you think there is an image of an object figured in the nauplius eye? I myself think that the sensory cells of a nauplius eye can only distinguish between light and dark.

Kontrovitz: Probably each rhabdom or pair of rhabdoms can distinguish, light and dark, therefore, they may also be able to detect movement. That is, there may be alternating detection of light and dark among the rhabdoms of a single eye cup.

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The Concept of Cyclicity of Morphogenesis

E. I. Schornikov
Far East Science Centre, Academy of Sciences, Vladivostok, USSR

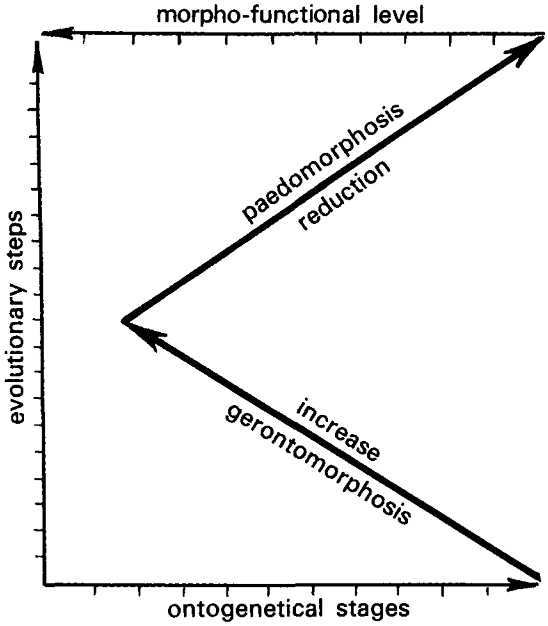
Abstract

The general pattern of phylogenesis of genetically determined positive characters has a two-phase cycle: first the characters evolve to achieve a morpho-functional maximum by means of accelerations (gerontomorphosis) and then reduce through retardations (paedomorphosis). Because of mosaic morphogenesis, each of the characters evolves through this cycle relatively independently. The ontogeny of a number of structures in Bythocytheridae ostracods has been considered from the standpoint of the concept presented and the concept proves to be useful for comparative morphological analysis.

In comparative morphological analysis, the most important point is to ascertain the sequence and direction of transformations of individual structures. The concept presented, which I define as the concept of cyclicity of morphogenesis, renders a great assistance in solving such problems. It generally runs as follows: "The general pattern of phylogenesis of genetically determined positive characters has a two-phase cycle: first the characters evolve to achieve a morpho-functional maximum by means of accelerations (gerontomorphosis) and then reduce through retardations (paedomorphosis)." Genetically determined positive characters imply various structures: organs, their parts, tissues and finally the majority of taxonomic characters except for negative taxonomic characters determined by the absence of structures (which this group of organisms has never had). Intracellular structures are not considered in this context since their evolution is perhaps governed by other regularities. Each of the positive characters evolves through this cycle relatively independently because of mosaic morphogenesis.

Phylembryologic transformations are known (Haeckel, 1866; Mehnert, 1898; Beer de, 1930; Severtzov, 1939; Gould, 1977) to occur due to heterochrony and heterotropy. Increase of structures is accomplished through accelerations. These generally result from the fact that, in the course of development of a structure, new stages (positive anabolies after Severtzov) are added at every evolutionary step and the time of a structure's introduction is shifted to earlier and earlier stages in the ontogeny of an organism. This produces an image of gerontomorphosis when the structure of a juvenile descendant proves to be similar to that of an adult ancestor. Thus, it produces the picture of recapitulation which is described by the "biogenetic law" of Müller-Haeckel.

Decrease (successive imperfection) of structures is accomplished through retardations. They generally result from the fact that final stages in the ontogeny of structures are dropped at every evolutionary step of reduction. The deletion of final stages of a structure's development causes the



TEXT-FIG. 1—Morphogenetic cycle scheme.

time of its introduction to shift to later and later stages in the ontogeny of an organism. Severtzov defines the reduction accomplished in such a way as rudimentation.* This gives a picture of paedomorphosis when the structure of an adult descendent proves to be similar to that of a juvenile ancestor. The stages in ontogeny of a structure prove to be similar to those anticipated in adult descendants if the reduction in further phylogeny is accomplished at the expense of rudimentation. Thus it reveals the prediction of development, anticipation in the sense of Schindewolf (1950), which he contrasts to recapitulation. In phylogenetic transformations of this type, the information about the final stages of the former increase of a structure is lacking in the phenotype. However, it does not seem to disappear from the genotype judging by the cases of atavism and the occurrence of atavistic features in the regeneration of structures. Here the information is impressed in the phenotype rather than deleted.

To make further analysis easier let us consider the following evolutionary model of a hypothetical structure (Text-fig. 1). Let us assume that the structure made its appearance as a new feature in the final stage of ontogeny. It is affected by natural selection during an indefinitely long period of time and in an imperceptibly changing environment, with the organism and its successive descendants possessing a lot of other evolving structures.

Under conditions of positive natural selection the structure is increasing. Newer and newer stages of its development are added and its introduction is shifted to earlier and earlier stages in ontogeny. Thus, in the first phase of the morphogenetic cycle, morpho-functional characters of the developing structure evolve to achieve a maximum possible for the given group.

However, the probability exists (and hence the tendency as well) that this positive selection may be replaced by a negative one. This may arise due to environmental fluctuations so that the need for the structure to function will disappear. Besides this, in a stable environment another structure may emerge which functions better than the previous one. The structure then continues to

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* He focuses, however, on the changes arising at early stages in the ontogeny of structures.

evolve through reduction at the expense of rudimentation. At every evolutionary step the structure appears to be more and more successively imperfect as its final stages of development are dropped and its introduction is shifted to later and later stages in ontogeny. In the long run the structure is completely eliminated Hence, the complete cycle of morphogenesis of a structure, from introduction to deletion, has two phases. The successive evolution of a structure through both phases in the cycle of morphogenesis is regular.

In addition to rudimentation, there are two more ways in which structures are reduced: fusion and aphanisis (Severtzov, 1939). Aphanisis is the retrogressive development of a structure at a certain point in ontogeny (for example, the reduction of tail and gills in amphibian larvae). Aphanisis is also defined an negative anaboly by Severtzov. In fact, it implies just the same additional stages in the development of a structure. They cause the formation of new structures by means of merging senile ones (fusion) or their reverse development (aphanisis) rather than by their morpho-functional increase. While a structure evolves through the cycle of morphogenesis, it submits to the same regulation as at any other stage of its development. With the increase of the character for which fusion and aphanisis are responsible, the beginning of fusion and aphanisis is shifted to earlier and earlier stages of ontogeny; with the decrease of the character, the beginning of fusion or aphanisis is shifted to later and later stages of ontogeny. Here we encounter the reduction of reduction so to speak. For example, neoteny in its classical sense (axolotl) should be regarded as the reduction through rudimentation of reduction of gills by means of aphanisis. That is, the stage which must have caused the reduction of gills of sexually mature individuals has dropped out of ontogeny.

The reduction through rudimentation is regular and retrogressive as to the sequence of formation of structures during ontogeny of an ancestral group. This is responsible for producing a good deal of parallelism in descendant groups. Particularly large series of parallelisms and gradations are produced in the course of reduction of serial structures in descendant groups.

Every specialist can probably cite many examples from the group of organisms he studies indicating some gaps in the morphogenetic cycle of different structures: increase through addition of terminal stages and reduction through rudimentation. The above elaborated model in its pure form, however, is unlikely to be found in nature. Real situations are generally more complex.

First of all heterochrony (varying or different timing) results not only from shifting the time of introduction of a structure, but from changing the rates of its histogenetic transformations and growth as well.

It is unreasonable to regard an organism's sexual maturity as absolute. It is not the reproductive stage alone that evolves but the whole organism at all the stages of its complex life cycle. New features may be introduced at any stage of ontogeny and new stages of a structure's development may emerge in any period of its ontogeny (deviation, archallaxis after Severtzov). An evolving group partly retains its structures over an extremely long period of time. The pattern of its morphogenesis may be an extremely complex zigzag. Periods of increase may be repeatedly followed by periods of decrease of structures. It may also retain stability during fairly long periods of time or in a vast number of descendant groups. One may then speak of bradygenesis or of the advance in organization of a recent group, if those are the basis of a system.

In the course of evolution, a developing structure may undertake a great number of evolutionary steps more or less towards the close of the cycle. It may enter a trap of fusion and aphanisis on its way and drop out of ontogeny without having attained its complete "natural" development. The evolving structure is often affected by opposite processes: displacement of its introduction to an earlier stage accompanied by retardation of development, and vice versa: fluctuation of growth and transformation rate during ontogeny; reduction through aphanisis of some parts of a structure with the rest continuing to develop, etc. This makes the picture of phylembryogenesis rather tangled and its analysis rather difficult. Yet, the suggested concept of cyclicity of morphogenesis helps us to understand better these rather tangled situations.

In this respect we consider some examples of phylembryogenetic transformations of structures in ostracodology. Morphological evolution is mosaic due to heterochronous evolution of all the organs of a complex multicellular organism. While studying heterochronies, one should first of all choose a scale of ontogeny for the organism as a whole, relative to which one might estimate displacements in development of the various organs. Yet, it is hard to find such "objective points of standardization" since in the evolution of any organ, or of any system of organs regarded as standard in the group of organisms being studied, heterochrony may also occur.

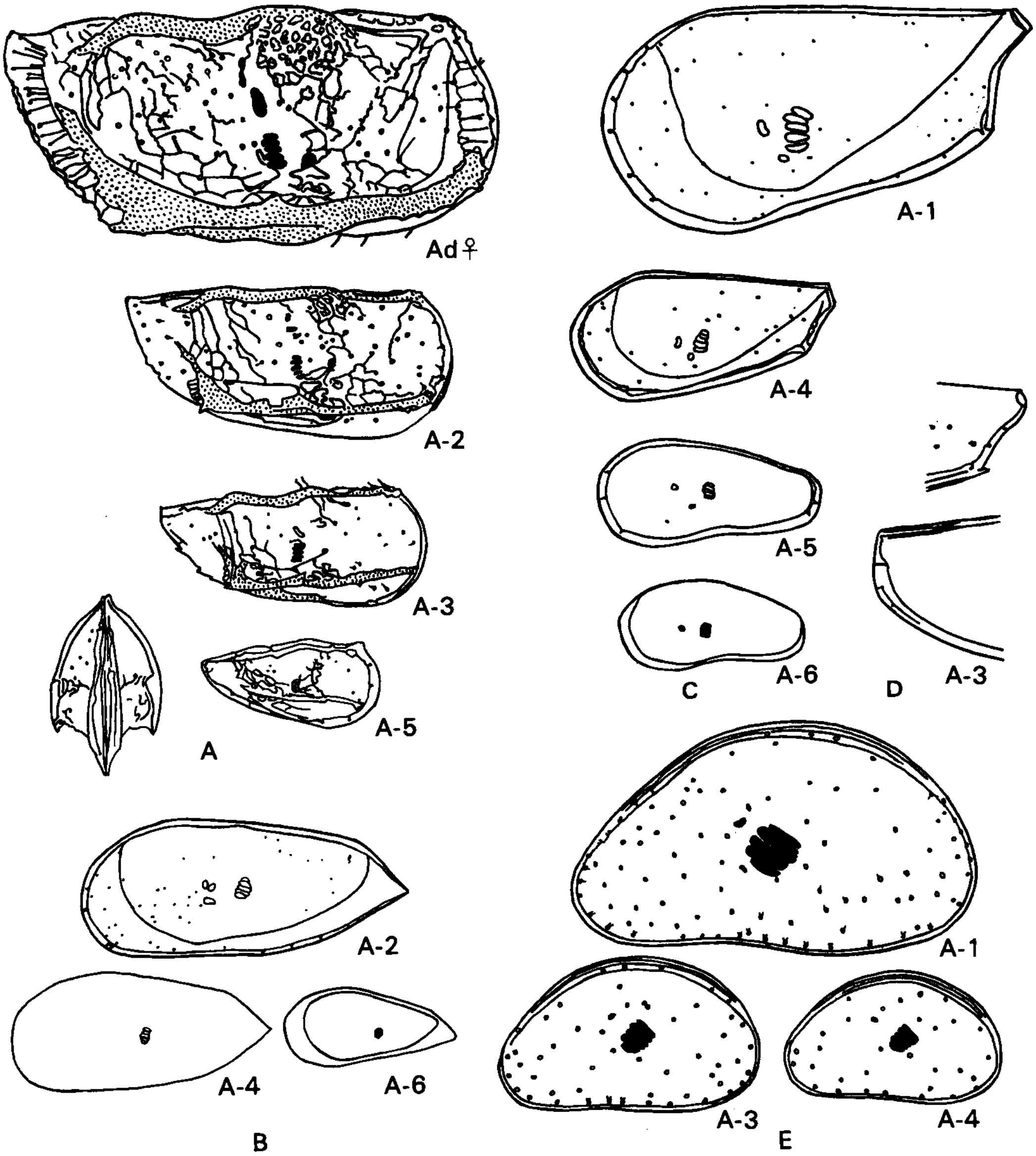
Ostracods are particularly convenient to study since adult individuals do not moult and each group has a definite number of instars. This simplifies the comparison of the structures studied at strictly fixed stages of ontogeny.

The ontogeny of the Bythocytheridae has been studied in detail (Schornikov, 1981, 1982b). The ontogeny of even rather similar forms of ostracods was found to be characterised by plenty of heterochrony. In a number of cases, the instars of species compared differed from one other to a greater extent than the adults at certain stages of development. In the evolutionary peculiarities of individual structures, one may find both recapitulations, throwing light upon the phylogenetic history of formation of structures, and anticipations indications of possible pattern of reduction through the excision of terminal stages. With regard to comparative morphology, the analysis of abnormalities which are found is also of a particular interest.

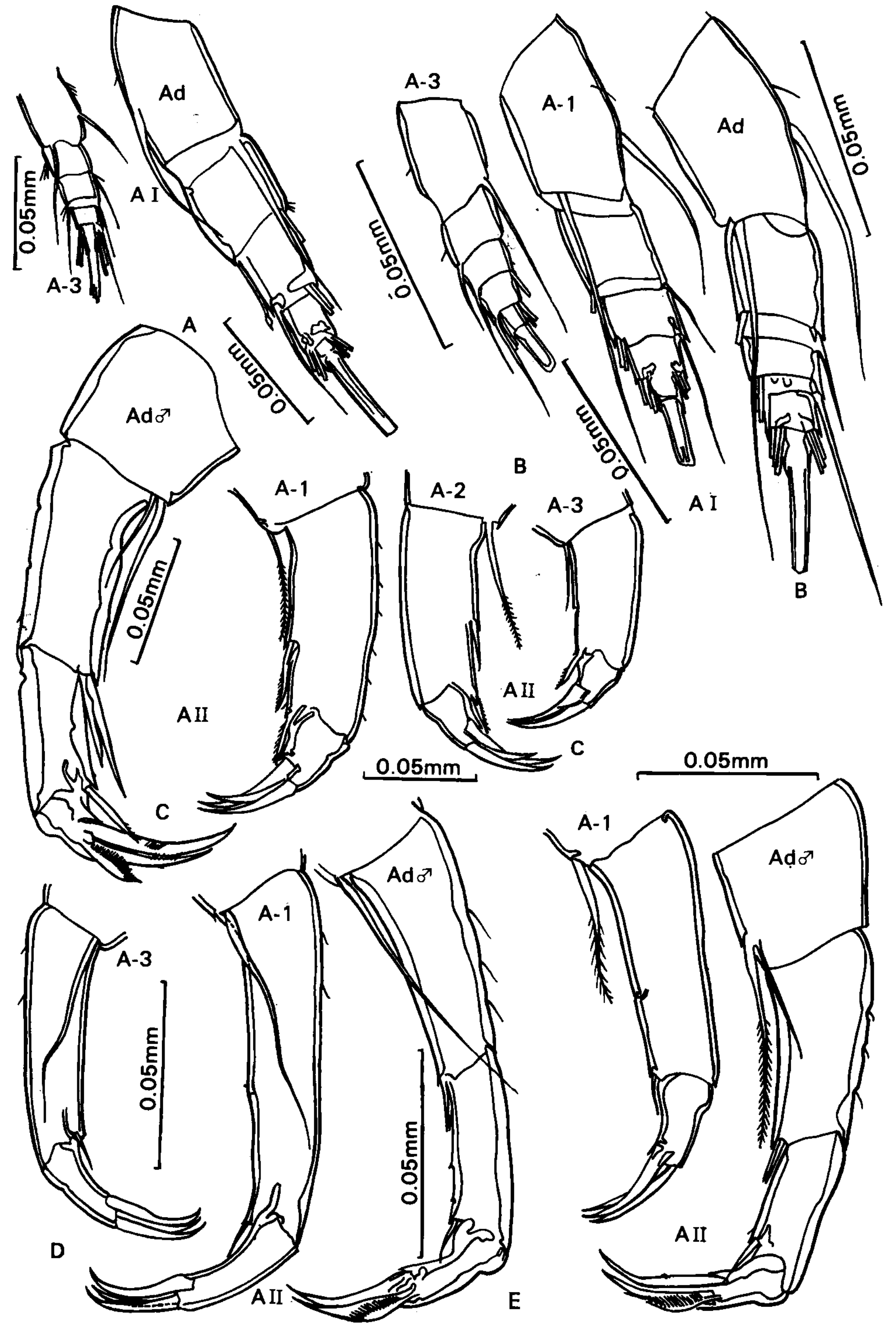
Shell shape

The majority of larval shells in the Podocopida are known to have a triangular shape (Hartmann, 1966–1975; Schornikov, 1981). Eggs of some species already acquire a triangular shape in the final stages of development and yield instars with a triangular shell. The majority of species have eggs, or at least nauplius and sometimes the A-7 stage of a rounded shape. A triangular shape emerges and is conspicuous only in successive instars; in final instars shells assume shapes resembling the outlines of adult animals. The evolution of the Podocopida through the specific stage of ontogeny which consists of the assumption of a triangular shape and its successive loss, does not result from the peculiarities of the animal's morphology and ecology. For example, Philomedinae, Bairdiidae and Cytheruridae may be found living together, yet the first one never has a triangular shell, the second one hatches in triangular form but loses this shape after the second ecdysis, and the third one only reaches a triangular shape during the analogous ecdysis and retains it until nearly the adult state. In this case we seem to encounter recapitulation showing that the ancestors of the Podocopida had a triangular shell, but we have no evidence to prove the hypothesis since the early evolution of the Podocopida is practically unknown.

It seems that shells of the Bythocytheridae have a rounded shape in their early instars, as do the Cytheracea investigated in this respect. According to the evidence obtained, (Szczechura, 1964; Herrig, 1967; Schornikov, 1981, 1982a, b) larval shells of Jonesini and Bythocytherini have a triangular shape by at least the A-6 stage and retain it until nearly the adult state (Text-figs. 2A, B). Due to heterochrony, the appearance of this character in the Pseudocytherini shifted to the A-5 stage (Text-fig. 2C), and in the Sclerochilini it was completely eliminated from ontogeny (Text-fig. 2E). Shell shapes of adult Sclerochilini resemble the earliest hatched instars of other Cytheracea (paedomorphosis). It is worth mentioning that the shells of adult Sclerochilini are more reniform than rounded. The rounded shape in the early instars was only a pre-adaptation to reach the reniform shell characteristic of adult Sclerochilini. This is one of the most rational shell configurations from the viewpoint of mechanical strength and conformity to a body shape. A reniform shell



Text-fig. 2—Shell shape transformations in the ontogeny of the Bythocytheridae.
A, *Nodobythere nodosa* Schornikov, 1981; B, *Jonesia camtschatica* Schornikov, 1981; C, *Pseudocythere moneroni* Schornikov, 1981; D, *Pseudocythere similis* Müller, 1908 (right and left valve posterior edges of an abnormal instar); E, *Convexochilus meridionalis* (Müller, 1908) (A–C, after Schornikov, 1981; D, E, after Schornikov, 1982b). Abbreviations: Ad, adult; A-1, A-6, instars.



Text-fig. 3—Sclerochilini antennule (AI) and antenna (AII) ontogeny.
A, C, *Sclerochilus* (*Praesclerochilus*) *kerguelensis* Schornikov, 1982; B, D, *Convexochilus meridionalis* (Müller, 1908); E, *Convexochilus compressus* (Müller, 1908) (after Schornikov, 1982b). For abbreviations see Text-fig. 2.

developed successively through the addition of new stages of development which appear within a tribe also due to heterochrony.

The abnormal A-3 instar of *Pseudocythere similis* Müller, 1908 investigated by Schornikov (1982b) has a normally developed left valve (equipped with a ventracaudal spine), and a right valve analogous to that of the A-5 instar in the shape of the rounded posterior border (Text-fig. 2D). Analogous heterochrony during the transformation of originally symmetrical structures may be regarded as one of the mechanisms of asymmetrical evolution through paedomorphosis.

Antennule

Among the Cytheracea there are a good many families and genera which have a reduced number of true podomeres in the antennule as compared with the Bythocytheridae. In such cases the two penultimate podomeres are only incompletely segmented or not segmented at all. These are the very podomeres which are the last to be segmented in the Sclerochilini. Thus, parallel evolution by means of paedomorphosis occurs here.

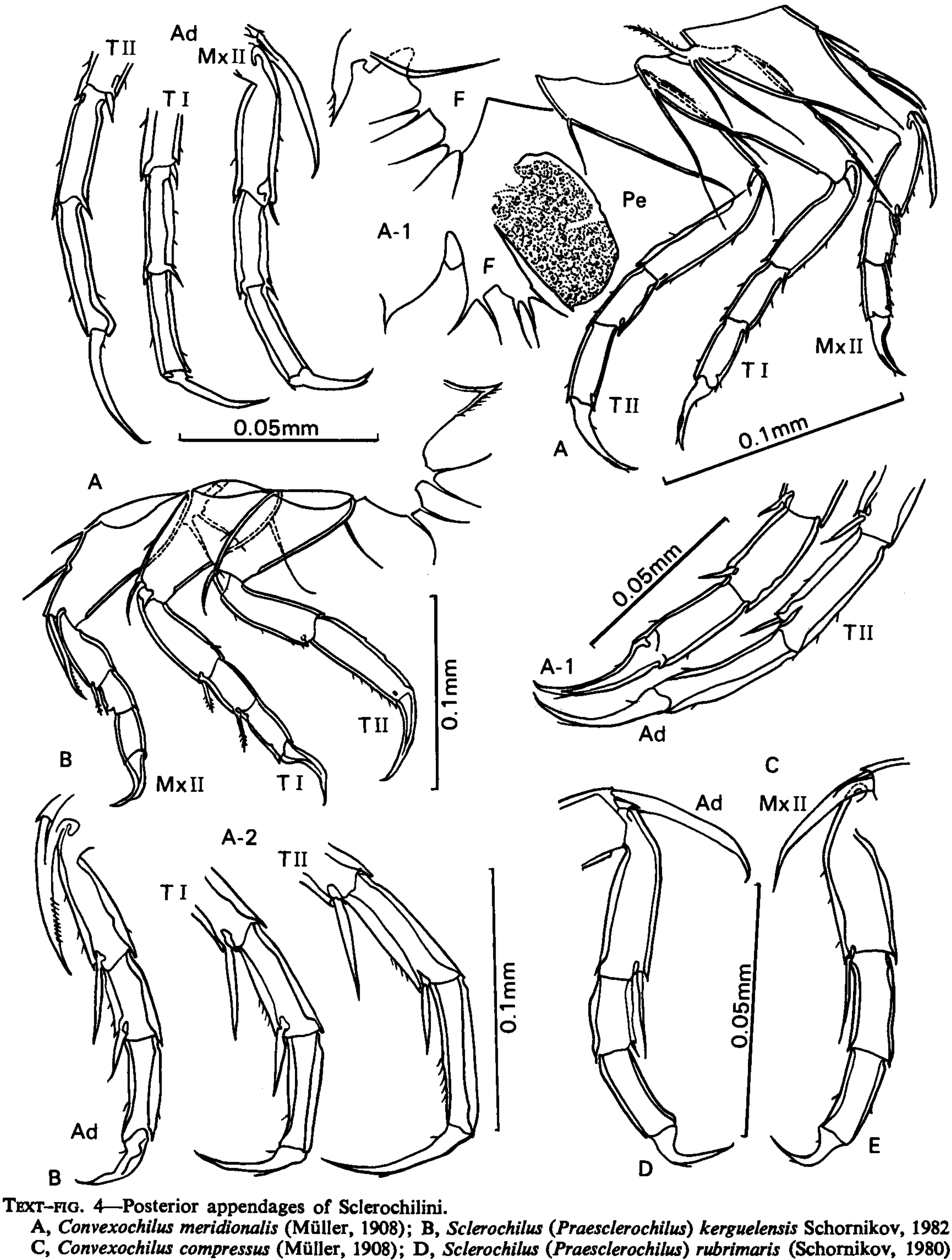
Heterochronies are found in the development of the dorsomedial seta of the second podomere (Text-figs. 3A, B). *Sclerochilus* (*Praesclerochilus*) *kerguelensis* Schornikov, 1982 have it in an anlage in the A-4 instars, and at the A-3 stage it becomes conspicuous. In the *Convexochilus* instars, it emerges only at the A-2 stage, but in a quite conspicuous rather than a small anlage form. It develops further at a faster rate and becomes much larger in adult *Convexochilus* than in *S.* (*P.*) *kerguelensis.* This case implies the violation of Mehnert's law as a result of two contrary processes overlapping: a retardation process implying a backward shift of an organ's anlage, and an acceleration process implying the appearance immediately of a large seta and successive accelerated development.

Antenna (Text-figs. 3C, D, E)

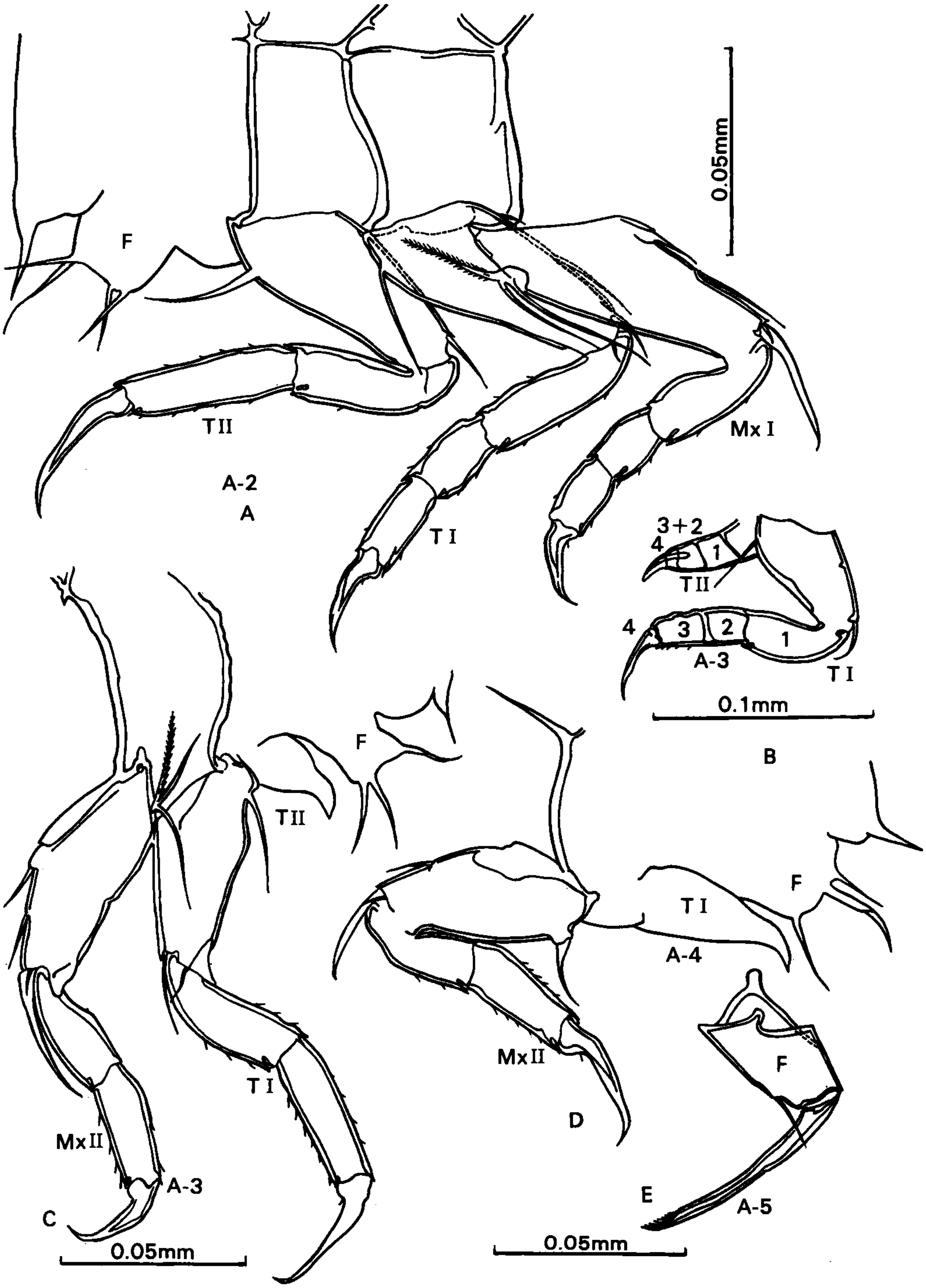
Sclerochilini instars have this appendage equipped with only two apical claws up to the A-4 stage. *Convexochilus* instars already have a rather long third (intermediate) claw at the A-3 stage, and *S.* (*P.*) *kerguelensis* have only its small anlage. It continues to increase at a faster rate than that of *Convexochilus,* and their relative size becomes equal at the close of development.

The pattern of development of ventrodistal setae of the endopidite's second podomere is in accordance with Mehnert's assumption that the displacement of an organ's appearance to a later stage of ontogeny testifies to the beginning of its reduction. Thus, the seta homologues of the endopodite second podomere emerge earlier in the ontogeny of *S.* (*P.*) *kerguelensis* than in that of *Convexochilus,* and it appears to be much longer in adults. The internal seta of *S.* (*P.*) *kerguelensis* emerges later than the external one and it appears to be shorter in adults. In *Convexochilus* both setae emerge simultaneously and appear to be equal in size in adults. A good many Bythocytheridae have the first podomere of the endopodite equipped with two ventrodistal setae. The internal one emerges only at the adult stage and is always shorter than the external one. Yet some of the Bythocytheridae have only one seta here, the internal one having failed to emerge because of paedomorphosis. Among them, however, abnormal forms with both setae are found (atavism).

Many adult representatives of different groups of Cytheracea which underwent the reduction of armament and segmentation of antennal endopodite, appear to be similar in certain characters to various instars of Bythocytheridae. Thus, *Cytheromorpha, Microcytherura,* Leptocytheridae, *Cytheroma,* a good many of the Loxoconchidae, and some of the Cytheruridae and Paradoxostomatidae have only 2 apical claws like the A-4 instars of the Sclerochilini. *Cythere, Schizocythere* and a good many of the Cytheruridae, Xestoleberididae and Microcytheridae have a rudiment of the 3rd apical claw like the A-3 instars of *S.* (*P.*) *kerguelensis.* In the Loxoconchidae, Bythocytherinae and Jonesiinae, the 2nd podomere is not segmented into two parts as in the A-1



TEXT-FIG. 4—Posterior appendages of Sclerochilini.
A, *Convexochilus meridionalis* (Müller, 1908); B, *Sclerochilus* (*Praesclerochilus*) *kerguelensis* Schornikov, 1982; C, *Convexochilus compressus* (Müller, 1908); D, *Sclerochilus* (*Praesclerochilus*) *rubrimaris* (Schornikov, 1980); E, *Sclerochilus* (*Praesclerochilus*) *rectomarginatus* (Hartmann, 1964) (A–C, after Schornikov, 1982b; D, E, after Schornikov, 1980). Abbreviations: Mx II, maxilla; T I, T II, thoracopods; F, furca; Pe, pennis anlage; for the rest see Text-fig. 2.



TEXT-FIG. 5—Ontogeny of the posterior appendages of Sclerochilini.
A, C–E, *Convexochilus meridionalis* (Müller, 1908); B, *Sclerochilus* (*Praesclerochilus*) *kerguelensis* Schornikov, 1982; (before an ecdysis the homologues of the exopod podomeres which develop inside thoracopod anlages are distinct; after Schornikov, 1982b). Abbreviations: I-4, podomere homologues; for the rest see Text-figs. 2, 4.

instars of the Sclerochilini. Thus, a lot of parallelisms exist as a result of evolution through paedomorphosis.

Maxilla and Thoracopods (Text-figs. 4, 5)

Maxilla and thoracopods of adult specimens of the Sclerochilini investigated are armed identically and evolve synchronously up to the A-3 instar. Yet, at the A-2 and A-1 stages they are subject to heterochrony due to which instars at the same stage differ to a great extent. In the *Convexochilus compressus* (Müller, 1908) and *S.* (*P.*) *kerguelensis* of the A-2 stage, there emerges a seta on the 1st podomere of he maxilla exopodite and on two proximal podomeres of the I thoracopod, while at the A-1 stage these appendages are armed as those of adult individuals. In *Convexochilus meridionalis* (Müller, 1908) these setae emerge only at the A-1 stage, and simultaneously on two proximal podomeres of the maxilla and I thoracopod; on the II thoracopod they are encountered only in adults. Other variants of similar heterochronies are also possible. Thus, among tropical *Sclerochilus* species are known which have a reduced seta of the 2nd podomere of maxilla and both thoracopods (Text-figs. 4D, E).

In the development of maxilla and thoracopods, the transformation pattern of the terminal (4th) exopodite podomere is of a particular interest. This podomere, though minute in size, is conspicuous in the majority of adult Podocopida. The Cytheracea with rare exceptions (Psammocytheridae) lack it. As shown in Text-fig. 5B, in Sclerochilini instars just before ecdysis, the 4th podomere homologue can be distinguished under the integument of the corresponding appendage anlage. After ecdysis an appendage equipped with a 2-podomere exopodite is formed. The lack of the 4th podomere is linked more with the addition of a new stage in the development of the appendage causing the podomere to fuse with a claw (immobilization), than with the extinction of the final stage. Some Cytheracea, the Pseudocytherini in particular, have a rather distinct homologue of this podomere in the form of a bulb at the basal part of a claw with a short ventrodistal seta. In the majority of the superfamily representatives the margin of fusion is hard to establish. The podomere immobilization seems to have proceeded in parallel in different groups of Podocopida. In *Neonesidea frequens* (Müller, 1984), at least, the podomere fused with the claw independently of the Cytheracea.

Furca

In the Podocopida this undergoes a two-stage development. In the A-5 instar, the furca is the only locomotor organ in the posterior part of the body. It is leg-like and consists of 2 podomeres when highly developed (Macrocyprididae, Bairdiidae, *Isocypris*). It seems that the furca in this early instar should be regarded not only as cenogenesis, but also as an initial furca homologue in Ostracoda (palingenesis).

In all the Sclerochilini investigated furca develops in a similar way (Text-figs. 4A, B; Text-figs. 5A, C–E). In the A-5 instar it is strongly chitinized and resembles an appendage podomere with a large apical claw directed forward. While reaching the A-4 instar, the furca is abruptly transformed. From that moment the furca develops in two opposite directions; on the one hand, there is the reverse development (aphanisis) of the morphological elements of a leg-like furca on the other hand, the rest of the structure developing to form a lamelliform furca. Yet, in the Bythocytheridae it is not so well developed as in the Myodocopida or Cytherellacea, developing only through the initial stages of formation and turning out to be successively imperfect in regard to them (paedomorphosis). In the male Pseudocytherini, unlike the female, one more special stage is added in the development of the furca. After the last ecdysis, the front lobe of the furca extends considerably and the furca becomes rod-like. Such a furca, however, has nothing in common with the true rod-like furca of the Cypridacea and Bairdiacea.

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Ontogeny of *Bradleya normani* (Brady): Shape Analysis of Landmarks

ROGER L. KAESLER AND DAVID W. FOSTER
The University of Kansas, Lawrence, U.S.A.

ABSTRACT

The choice of a method of shape analysis is limited by the purpose of the research to which the method is to be applied. Three areas of investigation to which shape analysis lends itself are describing morphology; studying environmental, geographical, or stratigraphical change of morphology; and comparing similarity of morphology. Selection of a method is further dependent on whether the shapes of the objects being studied are defined by homologous landmarks or are defined by outlines. We encourage investigators first to ask biologically important questions and then to select the appropriate method of shape analysis. Although these caveats may seem unnecessary, we believe that too little attention has been directed toward applications in the rush to develop new methodologies.

Bradleya normani (Brady) is unusual among species of its genus because it lives in relatively shallow water. Its study may provide a better understanding of deep-water species of *Bradleya* that have been used extensively in paleoceanography. Our understanding of the evolution of ostracodes in general would be enhanced by investigation of heterochrony, but especially little is known of the ontogeny of deep-sea ostracodes because their immature instars are comparatively rare. Homologous landmarks on the carapaces of adults and five instars of *B. normani* (Brady) were studied by traditional multivariate morphometric methods that are orientated toward graphical representation of results, by tensor analysis, and by robust regression analysis. Multivariate discriminant function analysis and ordination by nonmetric multidimensional scaling provide useful graphical summaries of overall morphological difference, but they do not show directly in which areas of the carapace the change occurs. Tensor analysis gives a useful graphic and quantitative impression of ontogenetic changes of shape of regions of the carapace that are bounded by landmarks. Robust regression analysis focuses attention on changes of the relative positions of the landmarks themselves rather than on changes of shape of the regions bounded by landmarks. It also provides a numerical estimate of change between selected pairs of indivials, the average residual length. In general, different methods of analysis showed the same progressive change of shape from the youngest instar, A–5, to the adult, but the results of the methods also differed in minor ways. The greatest ontogenetic change in the location of the landmarks occurred in the growth from instars A-4 to A-3, and from instars A-3 to A-2. Sexual dimorphism is apparent but not pronounced among adults of *B. normani* (Brady). Few males were found, however, and dimorphism was not detected with the measurements taken. In choosing a method, one should bear in mind that results of analysis of shapes are most easily interpreted when they lend themselves to production of simple graphs.

INTRODUCTION

In a little book on Christian evangelism, theologian Harvie Conn (1982) of Westminster Theological Seminary included a chapter that asked, "If Jesus is the answer, what are the questions?" Today, as a result of explosive advances in computer technology and digitizing and their applications to micropaleontology, we are faced with a question that can be phrased similarly to Conn's: "If quantitative analysis of shape is the answer, what are the questions?" We stress applications of this new technology to micropaleontology because the rigid form of most of our material ensures a microfossil will have a consistent shape from one time to the next and because in most instances that shape is closely similar to the shape of the living organism. Biologists who deal with soft-bodied organisms do not have this assurance. As a result, they face obstacles to quantitative analysis of shape that sometimes seem insurmountable. Nevertheless, with some limitations and some modifications, the techniques many micropaleontologists now use to analyze shapes quantitatively can be applied to a broad range of biological problems as well. Because this is true, it follows that the need to decide what questions such techniques can help us answer is a concern of scientists in general and does not pertain to micropaleontology alone.

What can quantitative analysis of shape show us that mere visual examination of specimens cannot? Answers may range from "very little" to "a great deal." The methods of quantitative analysis of shape that have been used by micropaleontologists are able to describe morphology, to express the change of morphology, and to measure the similarity of morphology. Of course, different techniques are suited to different goals. Emphasis of most researchers during the early, developmental stage of quantitative analysis of shape, however, has been on techniques rather than on testing hypotheses (see, *e.g.*, Kaesler and Waters, 1972). As a result, disagreement has sometimes arisen over which method is best (Bookstein *et al.*, 1982; Ehrlich *et al.*, 1981), whereas in fact each method has both strengths and weaknesses that typically depend on the biological questions being asked.

As interest in quantitative analysis of shape grows, the number and kinds of applications will increase. At present, however, uses of shape analysis to solve micropalenotological problems can be grouped into three broad categories: quantitative taxonomy of morphologically intractable forms, studies of evolution, and population biology of fossil assemblages. Despite the spirited interest that phenetic or numerical taxonomy engendered in the 1960's and early 1970's (Sokal and Sneath, 1963; Sneath and Sokal, 1973), today one finds few classifications based solely on phenetics. Instead, the techniques of numerical taxonomy have been subsumed under the broader category of *quantitative morphology* or *multivariate morphometrics* (Reyment *et al.*, 1984). Nevertheless, the methods developed by numerical taxonomists are applicable to a wide variety of problems irrespective of whether the ultimate goal is a phenetic taxonomic classification.

The current interest in quantitative analysis of shape and the new developments in the field presage a new phenetic taxonomy. If such a new phenetic taxonomy develops, it is likely to be based on those methods of shape analysis that are best suited for measuring similarity of morphology, such as traditional methods of multivariate morphometrics (Reyment *et al.*, 1984) or harmonic distance analysis (Kaesler and Maddocks, in press), rather than on methods that are better suited for describing morphology or showing change in morphology. Moreover, analysis of shape will have its greatest impact in the study of groups of organisms in which homologies are difficult to establish or in which suitable morphological characters are not abundant. Among the microfossil groups that come to mind are such unornamented ostracodes as the marine macrocypridids, the freshwater cypridaceans in general, and the exclusively marine bairdiaceans, cytherellids, and krithids.

As a result of the development of the punctuation model of evolution (Eldredge and Gould, 1972, 1977; Gould and Eldredge, 1977) and Gould's work on the importance of heterochrony in the relationship between ontogeny and evolution (Gould, 1977, see also Alberch *et al.*, 1979), renewed interest in the phenomena of evolution has swept paleonotology. Paleontologists have been made aware, for the first time in decades, that they may be able to contribute to an understanding of the mechanisms of evolution rather than merely to document the fact of evolution (Stanley, 1979). One approach to the study of heterochrony implied by Gould's (1977) clock model of heterochrony is quantification of the change of morphology through ontogeny. Shape analysis is uniquely suited for expressing ontogenetic shape change quantitatively. Such methods as robust regression analysis (Benson *et al.*, 1982; Siegel and Benson, 1982) and tensor analysis (Bookstein, 1978) can be applied to this kind of study if suitable homologous landmarks are available (see, *e.g.*, Okada, 1982). Outlines can be evaluated by eigenshape analysis (Lohmann, 1983), which operates without specific landmarks and uses, instead, a kind of geometrical homology. One looks forward to the results of the melding of these two approaches, which could be done if geometrically homologous points were regarded as homologous landmarks.

Almost since its inception, population ecology has been so quantitative and so devoted to model building that its theorems, although often of considerable heuristic value, have typically had little to say about the real world. This is especially true for those mathematical models in which assumptions have been introduced to improve mathematical tractability at the expense of biological realism. But if theoretical population ecology has been difficult to relate to field ecology and natural history, it has been impossible to relate to paleoecology. There is scarcely a field of study that could be called population paleoecology. Even to begin to apply the models of the theoretical population ecologists requires that one be able to estimate realistically such parameters of populations as fecundity, intrinsic rate of increase, and carrying capacity. Paleoecologists, however, are rarely able to establish convincingly that two fossils found together actually lived in the same place or at the same time. How much less, then, can they test applicability of theoretical models that require nearly full knowledge of the biology of the organisms being studied? As a result, what has passed for population paleoecology has been study of population dynamics and survivorship of time-averaged assemblages of fossils that may have been ravaged by taphonomic processes. It is unlikely that shape analysis will improve the chances of paleoecologists to hold up their heads among population ecologists. We can, however, expect it to contribute importantly to the emergence of another kind of population paleoecology, one that is based on the study of stratigraphical or geographical variation of morphology. Methods of automatically digitizing shapes are becoming an integral part of shape analysis. Their introduction has motivated paleontologists to measure enough morphological characters on enough individual specimens to provide statistically meaningful measures of morphological difference (Healy-Williams and Williams, 1981). Mere demonstration of statistically significant difference in morphology of different statistical or biological populations is not enough, however. Of course the morphology of organisms from two conspecific populations separated perhaps by the passage of millions of years of geological time differs significantly. Statistical theory tells us that parametric differences are always significant, and if we have not found statistically significant differences between such populations we have simply not looked hard enough. Larger samples are indicated, and one need only increase sample size to the point where statistically significant differences can be demonstrated (Sokal and Rohlf, 1981, p. 262). Progress in the new population paleoecology will come about when one is able to detect *biologically* significant differences in morphology, not merely statistically significant ones, and to identify the causes of such ecophenotypic variation in morphology. For such work to be productive, one needs to understand better the degree of variation within a species or within a biological population to help determine what magnitude of difference is biologically significant for the specimens being studied.

MORPHOLOGY OF *Bradleya normani*

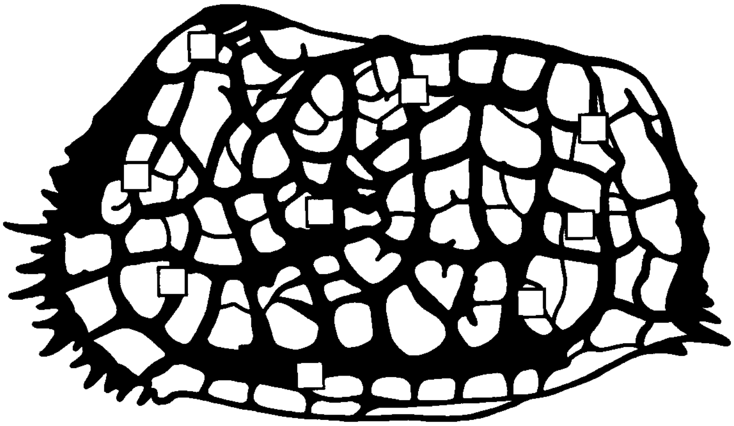
In the first part of our paper we have dealt primarily with generalities about shape analysis. Now we want to get down to specifics of the ontogeny of *Bradelya normani* (Brady) (Text-fig. 1). One of the distinguishing characteristics of B. *normani* (Brady) is its morphological variability. In addition to sexual diomorphism, the reticulum varies widely. In some adult specimens, the reticulum is quite coarse, and individual fossae are large and partially subdivided by one or two minor ridges, forming a kind of secondary reticulation. On others, the homologs of the minor ridges are strongly developed, resulting in a finer meshed reticulum without secondary reticulation. Whether the morphological variability of *B. normani* (Brady) is in response to differences in the environment is now under investigation.

We have made two approaches to the morphology of *Bradleya normani* (Brady). First, we have analyzed the change of shape during ontogeny independently of size by normalizing all specimens for size. Second, we have compared the results of several methods of shape analysis. We hope to demonstrate that on the basis of the morphological characters we studied, little change in shape occurs among the last three instars, including the adult. Moreover, the shape of the A-5 instar is more closely similar to that of the adult than the A-4 or A-3 instars, although this conclusion must be regarded as tentative because of small sample sizes of some of the early instars. Traditional methods of multivariate morphometrics, including cluster analysis (Sokal and Sneath, 1963; Kaesler, 1966), multivariate discriminant analysis (Reyment *et al.,* 1984; Foster and Kaesler, 1983), and nonmetric mutidimensional scaling (Kruskal, 1964a, b; Peterson and Kaesler, 1980), are useful because they provide the means for preparing simple, graphic summaries of quantitative results. They give a good impression of populations as a whole. Such newer, less tried-and-true methods as resistant-fit regression analysis (Benson, 1982; Siegel, 1982a, b; Siegel and Benson, 1982) and tensor analysis (Bookstein, 1987, 1982; Strauss and Bookstein, 1982) focus, instead, on morphology of individuals rather than on populations. These methods seem to be more useful for comparing individuals than for summarizing populations as a whole and are especially well suited for determining the biological effects of differential growth and changing loci of growth during ontogeny.

Why study *Bradleya normani?* Species of the genus *Bradleya* typically live in the deep sea. Because of the highly ornamented morphology of their carapaces and a few other accidents of micropaleontological history, they have been used extensively to help decipher the paleoceanographic history of the deep sea (Benson and Sylvester-Bradley, 1971; Benson, 1972, 1982; Whatley *et al.,* 1983). Unfortunately, because *Bradleya* is largely restricted to the deep sea, sample sizes from specific localities are likely to be small. This comparative rarity has precluded the study of species of *Bradleya* in a way consistent with what we have described as the new population paleoecology.

Bradleya normani (Text-fig. 1) offers some relief from the constraints imposed by the deep sea. Although it has been studied little since its first description, *B. normani* (Brady) (1865) may provide the key to a better understanding of other species of *Bradleya* that are more important from the viewpoint of the practicing oceanographer. *B. normani* (Brady) occurs in fairly shallow water in the Strait of Magellan. It is, therefore, much easier to sample, and it can be obtained in large numbers. Potentially of great importance is the morphological plasticity of its reticulum if this can be related to specific environmental parameters.

The overall thrust of our research on *Bradleya normani* (Brady) is directed at this morphological plasticity. Does the morphology vary systematically with environment? We have not yet begun to address this question, and we do not expect shape analysis will help much because of the need to



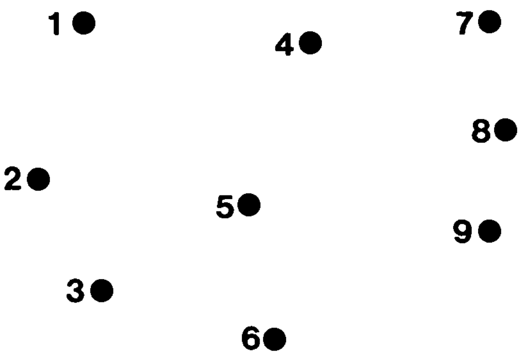
TEXT-FIG. 1—Adult *Bradleya normani* (Brady); squares indicate locations of nine pore canals, the homologous landmarks that were digitized for study.

study details of the surface ornamentation. Is the morphology of adults in a population predictable from the morphology of the immature forms? At present we are looking at ontogeny in hopes of ferreting the answer to this question. For the present, however, we intend to emphasize the comparison of techniques in hopes that other ostracode workers who apply methods of shape analysis to their research will find our comparisons useful.

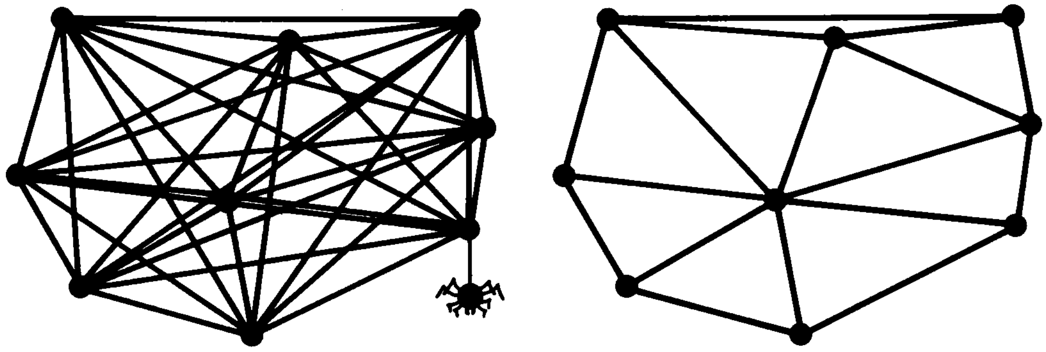
METHODS AND PROCEDURE

We have quite a few samples from the southern part of South America, but the specimens we measured for this part of our study came from a single sample, USARP 43. It was collected at a depth of about 135 m with a Sanders epibenthic sled dredge in mid-October, 1969, on cruise 69–5 of the R. V. *Hero*. The sample is from latitude 53°10.5′S, longitude 70°38′ W. We selected nine homologous points on the surface of adult specimens of *Bradleya normani* (Text-fig. 1). Most of the points are simple intramural pores, but some are celate sieve pores. We were not concerned with selecting pores that can be homologized throughout the genus or family because our study is aimed at population paleontology. Identifying these same nine homologous points on immature instars became increasingly difficult as we looked at earlier and earlier instars. In rare instances, for the very earliest instars studied, we had to approximate the position of a homologous point because it simply was not developed.

We digitized drawings made at 200× of 53 specimens, using a Houston Instruments Hipad dititizer driven by an IBM-PC microcomputer that is linked to the University of Kansas Honeywell mainframe computer. Also part of the system are a Hewlett-Packard 7470A plotter and an Epson printer. The procedure we used is as follows. First we identified the homologous landmarks on each specimen and drew them with a camera lucida. We then digitized the drawings of the landmarks and used a computer-based procedure to connect selected landmarks with lines to form triangles. The procedure for selecting landmarks and drawing triangles was adapted from one used in automated contouring (Watson, 1982). It selects homologous landmarks that produce triangles as nearly equilateral as possible given the configuration of the points. The lengths of the sides of the triangles were then computed, producing a matrix of morphological characters that



TEXT-FIG. 2—Configuration and numbers of the nine homologous landmarks with the outline of the ostracode removed.



TEXT-FIG. 3(*left*)—If lengths of all possible line segments connecting the nine homologous landmarks were measured, high intracorrelations would contribute to a great deal of redundancy in the data.

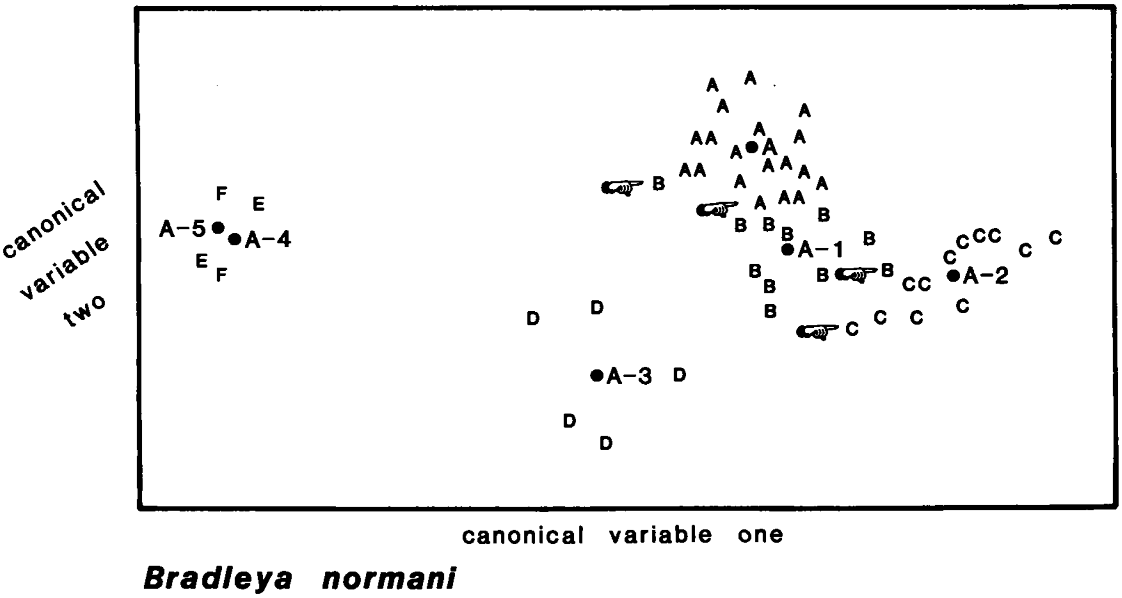
TEXT-FIG. 4 (*right*)—Selected homologous landmarks on an exemplar were connected to form a network of triangles by using an algorithm that selected triangles as nearly equilateral as possible. The triangles were identified by their vertices, and triangles with identical vertices were constructed for each specimen. The lengths of the sides of the triangles and the X and Y coordinates of the nine homologous landmarks comprised the morphological data for all subsequent analyses.

could be used as the basis for any multivariate statistical or graphic technique. Next an average specimen was computed for each instar, and the average lengths of the sides of the triangles were reconverted to X and Y coordinates. This matrix of X and Y coordinates was operated on by *robust regression analysis* and *tensor analysis*.

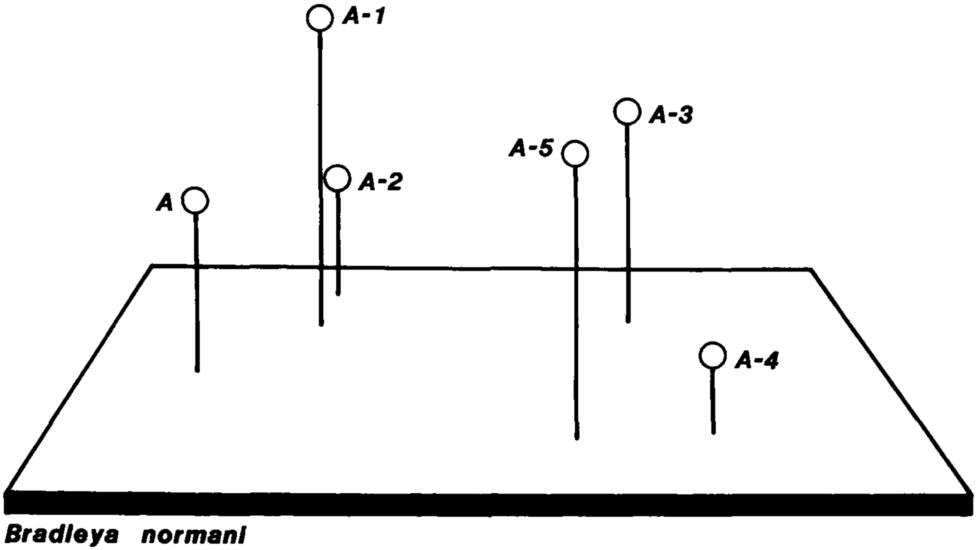
The nine homologous landmarks with the ostracode outline removed are shown in Text-fig. 2. It takes thirty-six lines to connect all the nine homologous landmarks to one another. Such a configuration is highly redundant because the lengths of many of the lines would be highly correlated with each other (Text-fig. 3). For this reason we chose to select triangles using the method briefly described above. The first ostracode in the study was used as an exemplar, and its homologous points were connected to make a network of triangles (Text-fig. 4). These triangles are identified by reference to their vertices. Triangles with the same vertices were then formed for all other ostracodes in the study. This insures that the characters used are the same throughout the study. The lengths of the sides of the triangles can then be used in any kind of traditonal multivariate morphometric analysis, such as discriminant function analysis or nonmetric multidimensional scaling. Robust regression analysis and tensor analysis, on the other hand, require that an average ostracode of each instar group be computed and the length of the sides of its triangles be reconverted to X and Y coordinates.

RESULTS

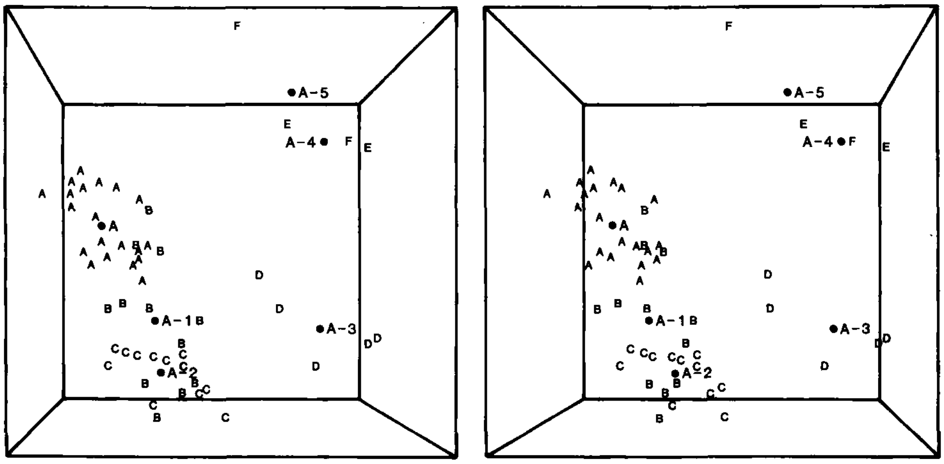
Text-figure 5 shows the results of multivariate discriminant function analysis. All 53 specimens are plotted. The large letters next to dots refer to the average ostracode of each instar from adult to A-5, the earliest instar in our collections. Small letters refer to individual ostracodes, the A's to adults, B's to A-1 instars, and so on. Forms that have been misclassified by the discriminant function are marked by pointing fingers. Recall that it is easy to identify the growth stage to which one of these ostracodes belongs by studying the animals' entire morphology. The misclassification resulted either from using only nine homologous landmarks and seventeen lengths of the resulting triangles or from anomalous individuals. As we pointed out earlier, this traditional multivariate morphometric method is particularly good for showing relationships between large numbers of individuls in a population, but differences between individuals may be swamped by the mass of points. It appears, however, that during ontogeny, late instars of *Bradleya normani* (Brady) change shape progressively so that adults are more similar to the very early instars than the A-2 or A-1 instars are. We did not detect sexual dimorphism. Such a result is not surprising because our study was not designed to show dimorphism. Sexual dimorphism of *Bradleya normani* (Brady) is apparent but is not pronounced. It is likely that the arrangement of the nine homologous points was such that the subtle sexual dimorphism was not expressed in their configuration. Moreover, males are quite rare in our collections.



TEXT-FIG. 5—Results of multivariate discriminant function analysis of 53 specimens of *Bradleya normani* (Brady), including adults and five instars. The symbols A, A-1, ..., A-5 indicate adults and respective instars. The somewhat smaller letters A, B, ..., F refer to individual ostracodes, respectively adults, A-1 instars, ..., A-5 instars. Misclassified individuals are marked by pointing fingers. Progressive morphological change is interrupted by a reversal of trend: adult specimens are moresimilar to early instars (A-4 and A-5) than late instars (A-1 and A-2) are.



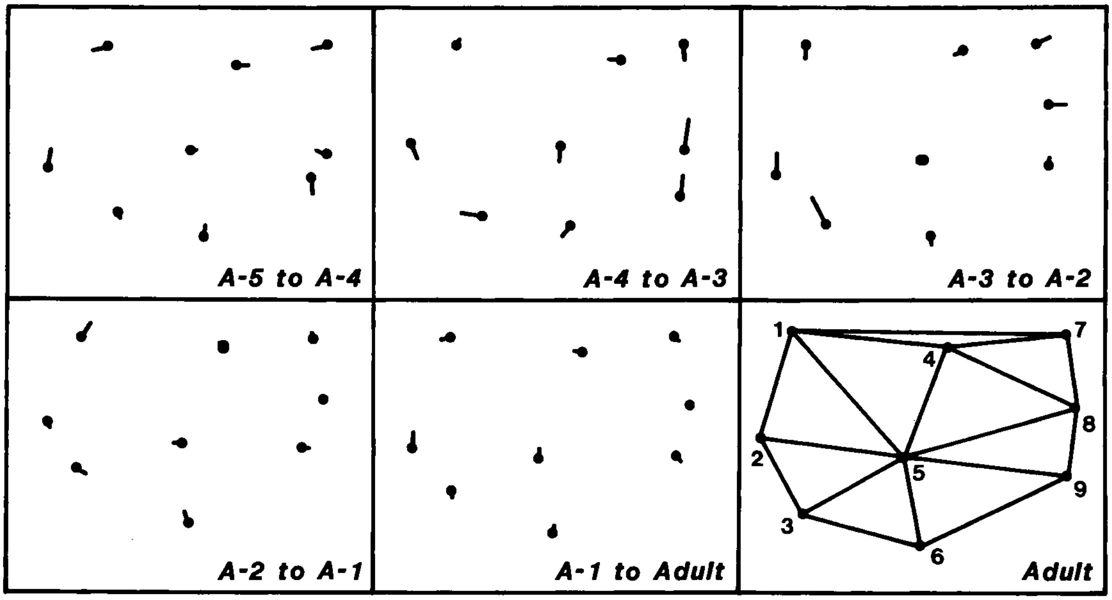
TEXT-FIG. 6—Results of non-metric multidimensional scaling of average *Bradleya normani* of each instar. As was true for results of multivariate discriminant function analysis, nonmetric multidimensional scaling shows A-5 instars to be more closely similar to adults than A-3 or A-4 instars.



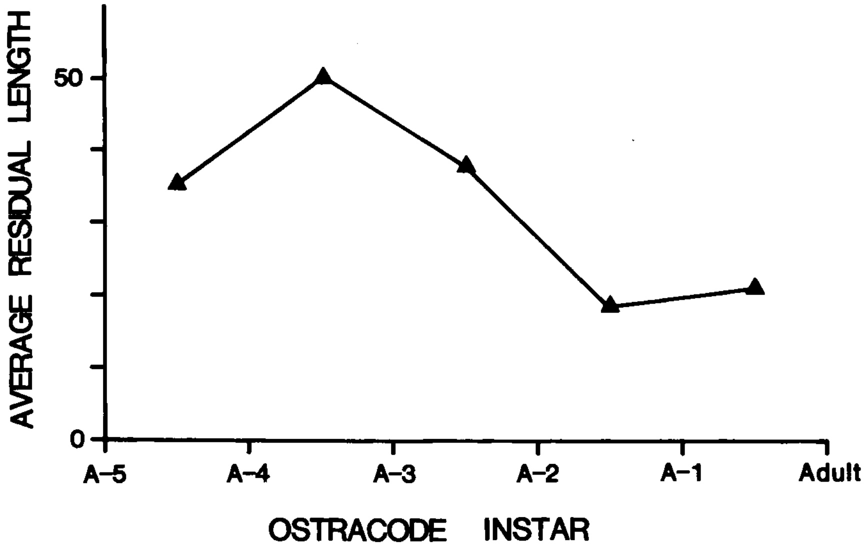
TEXT-FIG. 7—Stereopair of the nonmetric multidimensional scaling ordination of all 53 specimens of *Bradleya normani* (Brady). Symbols are the same as the ones used in Text-fig. 5. This figure is best viewed with a stereoscope.

The lollipop diagram of Text-fig. 6 shows the results of nonmetric multidimensional scaling of the average ostracodes of each of the six growth stages. Note again that the A-5 instar is more closely similar to the adults and last two instars than the A-3 and A-4 instars are. The progressive change in morphology from A-4 to the adult stage is also shown clearly on this figure. The similarities of the specimens in three-space are shown in the stereopair in Text-fig. 7, which is best viewed with a stereoscope.

Text-figure 8 shows the residual vectors from robust regression analysis of the growth stages of *Bradleya normani* (Brady). It is difficult to interpret this kind of diagram, but one gets two impressions from it. First, the residual vectors in the transformation from A-4 to A-3 and from A-3 to A-2 are longer than residual vectors associated with later transformations. This shows that the

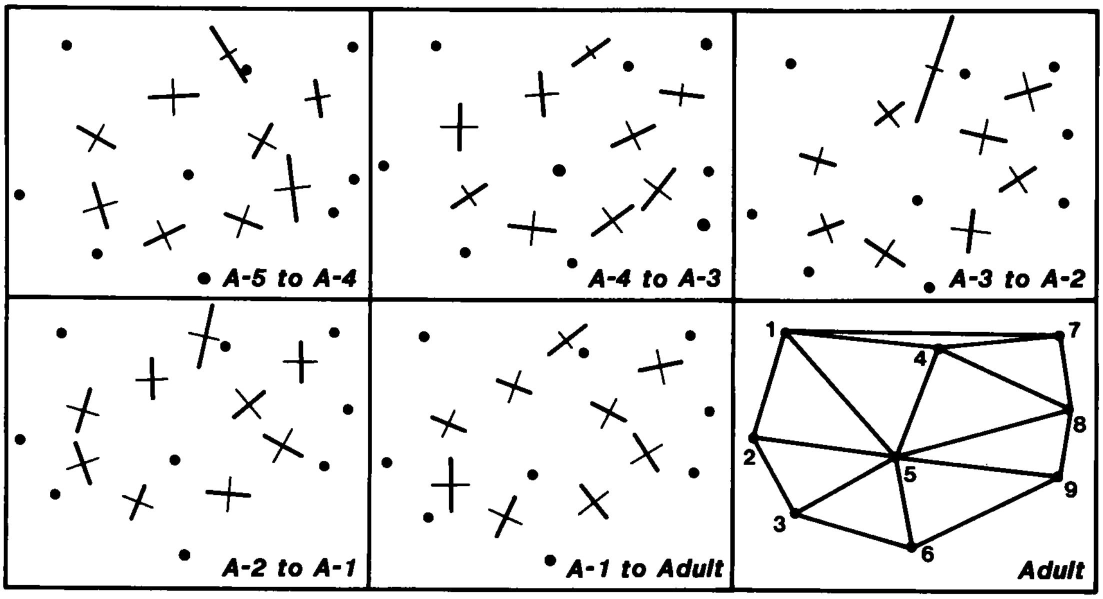


TEXT-FIG. 8—Residual vectors from robust regression analysis of data on 53 specimens of *Bradleya normani* (Brady). Long residual vectors, such as occur in the transformation from A-4 to A-3 and from A-3 to A-2, result from large changes in the relative positions of the homologous landmarks. Transformations from A-2 to A-1 and from A-1 to the adult stage have short residual vectors as a result of only miniscule change in the configuration of the landmarks during these transformations.



TEXT-FIG. 9—Average lengths of residuals show appreciably more change of shape of the configuration of the homologous landmarks occurred early in ontogeny than later.

greatest change in configuration of the nine homologous landmarks occurred in the transition from the A-4 to the A-3 instar. Second, residual vectors associated with the last two molts are negligible, indicating little change of shape late in ontogeny. Average lengths of the residuals (Text-fig. 9) convey the same impression as the previous figure: that the nine homologous points chosen for study show little change in the shape of *Bradleya normani* (Brady) during the last two molts.



TEXT-FIG. 10—Results of tensor analysis of *Bradleya normani* (Brady). The cross in the center of each triangle shows change of shape of that triangle during ecdysis. The heavy bar on the cross is the direction of greatest change. Homologous landmarks are shown in their position before ecdysis. Unlike robust regression analysis, which shows change of position of homologous landmarks, tensor analysis shows the change of shape of the area bounded by the landmarks and is thus singularly well suited for expressing allometry.

Text-figure 10 shows the results of tensor analysis. The cross in the center of each triangle shows the change of shape of that triangle during the transformation or molt from one stage to the next. The heavy bar on the cross is the direction of greatest change, and the homologous landmarks are shown in their position before each molt has occurred. Unlike robust regression analysis, which shows the change of position of homologous landmarks during ontogeny, tensor analysis shows the change of shape of the area bounded by the landmarks. As a result, it is singularly well suited for expressing allometry. In the ontogeny of *Bradleya normani* (Brady), morphological change expressed by the nine homologous landmarks seems to be evenly distributed over the carapace during the last two molts and, to a lesser extent, in the transformation from A-4 to A-3. The transitions from A-5 to A-4 and, even more so, the transition from A-3 to A-2, are marked by pronounced changes of shape in some parts of the carapace.

CONCLUSIONS

Now, what have we learned? First, evaluating the methods, we have confirmed that traditional multivariate morphometric techniques seem to be most useful in showing overall similarities of members of a population. Choosing between robust regression analysis and tensor analysis depends on what one is interested in. Burl Ives may have said it best: "As you go through life make this your goal: watch the donut, not the hole." Robust regression analysis focuses on the positions of the homologous points—the donut. Tensor analysis focuses on the shape of the area bounded by the homologous points—the hole in the donut. The choice between robust regression analysis and tensor analysis finally comes down to whether one is interested in positions of homologous landmarks or changes of shapes of the areas bounded by them. Finally, you may have other views, but as a result of this study we are convinced more than ever before that the choice of a method of analysis must be dictated by the biological questions asked and not merely by the availability of computer software.

With regard to *Bradleya normani* (Brady), we have identified a progressive change of shape from the A-5 instar to the adult with one major aberration as the A-5 instar departs from the trend and is more similar to the adult than would be expected. The greatest change in location of the landmarks occurs in the molt from A-4 to A-3 and from A-3 to A-2.

Finally, all shape analysis seems to be a search for ways to show the reader in graphic form how ostracodes change during growth. The most useful methods, therefore, are the ones that lend themselves to the production of simple graphic output from which a busy reader can gain a quick impression before he discards the paper in disgust or in favor of something simpler or more interesting.

ACKNOWLEDGEMENTS

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Multivariate Analysis of Leg Morphology of Macrocyprididae

ROSALIE F. MADDOCKS
University of Houston, U.S.A.

ABSTRACT

The fifth, sixth, and seventh legs and furcae of cypridacean ostracods are widely supposed to have considerable taxonomic significance and are relatively easy to dissect and illustrate. Nevertheless, some of the characters used in the past to diagnose new taxa have turned out to be invariant and, hence, without taxonomic importance, while many others are strongly correlated with each other or directly dependent on general size and, thus, not independent in their taxonomic significance. R-mode cluster and principal components analyses can be used to evaluate the independence of characters, so that the most appropriate characters may be selected for taxonomic and evolutionary applications.

To demonstrate this, 112 characters have been measured on these appendages and carapace for 71 species of Macrocyprididae, a relatively small and homogeneous family. The results show the potential of such methods for improving ostracod taxonomy. Q-mode cluster analysis of the same data provides evidence to test the generic classification of these species based on the carapace and subjective judgments. In general, the results confirm the prevailing opinion that the furcae and male fifth limbs offer more taxonomic information than the female fifth limb, sixth limb, and seventh limb. However, a few previously ignored characters may have taxonomic value, masked at present by possible non-linearity of their relationships.

INTRODUCTION

The posterior appendages of the Superfamily Cypridacea are widely recognized to have taxonomic significance. For more than 150 years, ostracod taxonomists have illustrated their descriptions of new species with drawings of these legs, giving special attention to the number and shape of the podomeres and setae. Although the accuracy of such descriptions has increased greatly over the years, only rarely are the proportions for new species compared with those of species already known, and almost never are the underlying mathematical relationships explored.

Today, as we celebrate the 22nd anniversary of the first ostracod symposium in Naples, and as the alpha taxonomy chapter in the history of ostracodology draws to a close, we should reconsider our priorities. Although a few new species still remain to be found, the time has arrived to start concentrating on the relationships among species rather than on the species themselves. The initiation of the Treatise revision makes it all the more urgent that we emphasize so-called beta taxonomy, because a sound generic and familial classification can be based only on systematic comparisons of large numbers of species.

It is also time to supplement the formal description of appendage anatomy with mathematical analysis of these anatomical relationships. We already know that the ontogenetic growth of the ostracod carapace follows certain geometric laws, and that mathematical analyses can help us to understand the architecture of adult shells. There is every reason to suppose that the *terra incognita* of appendage anatomy will yield to similar techniques. Let us abandon the uncritical use of ratios and shape-adjectives and find more powerful tools for understanding shape.

For example, size allometry is known to govern systematic changes of shape with increased size in organisms as diverse as land snails, australopithecines, and echinoids. It seems likely that the conspicuous miniaturization of Cenozoic cytheracean lineages and the increased size of deep-sea ostracods may also have been accompanied by allometric changes in shape. Such shape differences caused by size allometry would have no independent genetic basis and therefore no taxonomic value. We must learn how to recognize and allow for such morphologic trends, and only then will we be able to make sound taxonomic decisions.

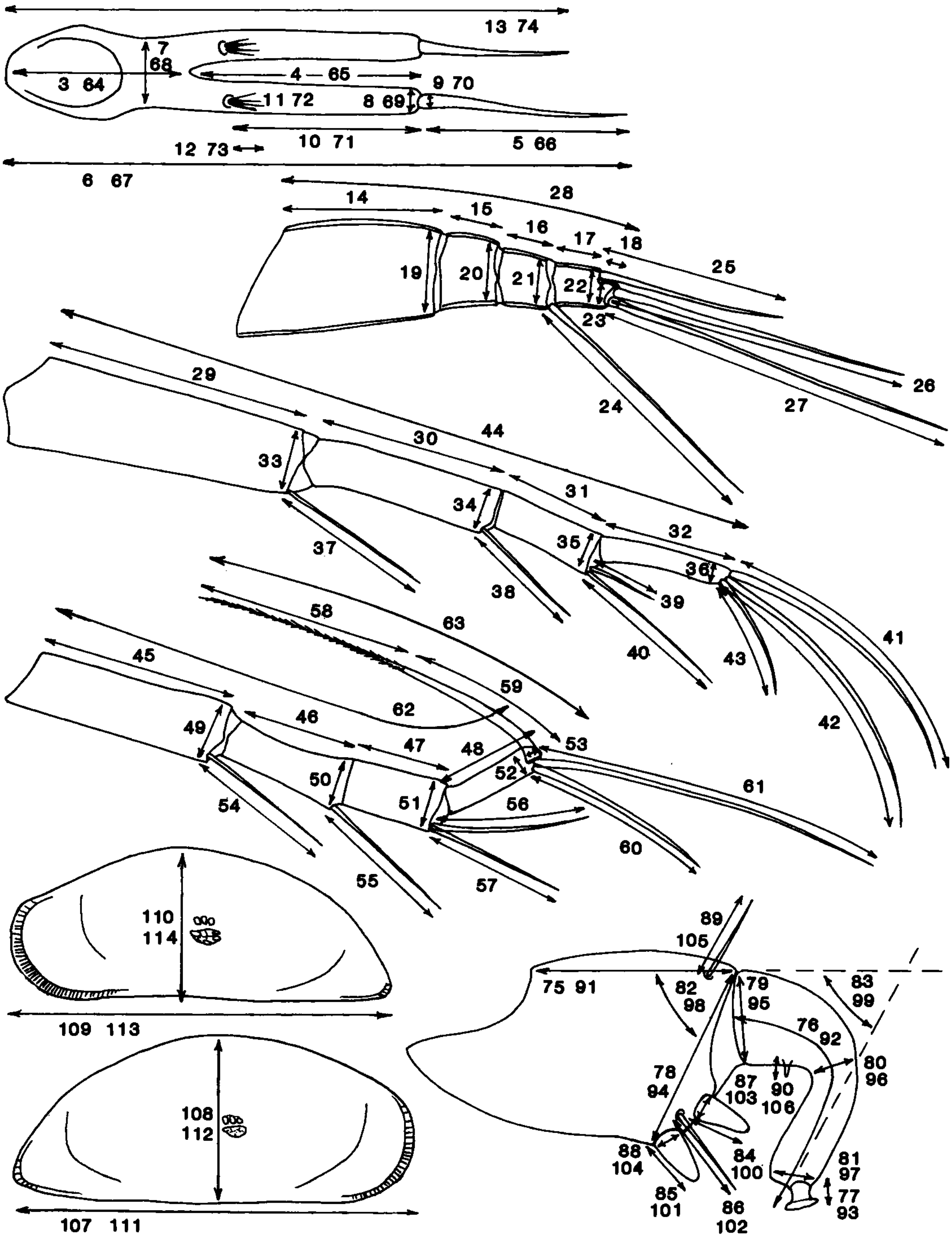
The present report illustrates some preliminary results from just a few of the techniques that might be useful for both of these objectives. Because this is a preliminary report from an on-going project, it emphasizes techniques that the taxonomist can use to evaluate potential taxonomic characters, in order to select from the multitude of characters available those few characters that carry the most information.

The data are taken from the Family Macrocyprididae, for which the author is currently preparing a comprehensive taxonomic revision. In addition to many fossil species, this monographic revision will include 71 living species for which the appendage anatomy will be described or redescribed. They will be classified into eight genera: *Macrocypris, Macrocyprissa, Macrocypria, Macrocyprina,* and four new genera.

The posterior appendages (fifth, sixth, and seventh limbs and furcae) were selected for analysis because they are relatively simple in structure and approximately two-dimensional, so that consistently accurate drawings can be made. They are also appropriate because they are very uniform in structure throughout this family, so that homologous characters are easy to recognize. Insights gained from these simple limbs may encourage us to study the more formidable cephalic appendages later.

For each of these 71 species, the female fifth limb, male right and left fifth limbs, non-dimorphic sixth and seventh limbs, and male and female furcae have been drawn by projection from the dissection slide, with uniform orientation and magnification.These drawings were then measured in mm with a transparent ruler. Text-fig. 1 shows the locations of 104 measured characters (variables 3 to 106), mostly lengths and widths of podomeres and lengths of setae. Characters 11 and 71 are counts of the number of setae (2, 3, or 4) at that location, while characters 82, 83, 98, and 99 are angles. The length and height of male and female right and left valves were added as characters 107 to 114. Variables 1 and 2 of the computer analyses are labels representing the species name and specimen number. Note that there is only one set of measurements for each species, so the results have only taxonomic rather than population significance. (Of course, the material for these 71 species was subject to the vagaries that govern all museum collections, so that for a few species the males are not known, while for others the female was missing, and for still others a particular leg was damaged or missing. Thus, the measurements for some species are compiled from more than one specimen, and the effective sample size and species composition differ for each analysis. Fortunately, computer algorithms are now available that can navigate around these missing values to select for each comparison those cases for which the characters are represented and to calculate a generalized inverse of the resulting correlation matrix.)

The computer analyses were done on the AS 9000 system at the University of Houston, using the BMDP Biomedical computer programs (Engelman *et al.*, 1983). The taxonomic revision of the



TEXT-FIG. 1—Locations of 112 measurements. 3-13, male furca; 14-28, female fifth limb; 29-44, sixth limb; 45-63, seventh limb; 64-74, female furca; 75-90, male right fifth limb; 91-106, male left fifth limb; 107-110, male carapace dimensions; 111-114, female carapace dimensions.

family Macrocyprididae was supported by National Science Foundation Grant DEB-76-83081. The generosity of scores of museums and individuals in lending or donating specimens and samples of Macrocyprididae for this project is most gratefully acknowledged.

STATISTICAL METHODS

Many statistical methods assume underlying normality of the variables, and excessive deviation from normality may invalidate the results. On the other hand, it is obvious that those characters of greatest taxonomic usefulness at the generic level will not be continuously distributed within a family. For both reasons, these data were tested for normality. Table 1 gives the significance levels of the Shapiro and Wilk's W statistic test for normality for raw and log-transformed measurements for each character. Fully 84 of 112 variables do not meet this assumption ($P<.05$). After logarithmic transformation, often recommended as a remedy in such situations, matters are only slightly improved. Now, 62 of 112 variables may be considered normally distributed, but 13 of the remaining 50 are variables that were normal before this transformation.

An inspection of individual characters shows some predictable trends and a surprise. Very small dimensions and those with limited range of values are not normally distributed, nor are those characters that are traditionally considered to have taxonomic value at the generic level. Thus, the male and female furcae and the male right and left fifth limbs have many characters that do not meet the assumpton of normality either before or after transformation. Many characters of the sixth and seventh limbs, on the other hand, are approximately normally distributed after logarithmic transformation, suggesting that part of their variability may be a geometric function of general size. This supports the judgment of many workers that these limbs have little taxonomic value at the ge-

TABLE 1—SIGNIFICANCE LEVELS FOR THE SHAPIRO AND WILK'S W STATISTIC TEST OF NORMALITY FOR RAW DATA AND LOG-TRANSFORMED DATA.

Character	Raw Data	Log Data	Character	Raw Data	Log Data
3	.23	.00	23	.00	.02
4	.23	.00	24	.04	.00
5	.09	.00	25	.14	.00
6	.01	.00	26	.00	.36
7	.01	.24	27	.04	.26
8	.00	.00	28	.02	.07
9	.00	.00	29	.10	.45
10	.02	.00	30	.01	.11
11	.00	—	31	.07	.20
12	.00	.00	32	.00	.00
13	.01	.00	33	.00	.13
14	.07	.43	34	.23	.06
15	.11	.08	35	.00	.03
16	.00	.04	36	.00	.00
17	.56	.00	37	.09	.00
18	.00	.00	38	.17	.29
19	.02	.53	39	.00	.39
20	.02	.03	40	.00	.06
21	.09	.01	41	.16	.00
22	.04	.00	42	.06	.00

(*Continued*)

TABLE 1—*Continued*

Character	Raw Data	Log Data
43	.00	.12
44	.03	.17
45	.03	.43
46	.00	.24
47	.06	.85
48	.00	.29
49	.00	.06
50	.00	.19
51	.00	.35
52	.00	.08
53	.00	.00
54	.24	.02
55	.24	.48
56	.00	.12
57	.02	.33
58	.04	.13
59	.01	.06
60	.00	.78
61	.00	.01
62	.05	.79
63	.02	.08
64	.00	.50
65	.02	.00
66	.45	.00
67	.49	.00
68	.00	.11
69	.00	.00
70	.00	.00
71	.00	.00
72	.00	—
73	.02	.01
74	.26	.00
75	.00	.19
76	.00	.17
77	.00	.01
78	.00	.09
79	.01	.53
80	.00	.11
81	.01	.09
82	.58	—
83	.50	—
84	.01	.00
85	.00	.01
86	.26	.00
87	.00	.00
88	.00	.00
89	.00	.00
90	.00	.00
91	.00	.03
92	.00	.02
93	.00	.01
94	.12	.06
95	.01	.09
96	.00	.14
97	.00	.00
98	.00	—
99	.00	—
100	.00	.00
101	.00	.09
102	.00	.00
103	.00	.00
104	.00	.00
105	.00	.00
106	.00	.00
107	.31	.44
108	.01	.92
109	.48	.67
110	.03	.99
111	.14	.96
112	.00	.19
113	.11	.32
114	.02	.82

neric level. Surprisingly, carapace lengths are normal even before transformation, while heights become normal after transformation. Is there any *a priori* reason why the carapace sizes of the species belonging to an ostracod family ought to be normally or log-normally distributed? It would be interesting to test this for other families and see whether any ecological or evolutionary principle underlies this phenomenon.

Even more critical to many statistical methods is the assumption of homoscedasticity (independence of means and variances). Plots (not shown) of mean versus variance for these limbs and the carapace showed very significant heteroscedasticity, not removed by logarithmic transformation. Taxonomists need to be aware that this tendency for larger structures to have greater variances is likely to divert attention from statistically more reliable characters.

R-mode cluster analysis is a quick and robust technique for revealing the presence of structure in a correlation matrix and is a useful preliminary to more sophisticated methods. The results can help the taxonomist evaluate the relative independence of a large number of potential taxonomic characters. The configuration of clusters may also suggest hypotheses about underlying causes for these correlations, for further testing. Here, matrices of correlation coefficients calculated from raw or log-transformed data were clustered by the average-linkage method.

Q-mode cluster analysis is an efficient method of comparing species on the basis of large numbers of characters. The resulting clusters can be compared with an *a priori* classification. Good agreement may be interpreted either as support for the *a priori* classification or as meaning that the characters used are effective and appropriate. Poor agreement may suggest that changes are desirable either in the *a priori* classification or in the list of characters. Here, clusters were formed by the single-linkage method from a matrix of Euclidian distance coefficients, calculated from raw or transformed data.

Principal component analysis is a mathematical model for identifying a smaller set of variables (interpretable as causes or end members) whose action could account for the correlations among the original variables. The computations extract from the original correlation matrix a series of orthogonal (uncorrelated) eigenvectors (principal axes or principal components), each of which in turn accounts for a maximum possible amount of the remaining variance. For morphological data the first principal component is usually interpreted as an expression of general size and the effects of size, while successive components quantify aspects of shape. The number of eigenvectors (with eigenvalues greater than 1.0) and the pattern of their loadings (a measure of their influence, mathematically a standard partial regression coefficient) on the original variables may suggest hypotheses about underlying causes. The taxonomist may apply these results to select those characters most likely to provide independent genetic informaton.

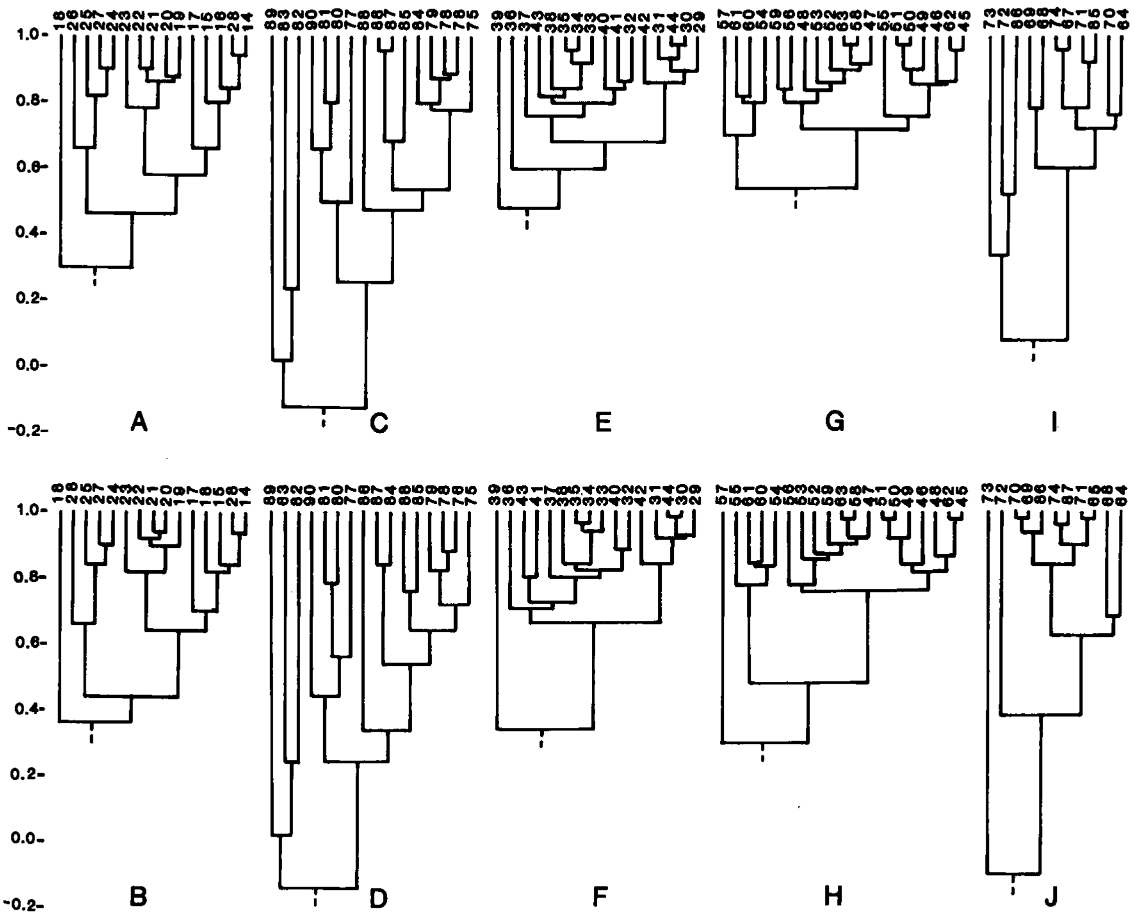
The mathematical theory and biological applications of multivariate methods are discussed in many modern textbooks, of which the following have been particularly useful in this study: Davis (1973), Reyment *et al.* (1984), Sneath and Sokal (1973), Sokal and Rohlf (1969).

FEMALE FIFTH LIMB

R-mode cluster analysis for untransformed data (17 characters, 59 species) produced three distinct clusters, composed of podomere lengths, podomere widths, and seta lengths (Text-fig. 2A). The isolation of character 18 may result from its small size and less accurate measurement. The pattern suggests that lengths and widths may be independent to some degree, justifying such verbal descriptions of this leg as "elongate" or "robust." Almost exactly the same pattern was produced from log-transformed data (Text-fig. 2B), suggesting substantial linearity in these relationships. The high levels of similarity confirm the traditional judgment that most of these characters have no independent taxonomic value.

Q-mode cluster analyses (not shown) yielded small groups of related species, but larger clusters transgressed generic and other plausible relationships, supporting the view that this leg has little taxonomic value.

Principal components analysis of untransformed data produced high squared multiple correlations for all characters except 18 (Table 2). The first eigenvector explains 59 percent of the variance and is readily interpreted as general size. Eigenvector 2 explains 15 percent and can be interpreted as setosity, with positive effect on seta length and negative effect on podomere length. Eigenvector 3 explains 7 percent of the variance and acts strongly only on seta 26, which may have taxonomic value. Results from log-transformed data (not shown) were very similar, suggesting that the relationships are largely linear.



TEXT-FIG. 2—Phenograms resulting from R-mode cluster analysis of measurements on female fifth limb (A, B), male right fifth limb (C, D), sixth limb (E, F), seventh limb (G, H), and female furca (I, J). A, C, E, G, I, untransformed data; B, D, F, H, J, log-transformed data.

MALE RIGHT FIFTH LIMB

R-mode cluster analysis of raw data (18 characters, 52 species) yielded four small clusters, one cluster composed mostly of podomere dimensions, another including the ventral pegs and seta, amother for dimensions of the distal hook and its sensory setae, and the last for the two angles and the dorsal seta (Text-fig. 2C). The analysis of log-transformed data (Text-fig. 2D) reproduced the last two clusters but mixed the first two. The results suggest that structures located in the same general region of the limb will tend to vary together rather than independently.

Q-mode cluster analysis of both sets of data (not shown) yielded poorly defined clusters with

TABLE 2—PRINCIPAL COMPONENTS ANALYSIS FOR FEMALE FIFTH LIMB.

Character	SMC†[1]	Eigenvectors†[2]		
		1	2	3
14	0.99233	0.767	-0.491	0.005
15	0.96271	0.871	-0.226	0.098
16	0.97122	0.674	-0.600	0.233
17	0.93095	0.668	-0.406	0.359
18	0.65773	0.437	-0.112	-0.156
19	0.87004	0.879	0.070	-0.132
20	0.92388	0.890	0.014	-0.245
21	0.89161	0.862	0.076	-0.349
22	0.91871	0.901	0.130	-0.327
23	0.82122	0.817	0.068	-0.419
24	0.91340	0.697	0.611	0.180
25	0.88149	0.725	0.524	0.316
26	0.80599	0.666	0.269	0.576
27	0.85568	0.699	0.589	0.037
28	0.99814	0.855	-0.482	0.104
Eigenvalues†[3]		0.5935	0.7376	0.8159

†[1] Squared multiple correlations of each variable with all other variables.

†[2] Loadings of each eigenvector (principal component) on the variables.

†[3] Variance explained by each eigenvector, as cumulative proportions of total variance.

many leftover species. The individual clusters were more homogeneous at the generic level for log-transformed than for raw data, suggesting non-linearity for some of these relationships.

Principal components analysis of untransformed data yielded moderate to high squared multiple correlations (Table 3), with seta 89 being the most independent. Eigenvector 1 explains only 44 percent of the variance, confirming the taxonomic value of the shape of this leg. While it is unusual for the first principal component (general size) to have negative loadings, that is quite logical here: Large species of Macrocyprididae tend to have more recurved hooks (smaller angle

TABLE 3—PRINCIPAL COMPONENTS ANALYSIS FOR MALE RIGHT FIFTH LIMB

Character	SMC	Eigenvectors			
		1	2	3	4
75	0.78744	0.825	-0.129	0.295	-0.012
76	0.91829	0.915	0.167	0.080	-0.022
77	0.55937	0.276	0.659	0.322	0.231
78	0.94266	0.934	0.184	0.063	0.049
79	0.91607	0.912	-0.026	0.064	0.195
80	0.95180	0.796	0.498	0.051	0.032
81	0.80534	0.541	0.715	0.000	0.001
82	0.52987	0.049	0.060	-0.628	0.574
83	0.49394	-0.375	0.334	-0.210	0.570
84	0.83618	0.901	-0.062	-0.018	-0.085
85	0.87428	0.768	-0.525	0.004	-0.014
86	0.52206	0.594	-0.285	-0.168	-0.178
87	0.95936	0.628	-0.513	-0.146	0.231
88	0.96436	0.611	-0.576	-0.078	0.284
89	0.65417	-0.330	-0.059	0.729	0.480
90	0.81940	0.327	0.748	-0.326	-0.198
Eigenvalues		0.4440	0.6256	0.7098	0.7843

83), while the dorsal seta (98) is found mostly in species of *Macrocyprina*, a genus whose species tend to be quite small. Two sensory setae and the proximal angle (77, 82, 90) also show little dependence on general size. Eigenvector 2 explains 19 percent of the variance; it controls the shape of the distal hook with its sensory setae and the shapes of the ventral pegs. Eigenvector 3 explains 8 percent of the variance and has its greatest effect on the shape (angle 82) of the proximal podomere and on the dorsal seta (89), both characters that may distinguish geographical species-groups in *Macrocyprina*. Eigenvector 4 explains 7 percent of the variance and also controls the angles and dorsal seta. These results confirm that there is considerable taxonomic value in the shape of the leg, but it appears that the shapes of the ventral pegs may have less importance than sometimes supposed. Analysis of log-transformed data (not shown) yielded fairly similar loadings for the first two factors but very different patterns for the others, suggesting non-linearity in the relationships of certain characters.

MALE LEFT FIFTH LIMB

The male fifth limbs tend to be asymmetrical in Macrocyprididae. The left limb varies from being nearly the mirror image of the right leg to being very much reduced and of quite different shape. It is not known whether the degree of asymmetry has taxonomic value above the species level. Because of this variability, the R-mode and Q-mode cluster analyses for this leg (18 characters, 53 species) are more difficult to interpret (not shown). Compared with those for the right leg, the principal component analyses (not shown) yielded a similar pattern of loadings for the first eigenvector, but conspicuous differences for the others, which highlight the individual characters that often show asymmetry. Future analyses may more appropriately focus directly on this asymmetry by calculating the differences between the values for the homologous characters of the two legs.

SIXTH LIMB

R-mode cluster analysis of untransformed data (18 characters, 65 species) yielded somewhat confused clusters that intermix setae with podomere lengths of widths (Text-fig. 2E). The apparent independence of dimensions 36 and 39 may result from less accurate measurement of these tiny structures. The high levels of similarity support the lack of taxonomic value at the specific and generic level for most characters of this leg. Slight differences in the analysis of log-transformed data (Text-fig. 2F) may be calling attention to non-linear components in these correlations.

Q-mode cluster analysis of raw data yielded poor structure and species clusters that could not be interpreted (not shown). Analysis of log-transformed data showed fair structure, in which the small species clusters were homogeneous at the generic level (not shown). This suggests that there may be some taxonomic information in this leg, hidden from the casual eye by non-linearity of relationships.

Principal components analysis of untransformed data yielded high squared multiple correlations for all variables except 36 and 39 (Table 4). Eigenvector 1 explains 73 percent of the variance and is readily interpretable as general size. Eigenvector 2 explains 9 percent and primarily controls proportionate lengths of the podomeres and distal setae. Analysis of log-transformed data (not shown) produced fairly similar results; non-trivial differences in the loadings for several setae suggest that non-linear trends may be at work.

TABLE 4—PRINCIPAL COMPONENTS ANALYSIS FOR SIXTH LIMB

		Eigenvectors	
Character	SMC	1	2
29	0.97998	0.757	0.601
30	0.98468	0.903	0.349
31	0.95508	0.846	0.444
32	0.98075	0.830	-0.417
33	0.93575	0.944	-0.067
34	0.92179	0.936	-0.095
35	0.96739	0.963	-0.071
36	0.72585	0.722	-0.014
37	0.85891	0.855	-0.048
38	0.85456	0.888	-0.134
39	0.74265	0.580	-0.294
40	0.91531	0.813	-0.474
41	0.89497	0.876	-0.342
42	0.89959	0.855	0.389
43	0.87084	0.846	-0.146
44	0.99697	0.950	0.251
Eigenvalues		0.7276	0.8249

SEVENTH LIMB

R-mode cluster analysis of untransformed data (21 characters, 64 species) produced three discrete clusters, one composed largely of dimensions for the three proximal podomeres, one for the distal podomere and recurved (feathered) seta, and one for most of the ventral and distal setae (Text-fig. 2G). Analysis of log-transformed data (Text-fig. 2H) reproduced substantially the same clusters with minor differences. There appears to be a strong connection between length of the recurved seta and length of the next-to-last podomere, while several of the other setae are highly correlated with each other but rather independent of the recurved seta.

Q-mode cluster analyses (not shown) of both raw and transformed data yielded good structure, with five or six reasonably homogeneous (at the generic level) species clusters plus a few leftovers. This supports the traditional view that the shape of this leg has good taxonomic value.

Principal components analysis of untransformed data produced high squared multiple correlations for all variables (Table 5). Eigenvector 1 explains 73 percent of the variance and has high loadings on all characters except 61. It may be interpreted as general size plus typicality of shape. Eigenvector 2 explains 13 percent of the variance and controls relative seta lengths; the negative effect on the recurved seta and positive influence on other setae demonstrate good taxonomic value for the relative proportions of these setae. Analysis of the log-transformed data yielded quite similar results (not shown), suggesting substantial linearity in these relationships. For both analyses, the strong dependence of the recurved seta on general size suggests that it may carry less taxonomic information than commonly supposed, while setae 54, 60 and 61 deserve greater taxonomic attention.

TABLE 5—PRINCIPAL COMPONENTS ANALYSIS OF SEVENTH LIMB

		Eigenvectors	
Character	SMC	1	2
45	0.99145	0.921	0.016
46	0.97804	0.876	0.287
47	0.97110	0.920	-0.278
48	0.96145	0.899	-0.182
49	0.89290	0.884	0.164
50	0.96855	0.939	0.096
51	0.98077	0.953	0.091
52	0.90407	0.900	-0.256
53	0.88819	0.836	-0.329
54	0.86501	0.708	0.580
55	0.82172	0.812	0.356
56	0.86216	0.814	-0.368
57	0.85052	0.810	0.261
58	0.98766	0.912	-0.308
59	0.93432	0.731	-0.578
60	0.90322	0.761	0.523
61	0.89969	0.522	0.807
62	0.99830	0.973	-0.026
63	0.99353	0.890	-0.409
Eigenvalues		0.7256	0.8624

FEMALE FURCA

R-mode cluster analysis for raw data (13 characters, 42 species) yielded several small clusters, representing lengths, thicknesses, and seta dimensions (Text-fig. 2I). The analysis of log-transformed data (Text-fig. 2J) reproduced the lengths cluster but not the others.

Both Q-mode cluster analyses (not shown) produced poor structure, with many leftover species, although the smaller species-clusters were fairly homogeneous at the generic level.

Principal components analysis of untransformed data produced high squared multiple correlations for all variables except 11 and 12 (Table 6); their tiny size makes them hard to measure ac-

TABLE 6—PRINCIPAL COMPONENTS ANALYSIS FOR FEMALE FURCA

		Eigenvectors		
Character	SMC	1	2	3
3	0.99813	0.840	-0.265	-0.049
4	0.99917	0.877	-0.194	-0.334
5	0.99860	0.423	0.755	0.226
6	0.99975	0.969	0.118	-0.106
7	0.89798	0.860	-0.095	0.270
8	0.88088	0.720	0.146	0.600
9	0.84172	0.875	-0.006	0.243
10	0.94669	0.801	-0.286	-0.489
11	0.57325	0.177	0.769	-0.407
12	0.32167	-0.155	0.722	-0.149
13	0.96717	0.929	0.158	-0.103
Eigenvalues		0.5615	0.7380	0.8385

curately. Eigenvector 1 explains 56 percent of the variance and may be interpreted as general size; the low loadings on setae 11 and 12 signal their independence of size. Eigenvector 2, which explains 18 percent of the variance, controls setae 5, 11 and 12. Eigenvector 3 seems to control taper of the rami and explains 10 percent. Similar results were obtained from log-transformed data (not shown).

In future analyses, the asymmetry of the furcal rami and the positions of the proximal setae should be more directly coded and the redundant variables deleted; this should improve interpretability of the results.

MALE FURCA

The furca is conspicuously dimorphic in some but not all species of two genera and may be slightly dimorphic in others. In such cases the male furca is smaller than that of the female and the rami are much reduced. The results presented below show that in future analyses the characters should be recoded to emphasize the taxonomic value of this dimorphism.

R-mode cluster analysis of both raw and log-transformed data showed poor structure without distinct clusters (13 characters, 52 species; not shown).

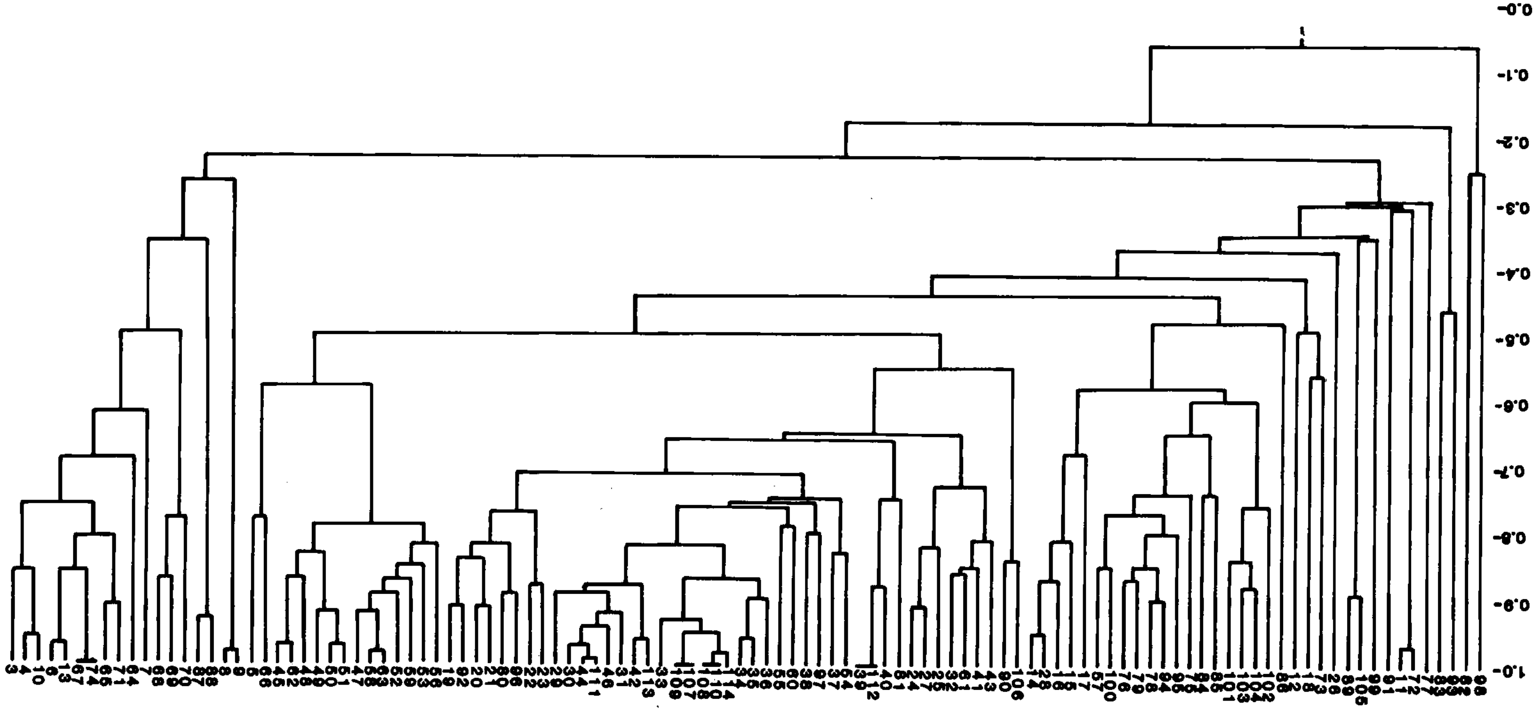
Q-mode cluster analysis of raw and transformed data showed poor structure with many leftover and misclassified species.

The principal component analyses of both raw and transformed data (not shown) were quite similar to those for the female.

THE TOTAL DATA SET

Cluster analysis of raw data (112 characters, 71 species) showed fairly good structure, in which the smaller clusters tend to be homogeneous both by body region and by type of character (Text-fig. 3). Repeatedly, the homologous characters of the male and female or right and left limbs cluster very closely, while podomere widths tend to separate from podomere lengths or carapace dimensions. The occasional misgroupings have heuristic value: For example, the close pairing of setae 37 and 54, which occupy comparable positions on successive legs, suggests an underlying influence related to serial homology. The connection of the recurved seta (58) with the next-to-last podomere of the seventh leg (47) is also striking. Other characters, such as seta 26 of the female fifth limb, the proximal setae of the furcae, and the angles of the male fifth limbs, continue to display independence and potentially valuable taxonomic characters.

Principal components analysis yielded the results shown in Table 7. Eigenvector 1 (general size) now explains only 42 percent of the variance. It has especially high positive loadings on podomere dimensions, lengths of major setae, and carapace dimensions, but it has negligible or even negative effects on some characters, especially of the male fifth limbs. Eigenvector 2 explains 16 percent of the variance and seems to control shape of the furca, with high positive loadings on dimensions of the furcal rami; it also comprehends shape aspects of the distal podomeres and major setae of the sixth and seventh limbs and controls proportions of the ventral pegs and seta of the male fifth limbs. The overall effect is to emphasize those taxonomic differences that separate *"Macrocypris" s. l.* from *"Macrocyprina" s. l.* Eigenvector 3 explains 7 percent of the variance; its loadings are generally positive for the fifth limb and negative for all others. It controls a variety of shape aspects of the fifth limbs and furcae. The subsequent eigenvectors individually explain only 3 percent of the variance or less; 14 additional eigenvectors (none of which have loadings higher than ±0.614) are necessary to explain 90 percent of the variance. The following is a complete list of all positive



TEXT–FIG. 3—Phenogram from R-mode cluster analysis of the total data set, untransformed data.

Table 7—Principal Components Analysis for the Total Data Set (3 of 16 Eigenvectors)

Character	Eigenvectors		
	1	2	3
3	0.097	0.816	0.026
4	0.129	0.867	-0.082
5	0.676	0.106	-0.280
6	0.369	0.793	-0.145
7	0.324	0.535	-0.124
8	0.182	0.316	-0.221
9	0.064	0.377	-0.201
10	0.043	0.915	-0.015
11	0.413	-0.162	-0.146
12	0.534	0.047	0.133
13	0.377	0.754	-0.075
14	0.595	0.309	0.284
15	0.709	0.147	0.418
16	0.457	0.363	0.457
17	0.460	0.235	0.636
18	0.576	-0.065	0.163
19	0.823	-0.154	0.319
20	0.802	-0.151	0.283
21	0.793	-0.194	0.168
22	0.787	-0.263	0.203
23	0.734	-0.242	0.170
24	0.592	-0.468	0.034
25	0.646	-0.415	0.151
26	0.487	-0.336	0.360
27	0.625	-0.499	-0.005
28	0.659	0.287	0.447
29	0.820	0.206	-0.267
30	0.879	-0.050	-0.345
31	0.879	0.085	-0.260
32	0.591	-0.622	-0.230
33	0.878	-0.352	-0.118
34	0.865	-0.228	-0.146
35	0.873	-0.325	-0.143
36	0.803	-0.321	-0.174
37	0.720	-0.307	-0.166
38	0.794	-0.307	-0.052
39	0.678	-0.236	-0.092
40	0.659	-0.480	-0.135
41	0.718	-0.576	-0.063
42	0.850	-0.027	-0.138
43	0.702	-0.441	-0.168
44	0.895	-0.141	-0.311
45	0.791	0.262	-0.350
46	0.877	-0.022	-0.369
47	0.748	0.448	-0.202
48	0.756	0.353	-0.145
49	0.780	0.044	-0.279
50	0.867	0.051	-0.235
51	0.872	0.078	-0.259
52	0.708	0.380	-0.204
53	0.654	0.376	-0.234
54	0.749	-0.169	-0.336
55	0.776	-0.054	-0.199
56	0.668	0.544	-0.008
57	0.870	0.098	-0.037
58	0.695	0.471	-0.222
59	0.572	0.663	-0.041
60	0.796	-0.241	-0.132
61	0.684	-0.507	-0.262
62	0.859	0.274	-0.297
63	0.672	0.560	-0.163
64	0.041	0.721	-0.206
65	0.166	0.804	-0·140
66	0.598	-0.112	-0.512
67	0.373	0.696	-0.393
68	0.244	0.481	-0.348
69	0.314	0.222	-0.521
70	0.240	0.580	-0.435
71	0.035	0.780	-0.027
72	0.368	-0.015	-0.226
73	0.504	-0.196	0.148
74	0.368	0.680	-0.410
75	0.672	0.386	0.321
76	0.781	0.164	0.398
77	0.302	-0.437	0.037
78	0.845	0.061	0.318
79	0.703	0.262	0.415
80	0.754	-0.285	0.263
81	0.596	-0.521	0.128
82	-0.009	-0.066	0.123
83	-0.234	-0.423	-0.159
84	0.711	0.125	0.407
85	0.508	0.582	0.389
86	0.378	0.267	0.453
87	0.386	0.418	0.291
88	0.369	0.493	0.260
89	-0.485	0.159	-0.013
90	0.565	-0.678	-0.056
91	0.424	0.277	0.081
92	0.843	-0.109	0.404
93	0.177	-0.316	0.044
94	0.842	0.068	0.311
95	0.819	0.009	0.257
96	0.795	-0.335	0.259
97	0.805	-0.323	0.105
98	0.025	0.013	-0.017
99	-0.450	0.097	-0.308
100	0.805	0.223	0.268
101	0.408	0.672	0.295
102	0.486	0.548	0.266
103	0.515	0.539	0.343
104	0.484	0.640	0.304
105	-0.457	0.230	-0.044
106	0.413	-0.493	-0.100
107	0.893	-0.239	0.022
108	0.913	-0.208	0.092
109	0.894	-0.206	0.005
110	0.916	-0.166	0.102
111	0.909	-0.117	-0.254
112	0.821	-0.191	-0.082
113	0.816	-0.073	-0.154
114	0.932	-0.186	0.027
Eigenvalues	0.4231	0.5819	0.6460

oadings of eigenvectors 4 through 16 that exceed 0.400: Eigenvector 4 on characters 24 and 68; on 39, 89, and 105; 6 on 13, 77, and 89; 7 on 11 and 72; 8 on 8 and 9; 9 on 87 and 88; 10 on 82 nd 98; 11 on 82; 12 on 82 and 83; 15 on 91. The following negative loadings of eigenvectors 4 hrough 16 exceed —0.400: Eigenvector 5 on character 9; 7 on 69. The recurrence in these lists of igh loadings on the furcae and male fifth limbs emphasizes the quantity of taxonomic informaion available in these limbs, but it also suggests that more appropriate measurement of characters night yield simpler structure.

Although these results are not easy to interpret biologically, they offer much that the taxonomist hould ponder before making decisions about characters and genera. Minor differences from the nalyses of log-transformed data (not shown) provoke speculation about non-linearity of certain elationships.

CONCLUSIONS

Although the Family Macrocyprididae is a relatively small, homogeneous family, these simple nultivariate methods have yielded an alarming amount of new information, which cannot be fully ligested in the space available here. In general, the results support the prevailing opinion that the urcae and male fifth limbs have relatively high taxonomic value at the generic level, while most haracters of the sixth limb and female fifth limb have little taxonomic usefulness. However, a few haracters singled out by these methods as having potential taxonomic value had previously not een recognized as such, perhaps because they may have substantial non-linear components to heir variability.

The would-be numerical taxonomist of ostracods should find these results highly encouraging. t has been shown that simple screening of the data for conformity to a continuous distribution such s the normal distribution can serve to flag certain characters as highly likely or unlikely to possess axonomic value at the generic level. The R-mode cluster analyses of characters have provided a reat deal of information about their interrelationships. The principal components analyses preent comparable insights in more rigorous form. The Q-mode cluster analyses have detected posible flaws either in the current generic classification of species or in the way certain characters were neasured. For all these methods, discrepancies between results from raw and log-transformed data ave spotlighted body proportions that may have a non-linear basis; those characters should now e investigated further by other, regression-based, multivariate methods. Also highly desirable vould be comparable analyses of individual and geographical variability within species. Meanwhile, hese preliminary results will be very useful in completing the taxonomic revision of the family Macrocyprididae, and similar analyses should be undertaken for other living families of ostracods.

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DISCUSSION

Kaesler: Your use of a test of normality to assess the value of characters is interesting. I assume non-normality implies taxonomic usefulness only when the departure from normality is in the direction of platykurtosis or multimodality rather than toward leptokurtosis. Would you care to comment on this distinction?

Maddocks: I had not intended to emphasize this normality testing. The programs I used ran, this test routinely together with other descriptive statistics, and I thought the results sufficiently interesting to be worth mentioning. *A priori,* we have no reason to predict any particular distribution of a character among the species of a family. If it should turn out that some of these characters do approximate some definable distribution, of whatever type, this might suggest hypotheses about speciation.

Schweitzer: I think your emphasis on the normal distribution is misdirected. As I understand it, you look for characteristics that vary greatly among taxa, while varying only a little within taxa. At no time do you invoke probabilistic assumptions, so the null model of a gaussian distribution is totally arbitrary. Suppose one character had a distribution that was uniform (a boxcar). Then your test for non-normality would be significant, regardless of the taxonomic utility (=discriminating power) of the character. Bookstein *et al.* (1985. Morphometrics in Evolution: The geometry of size and shape change, with examples from fishes. Acad. Nat. Sci., Philadelphia) detail five reasons for log-transforming lengths and distances. Normality doesn't enter into it. I liked your talk and I think studies of this kind are very powerful. My complaint is just that the normality testing is not necessary. A simple F-ratio is what you need to show which characters have the power to discriminate between species or genera.

Maddocks: I agree that normality testing is unnecessary for the techniques used, but it is always a good idea to examine the univariate distributions of the characters being studied before proceeding with more sophisticated analyses. In this case I thought it interesting that initial scan of the data provided a fairly good prediction of the relative taxonomic value of many characters.

A Preliminary Study on Ornamentation and Ultrastructure of Mesozoic and Cenozoic Ostracoda in China

YOU-TANG HOU AND YU-HONG ZHAO
Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, P.R. China

ABSTRACT

This paper deals with an abundance of material collected in China, which has been studied by many Chinese ostracodologists and published over the past thirty years or more. The present writers make use of the types of more than 500 species of Mesozoic and Cenozoic non-marine and marine Ostracoda which were examined by the scanning electron microscope. From examining several thousand SEM photographs they consider that the pattern of ornamentation may be divided into twelve types, and the ultrastructure of the pores into six types. Summarizing all the types of ornamentation and pore ultrastructure, the writers here put forward some preliminary views. It is suggested that the type of ostracod ornamentation may reflect the relationships between some genera and their evolutionary process, while the type of pore is probably related to the sedimentary facies. The study of both would accumulate more material and evidence leading to a much wider field for future ostracod research.

INTRODUCTION

It is very important in classification and evolution of Ostracoda to study the ornamentation and ultrastructure of ostracod shell, which has been rapidly developed recently because of the using of Scanning Electron Microscope and Transmission Electron Microscope.

The different shape of pore in subfamily Schizocytherinae was found (Hanai, 1970), which was related with dimorphism of Ostracoda. The ultrastructure of carapace, marginal pores and very fine setal pore of some ostracods were described by Langer (1973), who got some available conclusion. Puri and Dickau (1969) and Puri (1974) detected normal pores of some ostracods and discussed those using in taxonomy and phylogeny of ostracods. Rosenfeld and Vesper (1976) studied the variability of the sieve pores in both recent and fossil species *Cyprideis torosa* (Jone, 1850) and considered that the palaeoenvironment, especially the palaeosalinity, can be deduced by the sieve-pores. Development of sieve pores and ultrastructure of carapace-sensilla of some species were investigated by Keyser (1982, 1983), who discussed the possible function of the pores and bristle in the pore. Okada (1982a, b; 1983) paid a more attention to establish the relation between the ornamentation of shell surface and the cell in epidermis and to discuss the ultrastructure and function of pore of ostracods.

In China, the studying of the ultrastructure of carapace, ornamentation and trace elements of ostracod shell was started in the later of 1970's. The junior author, in his master thesis (1981) and his doctoral dissertation (1984) (both in press), described shape of pore canals of some ostracods, established five types of ultrastructure of carapace, and discussed the relationship between the trace elements in shell and the palaeoenvironment, in which the ostracods once lived.

Recently greater attention has been paid by Chinese ostracod researchers to shell ornamentation and pore ultrastructure of ostracods collected in China. This paper deals with a large amount of material which has been studied by many Chinese ostracod workers and published in the past thirty-odd years. The present writers make use of the holotypes and homotypes described and illustrated in these publications, amounting to more than 500 species and nearly 1,000 individuals of Mesozoic and Cenozoic non-marine or marine Ostracoda, which were examined by means of the scanning electron microscope. From several thousand scanning electron microphotographs they observed that the ornamentation of the shell and the ultrastructure of the pores show many patterns and consider that both kinds of patterns may be divided into twelve and six types respectively (see Tables 1 and 2).

TABLE 1—TYPES OF OSTRACOD ORNAMENTATION

A. Reticulate type
   1. Polygonal reticulate type
   2. Granular ridge-like reticulate type
   3. Transverse bar-bearing reticulate type
   4. Polyform reticulate type
   5. Round reticulate type
   6. Scale-like reticulate type

B. Spot-shaped type
   1. Punctate ornamented type
   2. Measles-like ornamented type

C. Echinulate type
   1. Spine-like echinulate type
   2. Granular echinulate type

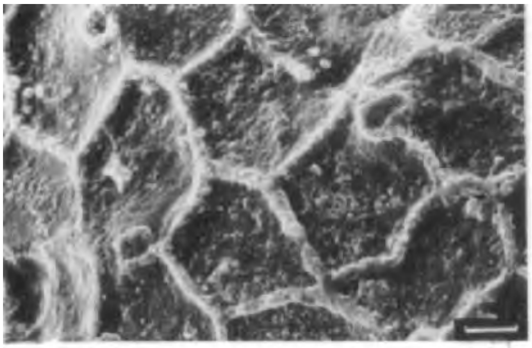
D. Striate type
   1. Corduroy-like striate type
   2. Fingerprint-like striate type

TABLE 2—TYPES OF OSTRACOD PORES

A. Types of simple pores
   1. Single circular pores
   2. Double circular pores
   3. Lip-like circular pores
   4. Funnel-shaped circular pores

B. Types of sieve pores
   1. Round sieve pores
   2. Elongate or irregular sieve pores

PLATE 1—Fig. 1. *Limnocythere nodosa* Bojie, Polygonal reticulate ornamentation, Bar=10 μm. Fig. 2. *Paracandona euplectella* (Robertson), Granular ridge-like reticulate ornamentation, Bar = 10 μm. Fig. 3. *Limnocythere bucerusa* Sou, Transverse bar-bearing reticulate ornamentation, Bar = 100 μm. Fig. 4. *Leucocythere plena* Y.H. Zhao, Polyform reticulate ornamentation, Bar = 10 μm. Fig. 5. *Cypridea favosa* Ye, Round reticulate ornamentation, Bar = 100 μm. Fig. 6. *Cypridea*? *dissona* Netchaeva, Scale-like reticulate ornamentation, Bar = 100 μm. Fig. 7. *Camarocypris ovata* Bojie, Punctate ornamentation, Bar = 30 μm. Fig. 8. *Sinocypris funingensis* Ho, Measles-like ornamentation, Bar = 100 μm.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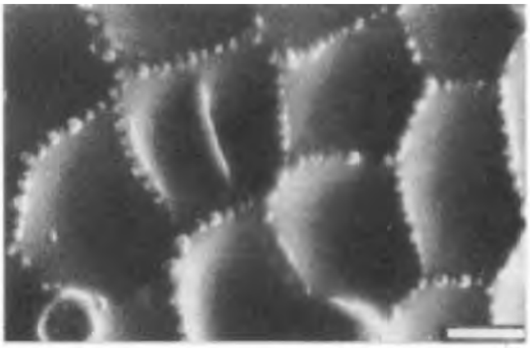
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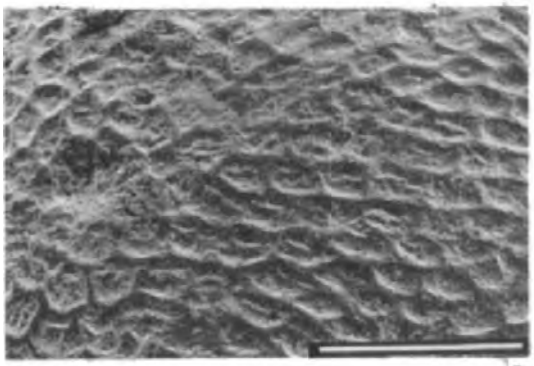
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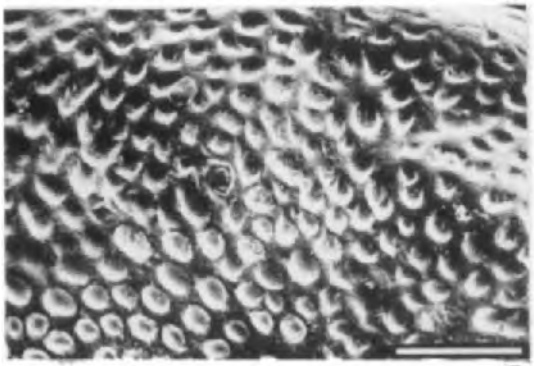
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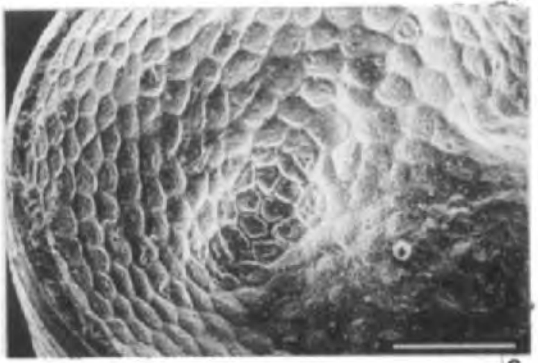
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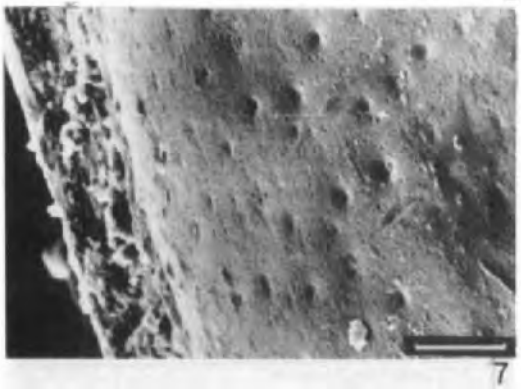
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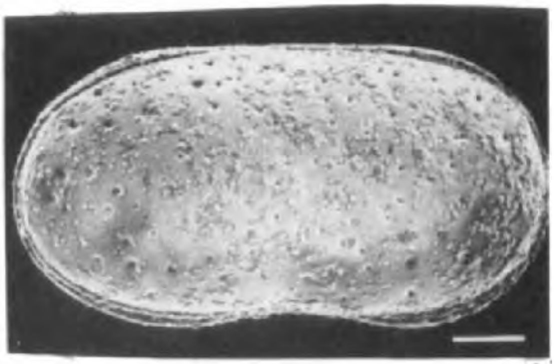
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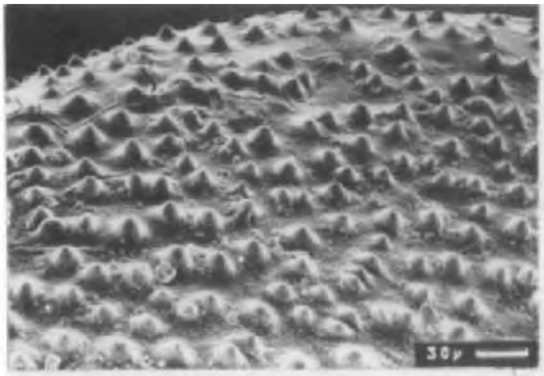

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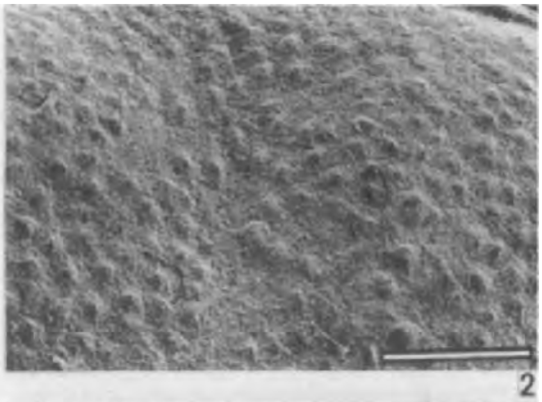

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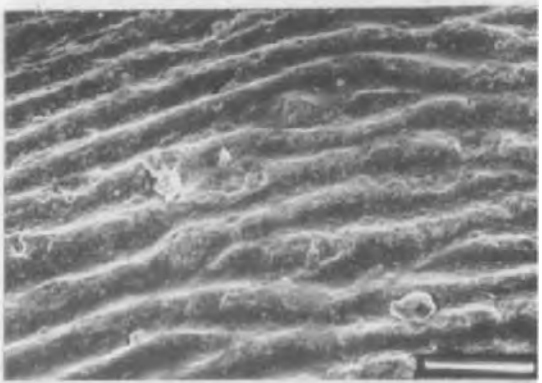

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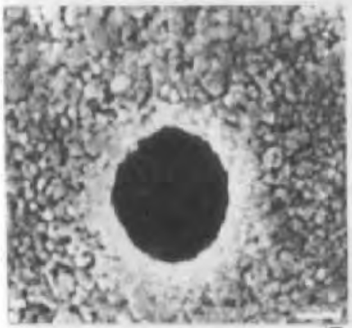

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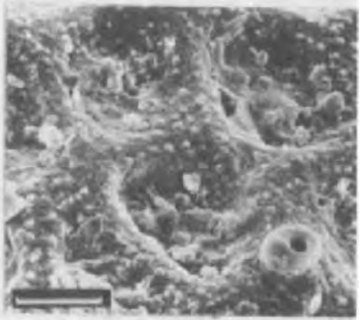

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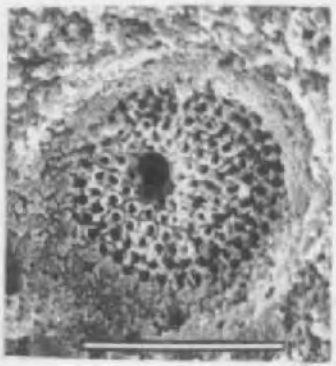

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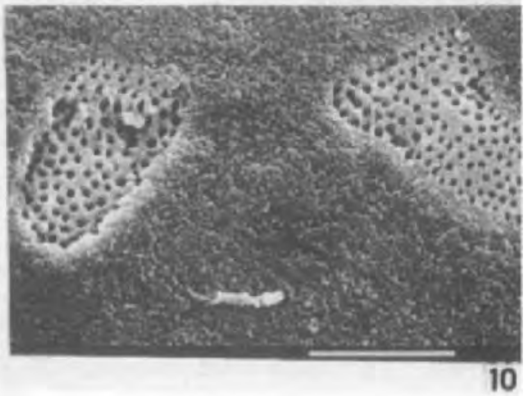

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TYPES OF SHELL ORNAMENTATION

Reticulate types

1. Polygonal reticulate type, with surface ornamentation composed of polygonal reticulation. Meshes very shallow and flat, as in some species of the genera *Limnocythere, Chinocythere* and *Ilyocypris.* especially clear in *Limnocythere bicostata* Bojie, *L. microcostata* Bojie, *L. longipileiformis* Bojie, *L. nodosa* Bojie, *L. dectyophora* Bojie (Pl. 1, fig. 1).

2. Granular ridge-like reticulate type, possesses reticulate ridges consisting of many micrograins arranged in regular order; reticulation generally appearing in pentagonal or hexagonal shapes as in *Paracandona euplectella* (Robertson) (Pl. 1, fig. 2).

3. Transverse bar-bearing reticulate type, with meshes rather irregular, rhomboidal, hexagonal or sub-quadrate in shape and unequal in size; each mesh with a transverse bar, which may be longer or shorter, as in *Limnocypridea bucerrusa* Sou, *L. inflata* Ye and *Ilyocyprimorpha netchaevae* Su (Pl. 1, fig. 3).

4. Polyform reticulate type, bearing a lot of secondary ornamentation in the shape of five-pointed stars or six to seven or three to four round pits in each irregular reticulate mesh, as shown on the surface of *Limnocythere* (*Xinanolimnocythere*) *tribulosa* Y.H. Zhao, *Leucocythere plena* Y.H. Zhao and *Abrotocythere quadracornis* Y.H. Zhao (Pl. 1, fig. 4).

5. Round reticulate type, with round meshes spreading all over the surface, sometimes slightly oblong in shape, often varying in size and area between adjacent meshes. All these features are usually observable in genera such as *Cypridea, Ilyocyprimorpha, Limnocypridea, Huabeinia, Quadracypris, Talicypridea,* etc., and occasionally in a few species belonging to the genera *Tuozhuangia* and *Chinocythere.* Species which are considered to show the typical ornamentation include *Cypridea bella* Chen, *C. favosa* Ye, *C. fuyuensis* Ding, *C.* (*Cypridea*) *semimorula* Chen, *C.* (*C.*) *cellularia* Chen, *Ilyocyprimorpha magnifica* Liu, *I. sungarienensis* Ten, *Limnocypridea datongzhenensis* Ye, *Huabeinia huidongensis* Bojie, *H. postideclivis* Bojie, *Tuozhuangia alispinata* Bojie, *Chinocythere xinzhenensis* Bojie, etc. (Pl. 1, fig. 5).

6 Scale-like reticulate type, ornamented with scale-shaped reticulation arranged densely on the surface and observable in such species as *Cypridea*? *dissona* Netchaeva (Pl. 1, fig. 6).

Spot-shaped types

1. Punctate ornamented type, with many punctate pits over the whole surface of the valves, with *Camarocypris elliptica* Bojie, *C. ovata* Bojie as representatives of this pattern (Pl. 1, fig. 7).

2. Measles-like ornamented type, shell surface completely covered by a number of very small round punctuations. *Sinocytheridea latiovata* Hou et Chen, *S. longa* Hou et Chen and *Sinocypris funingensis* Ho are representative (Pl. 1, fig. 8) of this type.

Echinulate types

1. Spine-like echinulate type, with a great number of small spines distributed over the surface;

PLATE 2—Fig. 1. *Dongyingia impolita* Bojie, Spine-like echinulate ornamentation, Bar = 30 μm. Fig. 2. *Cypridea* (*Sebastianites*) *tumida* Ho, Granular echinulate ornamentation, Bar = 100 μm. Fig. 3. *Ziziphocypris rugosa* (Liu), Corduroy-like striate ornamentation, Bar = 100 μm. Fig. 4. *Berocypris substriata* Bojie, Fingerprint-like striate ornamentation, Bar = 30 μm. Fig. 5. *Metacypris aphthosa* Y.H. Zhao, Single circular pore, Bar = 1 μm. Fig. 6. *Cypridopsis caohaiensis* Y.H. Zhao, Double circular pore, Bar = 1 μm. Fig. 7. *Ilyocypris neoaspera* Huang, Lip-like circular pore, Bar = 10 μm. Fig. 8. *Candona daliensis* Huang, Funnel-shaped circular pore, Bar = 1 μm. Fig. 9. *Cythere lutea lutea* O.F. Müller, Round sieve pore, Bar = 10 μm. Fig. 10. *Cushmanidea japonica* Hanai, Elongate or irregular sieve pore, Bar = 10 μm.

Dongyingia impolita Bojie and *Ilyocyprimorpha inandita* are representative of this pattern (Pl. 2, fig. 1).

2. Granular echinulate type, decorated with many small grain-like tubercules over the whole surface, with *Cypridea* (*Sebastianites*) *tumida* Ho as the typical example (Pl. 2, fig. 2).

Striate types

1. Corduroy-like striate type, with curved, continuous and disconnected striations present on the surface, as observed in the non-marine species *Ziziphocypris rugosa* (Liu), *Z. simakovi* (Mandelstam) and the marine species *Perissocytheridea trapeziformis* Hou et Chen, as far as known (Pl. 2, fig. 3).
2. Fingerprint-like striate type, bearing curved striations rather like fingerprints, sometimes branching or with two merging into one; distance between two striae unequal—as shown on the surface of *Berocypris substriata* Bojie, *B. striata* Bojie and *Virgatocypris striata* Bojie (Pl. 2, fig. 4).

TYPES OF OSTRACOD PORES

Types of simple pores

1. Single circular pores. Pores round in shape, simple, and evenly distributed; size and space between pores variable in different genera and species, usually found on the surface of many ostracod species collected from non-marine strata in China, with *Candona* and *Metacypris* as very typical patterns (Pl. 2, fig. 5).
2. Double circular pores. Pores appearing doubly-circular in form, connected with one another around a common centre, as in *Cypridopsis caohaiensis* Y.H. Zhao and *Cyclocypris* persicaria Y.H. Zhao (Pl. 2, fig. 6).
3. Lip-like circular pores. Pores appear to have a collar-like flange under high magnification, quite commonly occurring in non-marine ostracod species observed under the SEM, as in *Chinocythere, Limnocythere, Ilyocypris,* etc. (Pl. 2, fig. 7).
4. Funnel-shaped circular pores. Pores on the surface appear somewhat funnel-like and are only found in a few non-marine ostracod species, such as *Candona daliensis* Huang (Pl. 2, fig. 8).

Types of sieve pores

1. Round sieve pores. Pores circular in shape, with a large one in the centre or near the margin but absent in a few species; different in size and arrangement with different species and genera. So far only found in marine ostracods such as *Perissocytheridea trapeziformis* Hou et Chen, *Neocytherideis convexa* Hou et Chen, *Sinocytheridea latiovata* Hou et Chen, *S. longa* Hou et Chen, *Chthere lutea lutea.* O.F. Müller, *Eucythere* sp., etc. (Pl. 2, fig. 9).
2. Elongate or irregular sieve pores. Pores appearing elongate or irregular in shape, often in association with circular sieve pores on the same shell surface, as in *Cushmanidea japonica* Hanai (Pl. 2, fig. 10).

SUMMARY AND CONCLUSIONS

Summing up all the types of ornamentation and pore ultrastructure mentioned above, the writers here put forward their preliminary views:

1. Types of surface ornamentation can be similar to each other in different species of the same genus or of different genera.

2. Although some fossil ostracods can be found in different sedimentary conditions in different areas, their ornamentations bear obvious similarities to each other.
3. In general, similar ornamentation may occur in different species of the same genus distributed in different geological ages. For example, the geological range of *Limnocythere* is from Tertiary to Recent, but the ornamentation of different species in this genus is commonly polygonal reticulate. On the other hand, a close relationship exists between some species of *Cypridea* and some species of *Talicypridea* or *Quadracypris,* both of which possess the same kind of ornamentation belonging to the round-pit reticulate type.
4. Although the type of ornamentation varies in different parts of the same shell surface, as seen in *Limnocypridea succinata* Ding and *Neocytherideis convexa* Hou et Chen, the variation is stable in different individuals of the same species, as in *Limnocythere* (*Xianolimnocythere*) *trilubosa* Y.H. Zhao and *Abrotocythere quadracornis* Y.H. Zhao.
5. Types of pores are obviously different between Ostracoda collected from marine strata and from non-marine strata. They are probably not influenced by the type of ornamentation, but may be controlled by sedimentary facies, or more specifically, by salinity.

From a macroscopic view, it seems that the variation in ostracod ornamentation is not controlled by the factors of time and space, but possibly caused by some factors in the organism itself. Preliminary assessment of the large amount of material described in this paper reveals that there is probably a close relationship between the character of ostracod ornamentation and their evolution and therefore the study of shell ornamentation would provide evidence not only for evolutionary affinity, but also for their classification. It is especially significant in dealing with the problems of ostracod classification and evolution. The results of observations on the samples suggest that the different pore types are closely linked with sedimentary conditions such as salinity, etc., so the type of pore can be considered as one of the indicators for determining the sedimentary facies and conditions under which the ostracod lived.

To sum up, the type of ostracod ornamentation may reflect the relationship between some genera and their evolutionary processes, while the type of pore is probably related to the sedimentary facies. The study of both these features would accumulate more material and evidence leading to a much wider field for ostracod researchers in the future.

ACKNOWLEDGEMENTS

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Ultrastructure of Myodocopid Shells (Ostracoda)

I.G. SOHN AND LOUIS S. KORNICKER
U.S. Geological Survey, Washington, D.C. and
National Museum of Natural History, Washington, D.C., U.S.A.

ABSTRACT

Based on the study of scanning electron micrographs of cross-sections of ostracod shells representing 17 species in genera of the suborders Cladocopina, Halocypridina, and Myodocopina, five primary components are identified in the endocuticle: 1—laminate, 2—columnar, 3—fine granular, 4—coarse granular, 5—homogeneous. Crystalline nodules, rare *in vivo*, but common in preserved specimens, are considered to represent a secondary component. Preliminary experimentation with sun-dried shells of *Vargula hilgendorfii* indicates that crystalline nodules form in 10% buffered formalin, a commonly used preservative of plankton. Examination of two growth stages of this species suggests the same general combination of components during ontogeny.

Pelagic species of *Gigantocypris, Halocypris, Conchoecia,* and *Macrocypridina* have laminate endocuticles, but the pelagic *Codonocera polygonia* has both laminate and coarse granular components in the endocuticle. Benthonic species may have only one or a combination of any of the five components, but not more than four components in a species.

Based on this and previous studies, the ultrastructures of the endocuticles of the following taxa are known: *Metapolycope hartmanni, Polycope* sp., *Conchoecia atlantica, C. valdiviae, C. belgica, Halocypris inflata, Thaumatoconcha caraionae, T. tuberculata, Asteropterygion setiferum, Macrocypridina castanea, Gigantocypris muelleri, Scleroconcha folinii, Vargula hilgendorfii, Codonocera polygonia, Eusarsiella texana, E. disparalis, Spinacopia* sp.

INTRODUCTION

The purpose of this study is to examine cross-sections of the shells of myodocopid ostracods with scanning electron microscopy (SEM) in order to determine their ultrastructure. We report on the ultrastructure of 17 species in the suborders Cladocopina, Halocypridina, and Myodocopina, and we identify five different primary components in the shells (Table 1); crystalline nodules are considered to be a secondary component. The combinations of the various components of the shells are discussed relative to taxonomy and environment.

METHODS

Scanning electron microscopy techniques in the National Museum of Natural History were re-

TABLE 1—SHELL ULTRASTRUCTURE AND HABITAT OF MYODOCOPA

Taxon	Laminate	Columnar	Fine granular	Coarse granular	Homogeneous	Habitat	Source
Suborder CLADOCOPINA							
Metapolycope hartmanni Kornicker and van Morkhoven, 1976	—	X	X	—	—	B	Kornicker and van Morkhoven, 1976 fig. 7d.
Polycope sp.	—	X	X	—	—	B	Herein, Pl. 2, fig. 4.
Suborder HALOCYPRIDINA							
Conchoecia atlantica (Lubbock, 1856)	X	—	—	—	—	P	Herein, Pl. 1, figs. 6–9; Pl. 2, fig. 5.
C. belgica Müller, 1906b	X	—	—	—	—	P	Bate and East, 1972, fig. 10; 1975, Pl. 3, fig. 8.
C. valdiviae Müller, 1906a	X	—	—	—	—	P	Bate and Sheppard, 1982, Pl. 7, figs. 1, 2.
Halocypris inflata (Dana, 1849)	X	—	—	—	—	P	Bate and Sheppard, 1982, Pl. 4, fig. 4; Pls. 5–10.
Thaumatoconcha caraionae (Kornicker and Sohn, 1976)	—	X	—	—	—	B	Herein, Pl. 4, fig. 7.
T. tuberculata Kornicker and Sohn, 1976	—	X	X	—	—	B	Herein, Pl. 4, figs. 8–10.
Suborder MYODOCOPINA							
Asteropterygion setiferum Kornicker and Caraion, 1974	X	—	—	—	—	B	Herein, Pl. 1, figs. 10, 11; Kornicker, 1975, figs. 17, 18.
Codonocera polygonia Poulsen, 1962	X	—	—	X	—	P	Bate and Sheppard, 1982, Pl. 2, fig. 5.
Eusarsiella disparalis (Darby, 1965)	X	—	X	X	—	B	Herein, Pl. 4, figs. 3–6; Pl. 5, figs. 14, 15.
E. texana (Kornicker and Wise, 1962)	—	—	—	X	—	B	Herein, Pl. 5, figs. 7–9.
Gigantocypris muelleri Skogsberg, 1920	X	—	—	—	—	P	Herein, Pl. 1, figs. 1–5; Harding, 1965, fig. 8.
Macrocypridina castanea (Brady, 1897)	X	—	—	—	—	P	Herein, Pl. 2, fig. 1; Bate and East, 1975, Pl. 3, figs. 9, 10.
Scleroconcha folinii (Brady, 1871)	—	X	—	—	X	B	Herein, Pl. 2, figs. 2, 3.
Spinacopia sp.	X	—	X	—	—	B	Herein, Pl. 5, figs. 10–13.
Vargula hilgendorfii (Müller, 1890)	X	X?	—	X	X	B	Herein, Pl. 2, figs. 6–8; Pl. 3, figs. 1–7; Pl. 4, figs. 1, 2.

(X = present, — = absent, B = benthonic, P = pelagic)

cently described (Sohn, 1983, p. 10). Except for those specimens of *Vargula hilgendorfii* (Müller, 1890) that were sun-dried as soon as collected, the specimens prepared for scanning electron microscopy had been preserved in alcohol. The sun-dried specimens were fractured by pressing with a thick needle, and the fragments were mounted on stubs for study. The wet specimens were either

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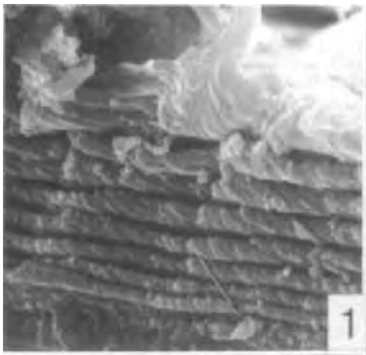
PLATE 1—Figs. 1–5. *Gigantocypris muelleri* Skogsberg, 1920. USNM 151241A. 1, 2, section made by cryofracture to show laminae, approx. ×1,450 and ×5,800, respectively. Area of 2 shown by arrow on fig. 1. Figs. 3–5, torn sections of the same specimen, approx. ×470, ×1,500, and ×4,700, respectively. Arrow on fig. 3 indicates epicuticle; area of 5 shown on fig. 4 by arrow; outer surface of valve towards bottom of plate. Locality 1. Figs. 6–9. *Conchoecia atlantica* (Lubbock, 1856). Adult male, left valve, USNM 149290. 6, 7, cut sections near dorsal margin above incisur of valve showing laminae, approx. ×2,000 and ×4,500, respectively. Adhering objects are bacterial contamination during preparation. Sections oriented with outer surface of valve towards top of plate. 8, 9, cut section in other area behind midlength at midheight of same fragment, approx. ×2,200 and ×4,500, respectively. Area of 9 shown by arrow on fig. 8; laminae separated during preparation. Sections oriented with outer surface of valve towards top of plate. Locality 2. Figs. 10, 11. *Asteropterygion setiferum* (Kornicker and Caraion, 1974). Adult female, right valve sliced with razor blade, USNM 143996. 10, epicuticle (arrow) and part of laminated endocuticle, showing that elongate process is confined to epicuticle, approx. ×5,100. 11, detail showing laminae, approx. ×9,800. Sections oriented with outer surface of valve towards top of plate. Locality 3.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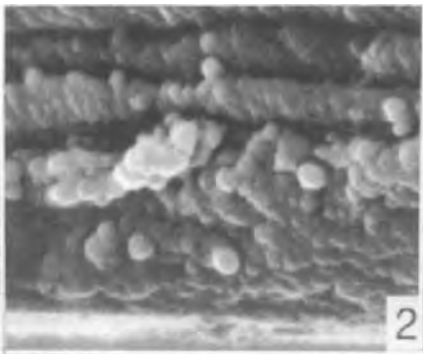
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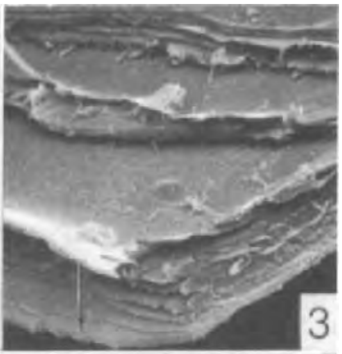
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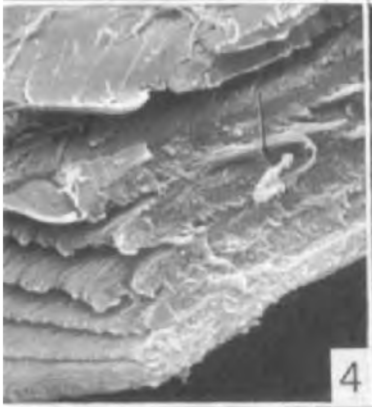
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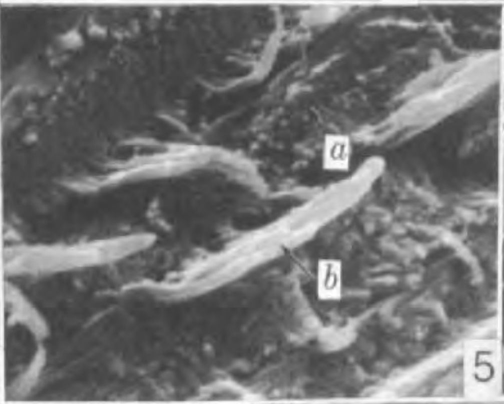
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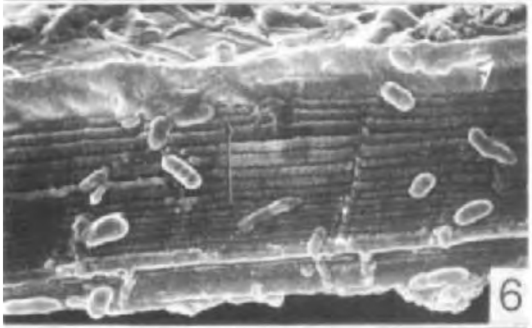
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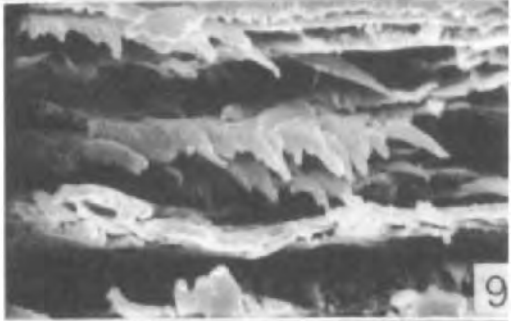
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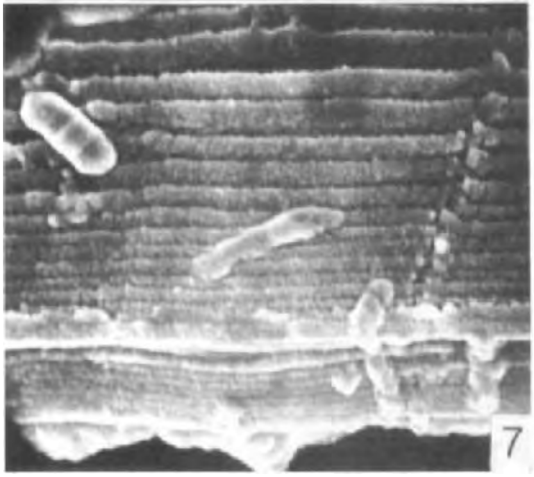
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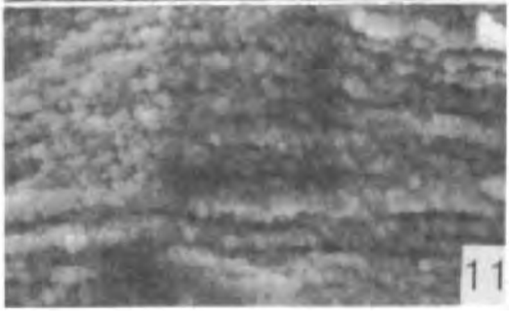
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cryofractured or cut with a sharp blade and then freeze-dried. When a carapace of a myodocopid is cut, the edges of the specimens may smear, masking the ultrastructure (lower part of Pl. 1, fig. 9); cryofracture more consistently gives better results. The technique of cryofracture consists of quick-freezing a specimen immersed in a drop of water at −40° C; the frozen drop is then fractured by hitting with a sharp edge.

The specimen illustrating the dorsal attachment of the two valves (ligament) on Pl. 3, fig. 7, is a sun-dried carapace of *V. hilgendorfii*. Before freeze-drying, the carapace was decalcified by soaking in a slightly acid wetting agent (Aerosol OT), and some of the organic matter was removed with dilute sodium hypochlorite.

DISCUSSION

We follow Kornicker (1969, p. 114) as well as Bate and Sheppard (1982, p. 29) in considering the shell of Myodocopa to consist of two parts: an epicuticle and an endocuticle (=procuticle). The epicuticle consists of a very thin layer above the outer surface of the thicker and more structurally complex endocuticle. The epicuticle appears to lack internally differentiated ultrastructures. Puncta as well as certain surface structures on the valves are confined to the epicuticle in the taxa examined. The mineralogy of myodocopid shells is poorly known. E. R. Roseboom (in Sohn and Kornicker 1969, p. 103) determined that the shell of *V. hilgendorfii* contains monohydrocalcite ($CaCO_3 . H_2O$). Crystalline nodules in the myodocopids are calcite (Sohn and Kornicker, 1969; Bate and Sheppard, 1982, p. 27).

The appearance of the ultrastructure may depend on the method of fracturing of the shell. Plate 1, figures 1 and 2, are of a cut cross-section normal to the valve surface of *Gigantocypris muelleri* Skogsberg, 1920, whereas Pl. 1, figs. 3–5, are of an oblique tear on the same specimen showing laminae in three dimensions. Similar influences of preparation are illustrated for *Conchoecia atlantica* (Lubbock, 1856) of which Pl. 1, figs. 6 and 7 are of clean cuts, whereas figures 8 and 9 illustrate frayed edges of some of the laminae.

We recognize five primary components in the ultrastructure of myodocopid shells (Table 1): 1, laminate; 2, columnar; 3, fine granular; 4, coarse granular, and 5, homogeneous.

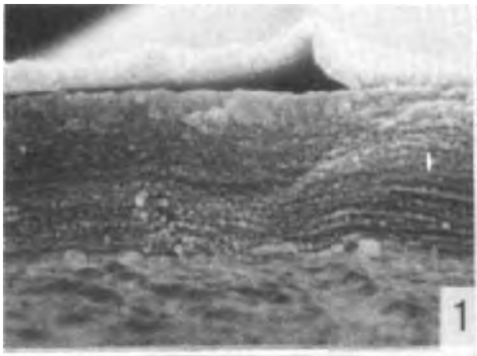
1. Laminate: This component consists of thin layers in cut sections; on torn sections, however, the layers have ragged edges "chitin" shown on Pl. 1, figs. 3–5. In *Gigantocypris muelleri*, finely granulated layers separate the "chitin" layers.

2. Columnar: This component consists of lineations perpendicular to the shell surfaces (Pl. 2, figs. 3, 4)

3. Fine granular: This component consists of unlayered small rounded granules (Pl. 2, fig. 4).

4. Coarse granular: This component consists of relatively large polygonal grains with con-

PLATE 2—Fig. 1. *Macrocypridina castanea* (Brady, 1897). Adult male, USNM 151167B, cross-section of carapace, approx. ×2,500. Locality 4. Figs. 2, 3, *Scleroconcha folinii* (Brady, 1871). Ovigerous female, USNM 141545, cut sections near central adductor muscles, approx. ×510 and ×4,900, respectively. Area of fig. 3 shown on fig. 2 by arrow. Note on fig. 2 thin epicuticle, which separated from endocuticle during preparation. Locality 5. Fig. 4, *Polycope* sp. Adult male, USNM 149325, broken section, approx. ×2,700. Note relatively thick epicuticle and shallow puncta confined to epicuticle (arrow). Locality 6. Fig. 5. *Conchoecia atlantica* (Lubbock, 1856). Adult male, left valve. USNM 149290. Broken section at inner fold of rostrum showing laminae of endocuticle and bacteria contamination on epicuticle, approx. ×2,200. Same specimen as Pl. 1, figs. 6–9. Locality 2. Figs. 6–8. *Vargula hilgendorfii* (Müller, 1890). Sun-dried carapace, crushed fragments, USNM 193163C. 6, broken section of right valve, approx. ×4,850, showing coarse granular, laminate, and columnar(?) components of endocuticle. 7, section of fragment showing in two dimensions the coarse granular middle component (arrow *a*), and the innermost layer (arrow *b*), approx. ×1,950. 8, montage of cross-section, approx. ×4,850, showing epicuticle (arrow *a*), four components of endocuticle (arrows *b*–*e*). Locality 7.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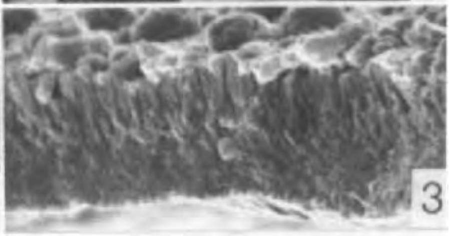
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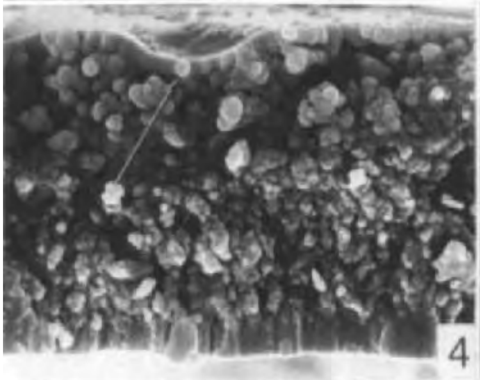
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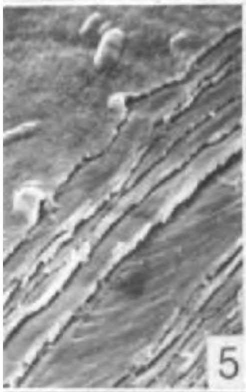
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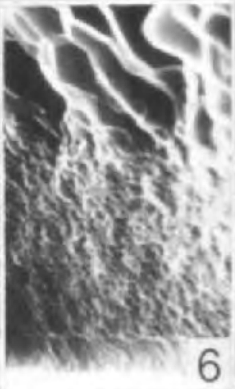
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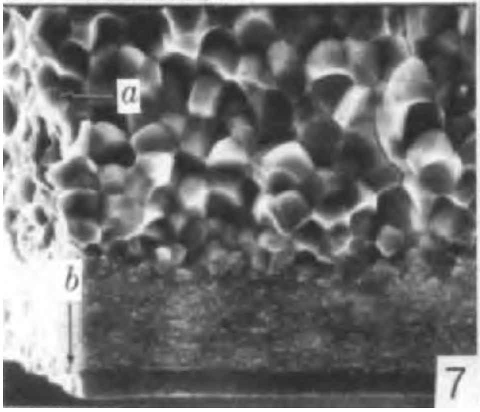

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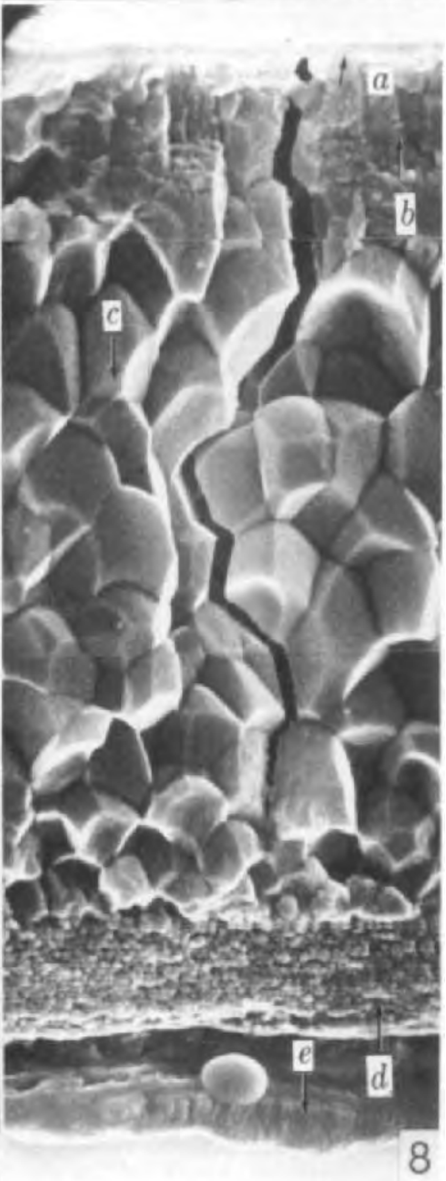

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choidal faces convex towards the outside of the valve (Pl. 2, figs. 7, 8). We think that the granules in this component (Pl. 4, figs. 3–6) and the net-like counterparts (Pl. 4, figs. 1, 2; Pl. 5, figs. 11, 12, 14, 15) are *post-mortem* artifacts resulting from dehydration of the monohydrocalcite-protein complex in the particular kind of nonlaminate ultrastructure forming the endocuticle.

5. Homogeneous: This component is dense and non-granular under magnifications examined (Pl. 2, fig. 8b).

In addition to the primary components, we recognize crystalline nodules as a secondary component. These calcite nodules are sparse *in vivo,* are common as a posthumous component in preserved specimens and can be produced in the laboratory (Pl. 3, fig. 6; Pl. 4, figs. 8, 9; Pl. 5, figs. 1–7, 9–13; Pl. 6).

OBSERVATIONS

The components are distributed among the taxa as follows:

Endocuticle with only laminate component: Taxa with laminate endocuticles are listed on Table 1, and this structure is illustrated on Pl. 1, figs. 10, 11 for *Asteropterygion setiferum.* The ultrastructure of the shell consists of a thin epicuticle (arrow on fig. 10) not readily distinguishable from the underlying lamina of the endocuticle. The surface ornaments or processes are extensions of the epicuticle (fig. 10). The endocuticle is uniformly laminated (fig. 11). Additional illustrations of the ultrastructure of this specimen are in Kornicker (1975, Fig. 18). *Macrocypridina castanea* has a similar endocuticle (Pl. 2, fig. 1); see also Kornicker *et al.* (1976, fig. 2d).

The ultrastructure of *Conchoecia atlantica* is illustrated on Pl. 1, figs. 6–9, and Pl. 2, fig. 5. This species has a thin dense epicuticle (arrow on Pl. 1, fig. 6). In an adult male of this species the laminations of the endocuticle become progressively thinner inward from the outer margin. However, the innermost group of relatively uniformly thinner laminae is separated from the main laminate component by a single thicker lamina (Pl. 1, figs. 6, 7). The endocuticle on the inside fold of the rostrum is also laminate (Pl. 2, fig. 5). Bate and Sheppard (1982, Pl. 7) illustrated a similar progressively thinning laminae in *C. valdiviae.* Bate and East (1972, Fig. 10) showed that a laminate ultrastructure is present in *C. belgica. Halocypris inflata* has a similar laminate ultrastructure (Bate and Sheppard, 1982, Pls. 4, 6, 8, 9).

The ultrastructure of *Gigantocypris muelleri* is illustrated on Pl. 1, figs. 1–5. This species has a thin, dense epicuticle (arrow in Pl. 1, fig. 3), and the laminae of the endocuticle become progressively thicker inward from the outer margin (Pl. 1, fig. 1). Figs. 3–5 show a torn cross-section, whereas figs. 1 and 2 illustrate a cross-section obtained by cryofracture. The torn sections demonstrate that the individual lamina is complex. Each lamina consists of both granular (arrow *a* on fig. 5) and fibrous parts (arrow *b* on fig. 5). Similarly laminated ultrastructures in *G. muelleri* were illustrated on additional specimens by Harding (1965, Fig. 8) and by Kornicker *et al.* (1976, Fig. 15f).

The alternating granular and fibrous layers (Pl. 1, fig. 5) of the laminate component in the slightly calcified pelagic *Gigantocypris muelleri* were not observed in the benthonic more heavily calcified taxa.

Endocuticle without laminate and with columnar, fine granular, or homogeneous components: The ultrastructure of *Scleroconcha folinii* is shown on Pl. 2, figs. 2, 3. The epicuticle is thin and pustulose. The inner part of the endocuticle is homogeneous, the outer part is columnar (fig. 3).

The ultrastructure of *Polycope* sp. is shown on Pl. 2, fig. 4. The epicuticle is thin and punctate (arrow on fig. 4). The endocuticle is finely granular with a thin columnar inner component (fig. 4)

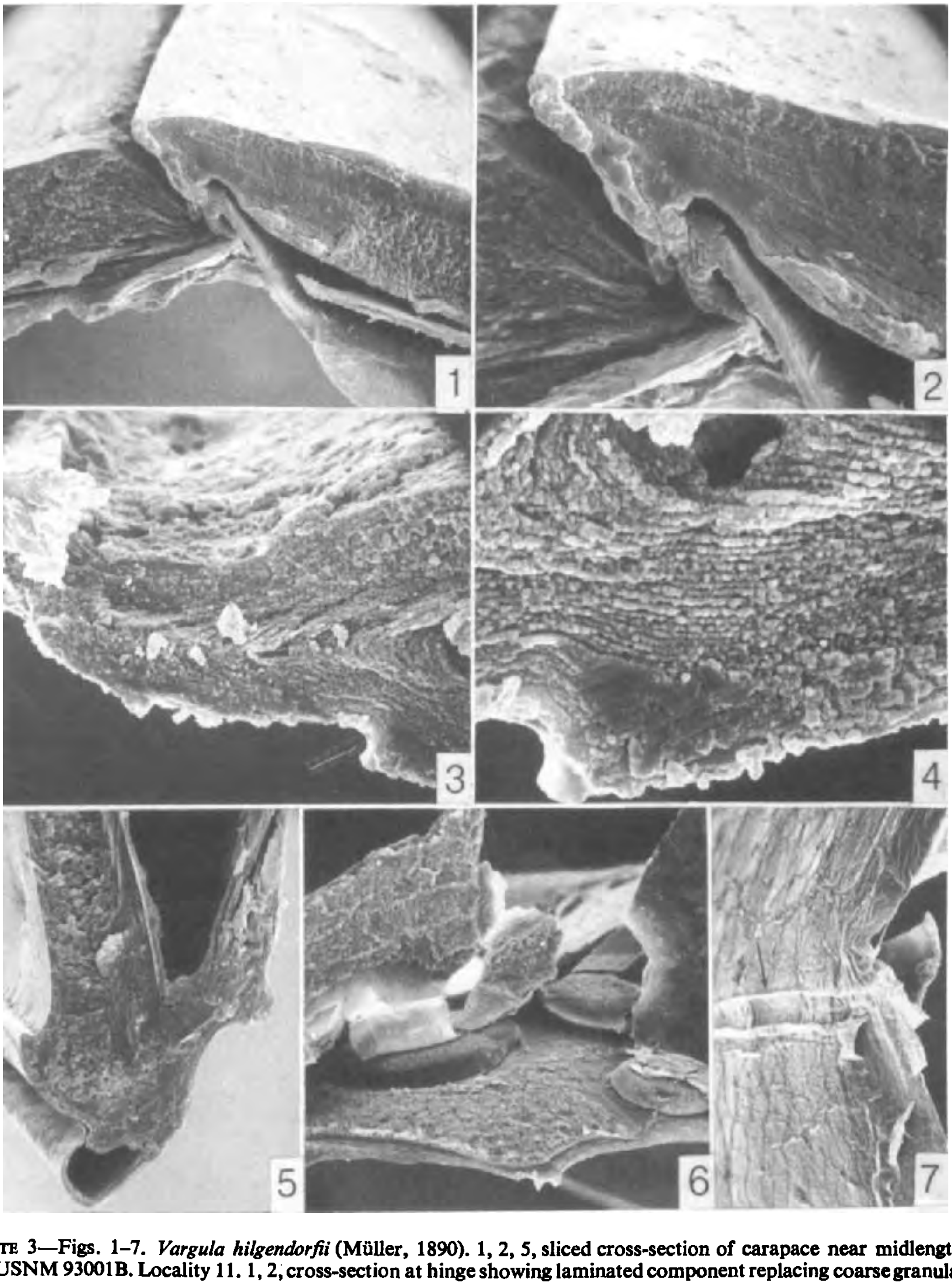

PLATE 3—Figs. 1–7. *Vargula hilgendorfii* (Müller, 1890). 1, 2, 5, sliced cross-section of carapace near midlength. USNM 93001B. Locality 11. 1, 2, cross-section at hinge showing laminated component replacing coarse granular component, approx. ×640 and ×1,267, respectively. 5, cross-section of the same specimen at free margin showing coarse granular and laminate components, approx. ×490. 3, 4, 6, cryofractured carapace that had been preserved in alcohol. USNM 193164. Locality 8. 3, detail of infold demonstrating laminate component folded inward to form infold, approx. ×1,000. 4, laminated infold, area shown by arrow on fig. 3, approx. ×1,850. 6, nodules postulated to have formed *in vivo*, approx. ×120. 7, sun-dried decalcified carapace demonstrating dorsal attachment of the valves (arrow shows ligament), approx. ×210. USNM 193163A. Locality 7.

Two species of *Thaumatoconcha* Kornicker and Sohn, 1976 have a thin epicuticle. The endocuticle of *T. caraionae* is columnar (Pl. 4, fig. 7). *T. tuberculata* has an additional fine grained granular component between the epicuticle and the columnar components (Pl. 4, figs. 8–10). The columnar component of *T. tuberculata* appears to be prismatic, possibly due to recrystallization as suggested by its nodose inner surface (Pl. 4, fig. 8, lower left in fig. 9). This structure might be due to coalescing nodules.

Endocuticle with laminate and coarse granular components, and with or without homogeneous, fine granular, or columnar components: The ultrastructure of *Vargula hilgendorfii* is shown on Pl. 2, figs. 6–8; Pl. 3; Pl. 4, figs. 1, 2; Pl. 5, figs. 1–6; Pl. 6, Pl. 7. The epicuticle is thin and punctate (arrow *a* on Pl. 2, fig. 8). The endocuticle consists of four components: 1, an outer homogeneous layer under the epicuticle (arrow *b* on Pl. 2, fig. 8); 2, a thick coarse granular middle layer in which the grains decrease in size toward the inside (arrow *a* on Pl. 2, fig. 7; arrow *c* on Pl. 2, fig. 8); 3, a laminate layer consisting of many thin laminae (arrow *d* on Pl. 2, fig. 8), and 4, an innermost thin, poorly defined columnar (?) layer (Pl. 2, bottom fig. 6, *b*, fig. 7, *e*, fig. 8). This innermost layer may represent the basement membrane shown in *Halocypris inflata* by Bate and Sheppard (1982, Pl. 6). but in this study it is provisionally considered part of the endocuticle.

Eusarsiella disparalis differs from *V. hillgendorfii* in that the component between the epicuticle and the coarse granular component is fine granular instead of homogeneous (Pl. 4, figs. 3, 4), and in the absence of the innermost columnar component (Pl. 4, figs. 5, 6). The coarse granular component is present in *E. texana* (Pl. 5, figs. 7, 8); however, the other components are indistinct due to the formation of crystalline nodules. The similarly recrystallized specimen of *Spinacopia* sp. (Pl. 5, figs. 10–13) has a coarse granular component above a laminate inner component.

Endocuticles with crystalline nodular component: Calcareous nodules are common components of myodocopid shells, but their distribution is variable (abundant in some carapaces, absent in others); and the distribution in one valve may differ considerably from that in the opposite valve of the same specimen. Although nodules have not yet been recorded in ostracods other than myodocopids, they are present in other Crustacea (Sohn and Kornicker, 1969; Neville, 1975, p. 316 and references therein). Because *post-mortem* nodules may form rapidly, it is difficult to identify nodules that may have formed *in vivo*. Myodocopid shells without nodules rapidly develop nodules when soaked in water, but not when soaked or preserved in alcohol (Sohn and Kornicker, 1969, p. 100).

We produced nodules during the present study in sun-dried *V. hilgendorfii* immersed for about 24 hours in about 10% buffered formalin. Because buffered formalin is the usual initial preservative of marine collections, especially plankton, nodules present in myodocopids preserved in this manner may not have been formed *in vivo*.

We had previously classified and illustrated nodules produced in the laboratory as spherical, hemispherical, discoidal, and anastomosing (Sohn and Kornicker, 1969, p. 100, 101, Pl. 1). The

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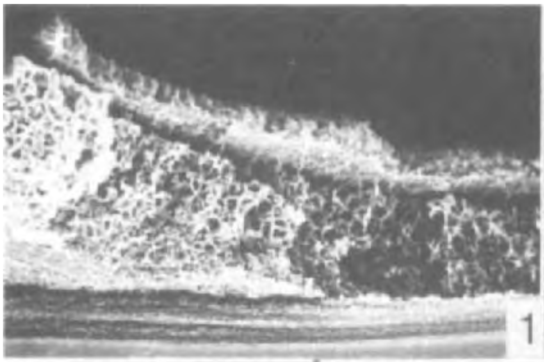
Plate 4—Figs. 1, 2. *Vargula hilgendorfii* (Müller, 1890). Cut cross-section of left valve of carapace preserved in alcohol showing net-like counterpart of coarse granular component. USNM 93001A. Locality 11. 1, shows epicuticle, frame of coarse granular component and laminate component, approx. ×420. 2, detail of frame of coarse granular component, approx. ×2,100. Figs. 3–6. *Eusarsiella disparalis* (Darby, 1965). Cross-section of left valve showing epicuticle and endocuticle. USNM 152311. Locality 10. 3, 4, cross-sections, epicuticle (arrow on fig. 5), fine granular, coarse granular, and laminate components, approx. ×930. 4 is 90° to section on fig. 3. 5, 6, details of outer and inner parts, respectively, of cross-section on fig. 3, approx. ×3,400. Fig. 7. *Thaumatoconcha caraionae* Kornicker and Sohn, 1976. Broken cross-section of left valve, adult male, showing epicuticle and columnar component of endocuticle, approx. ×890. USNM 143855B. Locality 12. Figs. 8–10. *Thaumatoconcha tuberculata* Kornicker and Sohn, 1976. Broken fragment of adult male. USNM 143796MZZ. Locality 13. 8, oblique view showing cross-section of epicuticle and columnar component, and inner surface of fragment, approx. ×180. Outer edge towards bottom of plate. 9, 10, detail of fig. 8 showing epicuticle, fine granular and columnar components of endocuticle, approx. ×870 and ×4,900, respectively; area of 10 shown on fig. 9 by arrow.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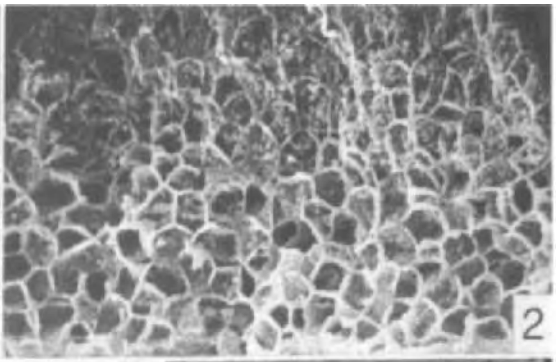
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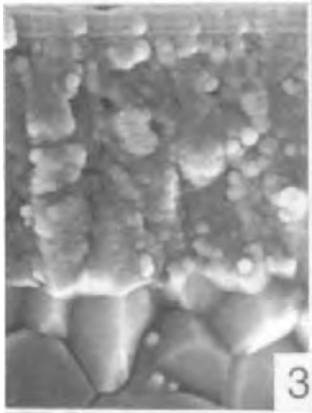
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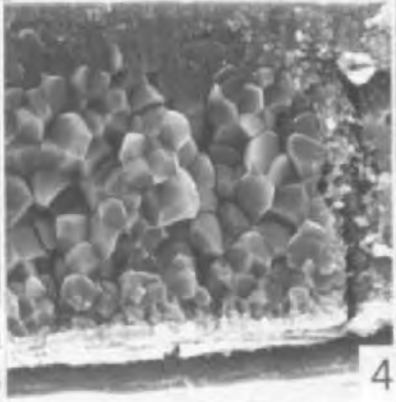
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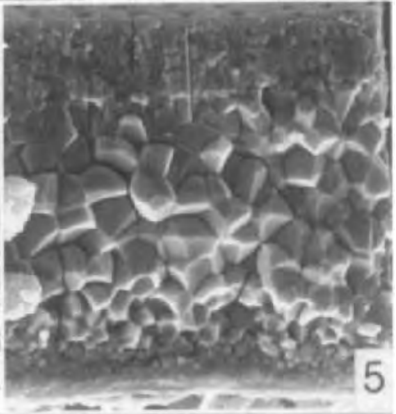
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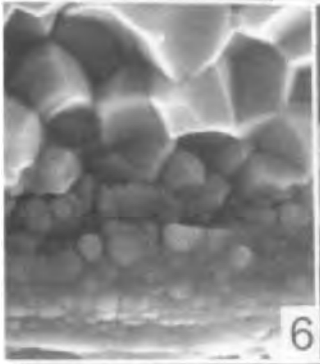
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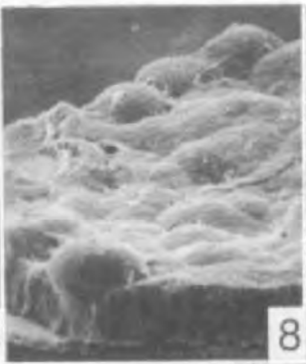
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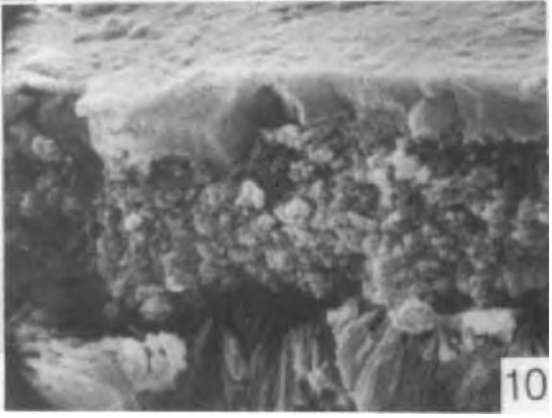
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ultrastrucrures of some of these forms are illustrated herein with SEM micrographs (Pl. 5, figs. 1–6; Pl. 6, figs. 1–8).

Discoidal and hemispherical nodules in a fragment of *V. hilgendorfii* illustrated on Pl. 3, fig. 6, and on Pl. 6, fig. 9, are postulated to have formed *in vivo* because this specimen was preserved in alcohol immediately after collection. Coalescing nodules in *Thaumatoconcha tuberculata* are shown on Pl. 4, figs. 8 and 9. Acicular nodules are shown replacing the coarse granular component in *Eusarsiella texana* (Pl. 5, figs. 7, 9). We assume that the concentric spheres in *Spinacopia* sp. are nodules (Pl. 5, figs. 10–13), but their method of formation is enigmatic.

Ultrastructures of shells at margins: The ultrastructure of the shell at the margins of *Vargula hilgendorfii* (Pl. 3, figs. 1–5) differs from the rest of the shell. The laminate layer at the margins replaces the coarse granular layer and forms the infold (Pl. 3, figs. 2–5). Pl. 3, figs. 3 and 4 clearly demonstrate the nature of the infold. Laminae also replace the coarse granular component along the attached margin (Pl. 3, figs. 1, 2) where the valves are joined by the ligament shown by the arrow on Pl. 3, fig. 7.

Ultrastructures of juveniles: The ultrastructures of the valves of two juveniles of *V. hilgendorfii* were examined (Pl. 7). The smaller juvenile (greatest length 1400 μm) has an ultrastructure that is more or less similar to that of the adult, except that the grains of the coarse granular component are less well defined (Pl. 7, figs. 1, 2). The larger juvenile (greatest length 1700 μm) has a homogeneous component similar to that of the adults. There are fewer grains in the coarse granular component (Pl. 7, figs. 3, 4), and the grains are relatively larger than in the adults. As in the adults, the coarse granules are convex upward and decrease in size towards the inside of the valve.

TAXONOMIC DISTRIBUTION OF COMPONENTS

This and prior studies of the ultrastructures in the mainly pelagic suborder Halocypridina indicate that taxa in the superfamily Halocypridacea have laminate endocuticles, and the mainly benthonic Thaumatocypridacea have columnar, or columnar and fine granular, endocuticle. The endocuticle in the suborder Cladocopina is fine granular and columnar. The endocuticle in the Myodocopina has a combination of one to four components.

PLATE 5—Figs. 1–6. *Vargula hilgendorfii* (Müller, 1890). Discoidal and anastomosing crystalline nodules prepared in the laboratory. USNM 193163B. Locality 7. 1, 2, discoidal nodule, approx. ×180 and detail of lower front, approx. ×900. 3–6, anastomosing nodule. 3, 4, detail of top surface near right side of fig. 3, approx. ×180 and ×900, respectively. 5, edge view of unbroken surface at right side of fig. 3, approx. ×2,250. 6, edge view of broken surface on bottom of fig. 3 showing dense ultrastructure, approx. ×890. Figs. 7–9. *Eusarsiella texana* (Kornicker and Wise, 1962). Cut sections showing coarse granular and laminate components, and nodules replacing coarse granular component. USNM 144004. Locality 9. 7, edge of valve, approx. ×300. 8, detail of coarse granular component, approx. ×1,650. 9, detail of nodule shown by arrow on fig. 7, approx. ×5,400. Note similarity to nodule illustrated on Pl. 6, fig. 8. Figs. 10–13. *Spinacopia* sp. Left valve with many spherical nodules replacing coarse granular component. USNM 149315. Locality 2. 10, cut section showing two components: coarse granular component partly replaced by nodules above inner laminate component, approx. ×2,250; 11, detail of nodules, approx. ×2,250. 12, detail of polygonal outline of coarse granule shown by arrow on fig. 11, approx. ×6,700. 13, detail of spherical concretion inside large nodule, approx. ×1,350. Figs. 14, 15, *Eusarsiella disparalis* (Darby, 1965). Etched replica of polished cross-section of left valve, showing polygonal outlines surrounding the granules. Same specimen as Pl. 4, figs. 3–6. 14, approx. ×700; outer surface to top. 15, detail from fig. 14, approx. ×5,650; outer surface of valve to right.


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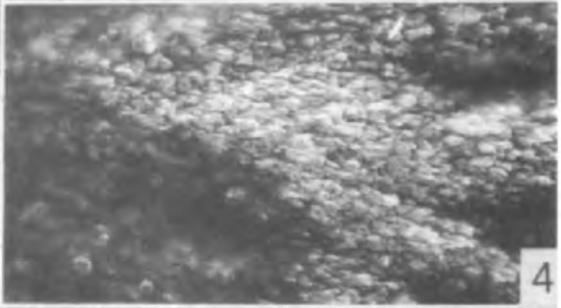
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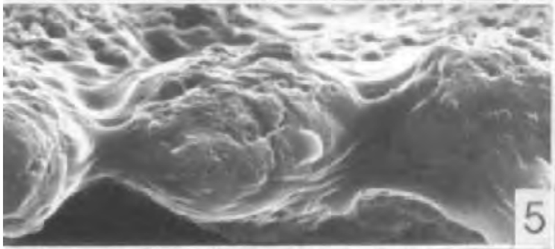
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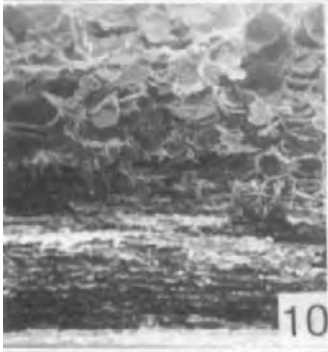
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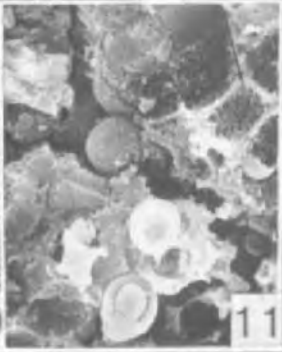
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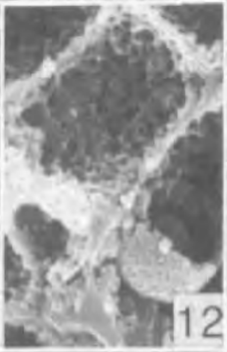
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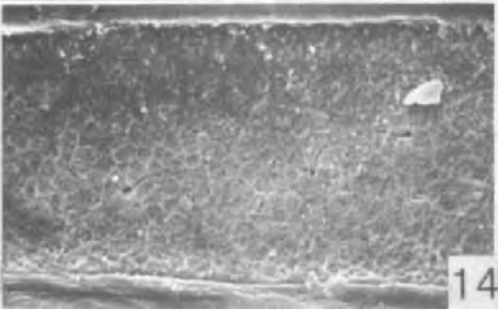
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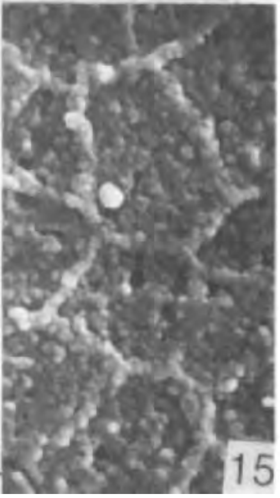
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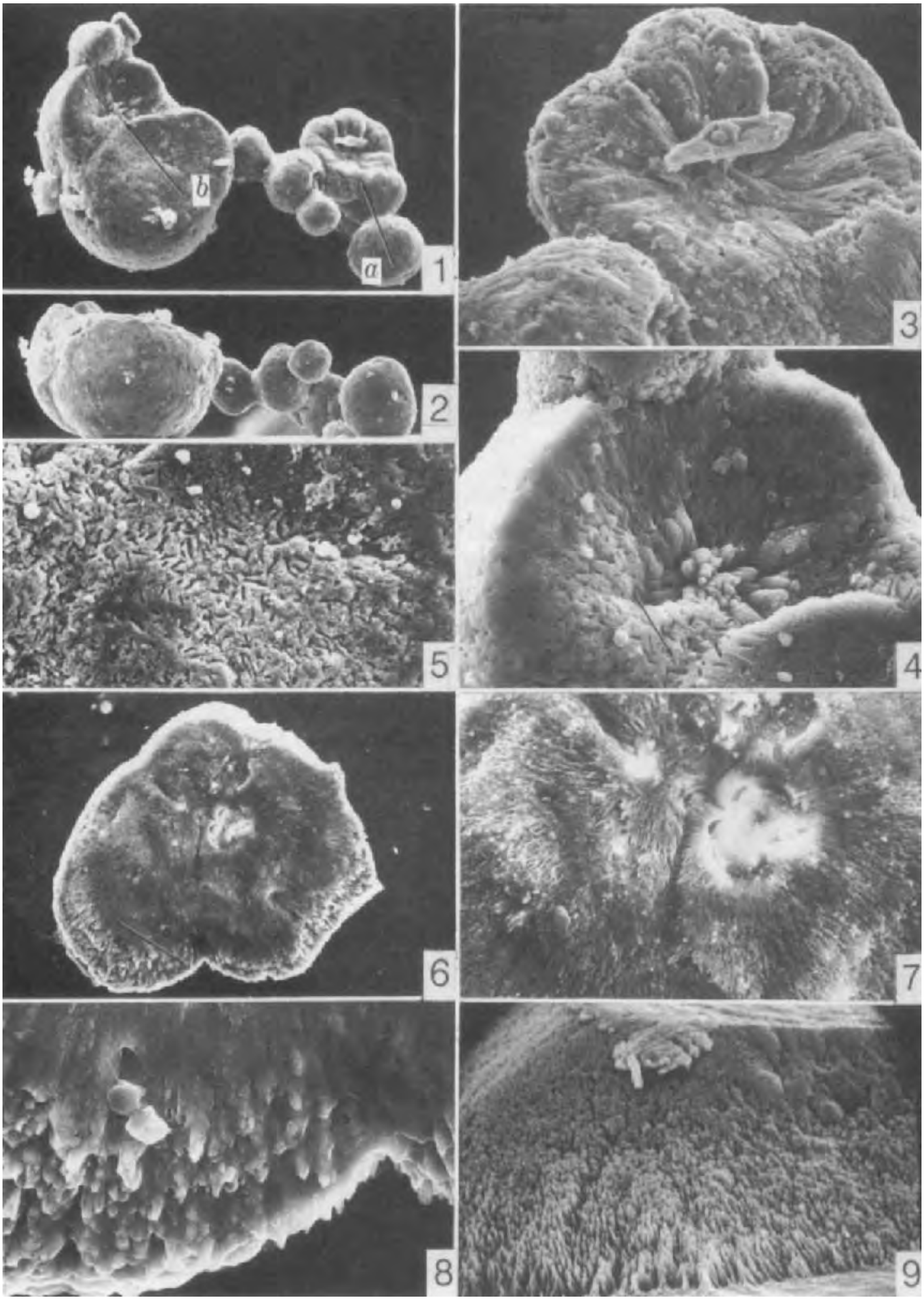
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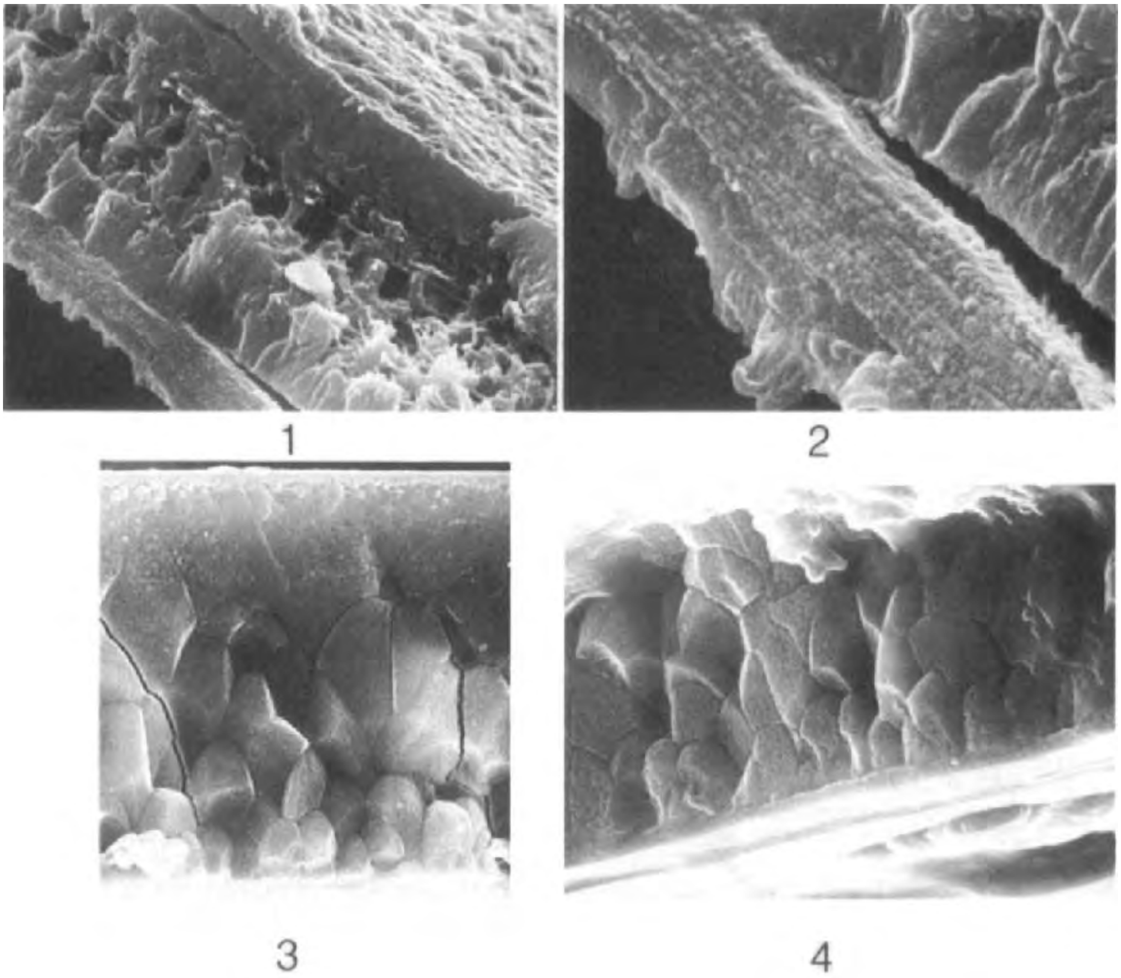

Plate 7—Figs. 1–4. *Vargula hilgendorfii* (Müller, 1890). Broken sections of juvenile sun-dried carapaces. Locality 7. 1, section showing homogeneous, coarse granular and laminated endocuticle, approx. ×3,100. 2, detail of lower middle part of fig. 1, approx. ×8,900. USNM 193163D, greatest length 1.40 mm. 3, 4, sections showing epicuticle, and homogeneous and coarse granular components of endocuticle, approx. ×3,100. Components below coarse granular component missing. USNM 193163E, greatest length 1.70 mm.

Plate 6—Figs. 1–8. *Vargula hilgendorfii* (Müller, 1890). Hemispherical, spherical and discoidal crystalline nodules produced in laboratory. USNM 193163B. Locality 7. 1, 2, top and end views of assemblage, approx. ×220. Note variation in size of spherical nodules. 3, detail of inner surface of hemispherical nodule shown by arrow *a* on fig. 1, approx. ×890. 4, detail of upper surface of hemispherical nodule shown by arrow *b* on fig. 1, approx. ×890. 5, detail of surface structure in area shown by arrow on fig. 4, approx. ×890. Short black lines represent spaces between adjacent crystals. 6–8, discoidal nodule, detail of upper surface, and detail of lower edge shown by arrow on fig. 6, approx. ×180, ×450, and ×890, respectively. Fig. 9. *V. hilgendorfii*, detail of upper part of nodule showing acicular structure, approx. ×3,050. USNM 193164. Locality 8. Same valve illustrated on Pl. 3, fig. 6. Top of nodule towards inner surface of valve.

CONCLUSIONS

Although the ultrastructures of only a few of the known myodocopid species have been examined, our data suggest the following:

1. The pelagic Halocypridacea (*Conchoecia, Halocypris*) have laminate endocuticles.
2. Species in the pelagic genera *Gigantocypris* and *Macrocypridina* (Cypridinidae) have laminate endocuticles.
3. Members of the pelagic genus *Codonocera* (Cypridinidae) have laminate and coarse granular endocuticles.
4. Members of the benthonic Cladocopa have columnar and fine granular endocuticles.
5. Benthic Thaumatocypridacea have columnar, or columnar and fine granular, endocuticles.
6. Benthic members of the Cypridinacea have a combination of one to four components in the endocuticles.
7. With few exceptions, pelagic Myodocopa have laminate endocuticles.

LIST OF COLLECTION LOCALITIES

1. *Gigantocypris muelleri* collected SW of the Kerguelen Islands, depth 3240 m, April 12, 1974, Sanders dredge (see Kornicker, 1976, p. 47).
2. *Conchoecia atlantica, Spinacopia* sp. collected off West Africa, R. V. *Atlantis II*, cruise 42, May 23, 1968, station 202, 8°48′S, 12°52′E, depth 527–541 m (new record).
3. *Asteropterygion setiferum* collected off Ivory Coast, 5°12′N, 4°09′W, depth 40 m (see Kornicker, 1975, p. 2).
4. *Macrocypridina castanea* collected near Bermuda, R. V. *Trident*, cruise 1, June 2, 1970, station 10–5B, 32°33′N, 64°04′W, depth 600 m, discrete depth sampler (see Kornicker and others, 1976, p. 3).
5. *Scleroconcha folinii* collected off Mauritania, R. V. *Thalassa*, January 29, 1971, station X048, 28° 50′05″N, 17°39′00″W, depth 270 m, (see Kornicker and Caraion, 1977, p. 40).
6. *Polycope* sp. collected in South Atlantic, Walvis Bay, off Ruanda, R. V. *Atlantis II*, cruise 42, May 23, 1968, station 201, 09°25′S, 11°35′E, depth 1964–2031 m, trawl (new record).
7. *Vargula hilgendorfii* collected and immediately sun-dried by Dr. Y. Haneda, September 1954, at Zushi Beach, Kanagawa, Japan (see Sohn and Kornicker, 1969, p. 100).
8. *Vargula hilgendorfii* same locality as 7, but preserved in alcohol instead of sun-dried.
9. *Eusarsiella texana* collected off Bird Key, Charlotte Harbor, Florida, July 1971, depth 1–3 m, Ockelman dredge (see Kornicker, 1986, p. 7).
10. *Eusarsiella disparalis* collected off Bird Key, Charlotte Harbor, Florida, May 1, 1974, depth 2–3 m, Ockelman dredge (see Kornicker, 1986, p. 8).
11. *Vargula hilgendorfii* collected by Dr. D. J. Pletsch, U.S. Public Health Service, at Chiba-Ken, Japan, Sept. 1948 (new record).
12. *Thaumatoconcha caraionae* collected in South Atlantic, R. V. *Atlantis II*, cruise 60, March 14, 1969, station 245A, 36°55′42″S, 53°01′24″W, depth 2707 m, large epibenthic sled (see Kornicker and Sohn, 1976, p. 21).
13. *T. tuberculata* collected in South Atlantic, R. V. *Atlantis II*, cruise 31, February 12, 1967, station 169A, 8°03′00″S, 34°23′00″W to 8°02′00″S, 34°25′00″W, depth 587 m, epibenthic sled (see Kornicker and Sohn, 1976, p. 21).

ACKNOWLEDGEMENTS

We thank Mr. Walter R. Brown and his staff for operating the scanning electron microscopes and Mr. Ronald Hower for assistance in freeze-drying and cryofracture of specimens. We also thank our colleagues Drs. Jean M. Berdan and T. R. Waller for reviewing the paper.

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DISCUSSION

De Deckker: I wish to inform you that nodules similar to those which you talked about have been found in "planktonic" free swimming ostracods in Australia. These ostracods belong to the large (more than 3 mm) genera *Australocypris* and *Mytilocypris.* I am convinced that these nodules are forming within the ostracods after death and after the ostracods became dehydrated after having been preserved in alcohol. This could therefore result from the effect of dehydration of a substance containing some Ca and CO_3 molecules.

Sohn: Thank you for the new information, because in our paper we state that nodules have not been reported in ostracods other than myodocopids. In our experiments we observed that alcohol (70% ethanol) was one of the few liquids that did not produce nodules.

De Deckker: Knowing that monohydrocalcite is an unstable mineral, it is therefore unlikely that one will find these nodules in the fossil record.

Sohn: Sohn and Kornicker (1969, p.102) suggested that structures described in the Lower Carboniferous *Cypridinella superciliosa* Jones, Kirkby and Brady, 1874, may be discoidal nodules, and on p. 106 we suggested that myodocopid nodules may contribute carbonate particles to marine sediments.

Siveter: Do you consider that the nodules you have described are synonomous structures to the calcareous discs and spherulites which Bate and Sheppard (Fossil and Recent Ostracods, British Micropal. Soc. 1982. Eds. Bate *et al.*) described from Recent myodocopids?

Sohn: It has been established that large calcite nodules or discs may form in myodocopid shells at two different times: 1, while the animal is alive; and 2, after it has died. Bate and Sheppard (1982) and Smith and Bate (1983, *Jour. Micropalaeontology,* 2: 105–110) interpreted the nodules in living myodocopids to be a step in the normal calcification of the shell. We think that nodules in living myodocopids are atypical and not the usual way in which myodocopids calcify. A study of myodocopids *in vivo* is necessary to resolve this problem.

Keyser: Do you look at the same places on the ostracod shell? I found, for instance, different crystallization on places where the muscles adhere.

Sohn: We have insufficient data to draw conclusions concerning the ultrastructure in the vicinity of the central adductor muscles. There are ultrastructure changes near the hinge and free margin (Pl. 3).

Carapace Sculpture in *Amphissites* (Kirkbyacea: Ostracoda)

PETER J. JONES
Bureau of Mineral Resources, Canberra, Australia

ABSTRACT

A constant pattern of polygonal reticulation and pore distribution has been demonstrated in specimens of *Amphissites centronotus* (Ulrich and Bassler, 1906) from the Upper Pennsylvanian of Texas, and two allied species from the Lower Carboniferous (Visean) of the Bonaparte Basin, northwestern Australia. The adult stages show a distribution pattern of normal cone-pores (macro cones) that has remained fairly stable over a period of 40 million years. Ontogenetic changes in the reticulation pattern between the A-1 stage and the adult stage demonstrate the results of cell division in the formation of carinae and the increase in size of the carapace.

INTRODUCTION

Modern studies of the surface sculpture and form of the ostracod carapace seem to have developed in two directions (Hanai 1982). Benson (1972, 1974, 1975, 1981) approached the subject from a biomechanical point of view, by the application of engineering and architectural design principles. Liebau (1977, 1978), on the other hand, distinguished evolutionary levels of "ornamental" genetics in an evolutionary trend of cytheracean "ornamentations". A third approach, one initiated by Hanai (in Hanai *et al.*, 1977) and developed by Okada (1981, 1982, 1983), has been the study of the developmental mechanisms that control the constancy of both the mesh pattern (Pokorny, 1969; Liebau, 1969, 1971, 1975a,b) and the distribution of normal pore canals (Triebel, 1941; Morkhoven, 1962; Hanai, 1970). These studies are based on mainly Cretaceous to Recent ostracods; Palaeozoic ostracods, by contrast, have received scant attention.

The presence of normal pores in the carapaces of palaeocope ostracods was known before the advent of scanning electron microscopy. Among the beyrichiaceans, pore canals (=mesh pores; Liebau, 1971) were recognized by Adamczak, (1958) in fluoridized specimens of *Kozlowskiella praetuberculata* Adamczak, 1958 [=*K. corbis* (Dahmer, 1927)]. Spjeldnaes (1951) suggested that the pores contained in the tubercles of *Craspedobolbina clavata* (*"Beyrichia jonesi"*) probably marked the sites of bristles or hairs (=sensilia; Okada, 1983). Liebau (1975) later showed that the homologous spinous tubercles in *Beyrichia peponulifera* Martinsson, 1962 have constant positions. Pore canals were reported among the hollinaceans by Bless (1968) in the domicilial wall in partly pyritized thin sections of a species of *Hollinella*. The development of scanning electron microscopy techniques combined with the use of stereoscopic photographs, has increased the number of of palaeocope species in which pores and surface structures could be seen in detail, *e.g.*, see Siveter

(1973, 1976, 1980, 1982) for Beyrichiacea, and Schallreuter (1983) for Ordovician palaeocopes. The last paper is important because two different types of sieve pores are described; the *Klimphores*-type consisting of many irregularly arranged micro-pores, and the *Miehlkella*-type consisting of one ring of 5 of 8 micro-pores. Among the Kirkbyacea, Langer (1973) reported 9 to 12 normal pore canals ("radiaporenkanale") in each valve of *Shleesha pinguis* (Ulrich & Bassler, 1906); these are mesh-pores, as they occur one per solum.

Benson (1975), in a discussion of the evolution of structural types, has suggested that modern ostracods of the box-frame structural "morphotype" (*e.g.*, Trachyhleberididae) were represented in Palaeozoic seas by the kirkbyaceans. This stimulating analogy needs to be pursued to determine whether the sculptural pattern of Kirkbyacea can be analysed by a methodology similar to that used by Liebau (1971, 1977) on homologous sculpture patterns in Trachyleberididae.

This paper is an attempt to find such a parallel scheme in the Kirkbyacea by analysing the carapace sculpture of three species of the genus *Amphissites,* the nominate genus of the family Amphissitidae Knight, 1928. It is a pilot study because it is based on four specimens only, and therefore lacks the numerical rigour that Liebau (1971) applied to his studies of the *Limburgina*-type ornament. However, the material is diverse in that it contains three species, one of which is some 40 million years younger, and is now separated from the other two by a distance of some 15,000 km. Despite these differences, homologous features can be recognized.

Material

Amphissites is marine benthic ostracod, which was widely distributed during Middle Devonian to Permian times. Sohn (1983) suggested that it was probably a swimmer, and that the marginal frills and flanges would have inhibited a burrowing habit. More than 100 species have been described.

The material studied here consists of four specimens that are referable to three species. Dimensions-length (L), height (H) and width (W) are given in microns.

Amphissites centronotus (Ulrich and Bassler, 1906)

BMR reference collections of ostracod assemblage slides contain many well preserved specimens of this species extracted from samples collected by the late Dr. Irene Crespin from the Upper Pennsylvanian (Virgilian) Graham Formation, Texas. A left valve (CPC 16641; adult, L=800, H=450) taken from one of these slides (labelled—"Graham Formation; Plummer Stn 619 on Salt Creek, 1 mile W. of Graham, Texas, U.S.A.") is figured for comparison with the Australian species. The median node on this specimen, and on some not figured here, possesses a short carina on the ventral side, which appears to be characteristic of *Amphissites carinodus* Cooper, 1957 (=*A. carinatus* Cooper, 1946; not 1941). In all other respects the Texan specimens resemble *A. centronotus,* where they probably belong.

Amphissites aff. *A. centronotus* (Ulrich and Bassler, 1906)

Carapace (CPC 16647; adult; L=860, H=460, W=400) collected from the Lower Carboniferous (late Visean) Bonaparte Beds, Bonaparte No.1 Well, core 6, 1,846 feet (561.4m), Bonaparte Basin, northwestern Australia. Both valves of this carapace were compared for intervalve differences, in order to check the intraspecific constancy of position of ornamental details (Liebau 1975). In other words they were used like two conspecific specimens to increase the data base.

Amphissites sp. *B.*

Right valve (CPC 16643; adult; L=980, H=630, W=380) collected from the same sample detailed above. Both the external and internal surfaces of this well preserved right valve were studied; unfortunately the specimen was damaged after it had been photographed.

Right valve (CPC 16645; A-1; L=930, H=580, W=280) collected from the Lower Carboniferous (late Visean) Bonaparte Beds, Bonaparte No.1 Well, core 8, 2404 feet (732.7 m), Bonaparte Basin, northwestern Australia. Despite some abrasion of the surface, the polygonal fossae pattern, and at least one important pore cone can be distinguished in this specimen. This right valve was compared with that of the adult for ontogenetic differences.

The two species from Australia will be formally described in a forthcoming publication. The specimens illustrated in the present paper are deposited in the Commonwealth Palaeontological Collection (prefix CPC) of the Bureau of Mineral Resources, Canberra.

Methods

Transparent overlays were drawn of SEM photographs (Pls. 1, 2) to determine the reticulation pattern and pore cone distribution of the four specimens to be examined. The overlays of right valves were reversed in order to make valid comparison with left valves. The number of options available in determining an ordered reticulation pattern in the adult carapace is limited by the number of meshes that have developed during the ontogeny. Thus, by tracing the mesh pattern in early instars, a "preferred" order of reticulation pattern may be detected in the adult stage. Even with the present limited material, study of the changes from the (A-1) stage to the adult stage of *Amphissites* sp. *B* proved to be rewarding. The (A-1) stage laid the foundation for the interpretation of the adult stage (Text-figs. 2a, b).

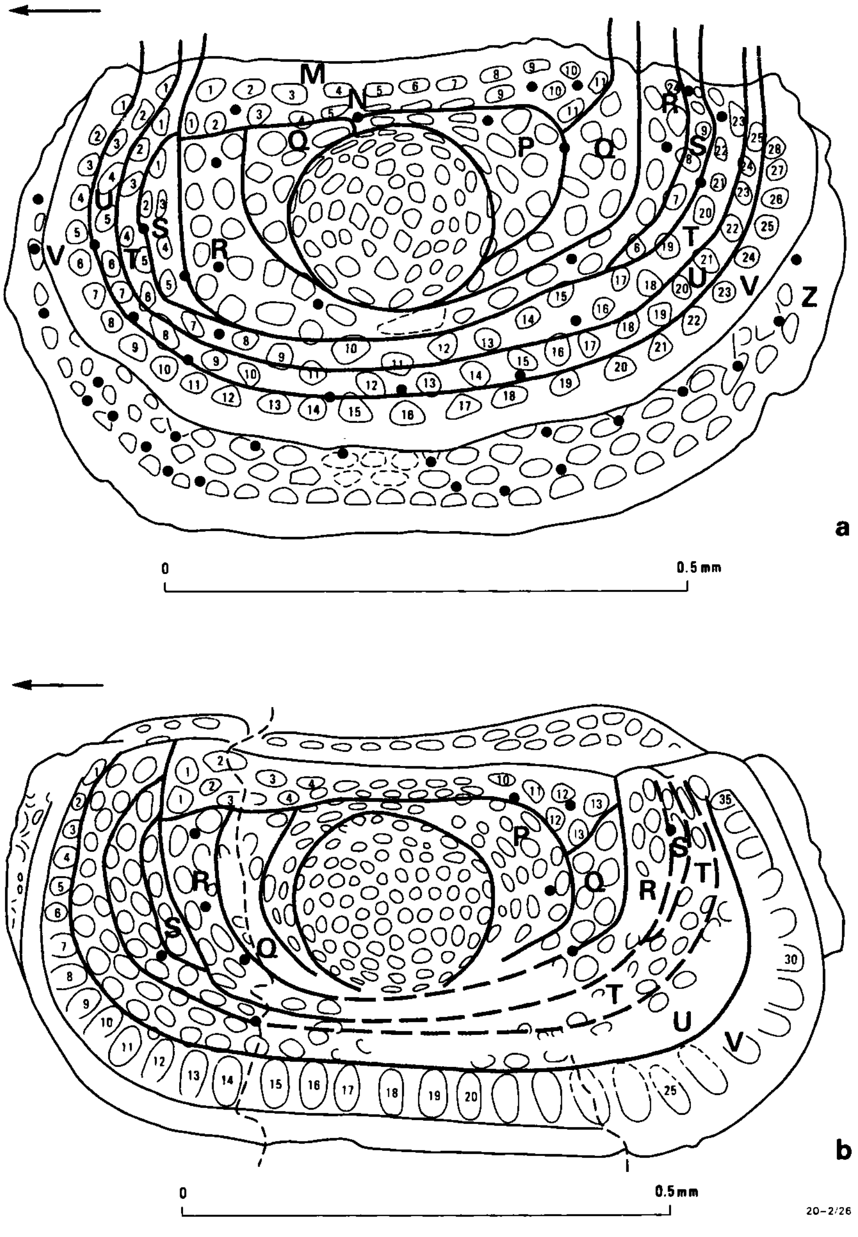
RETICULATION

The lateral reticulation of the three species of *Amphissites* examined here is clearly ordered (Text-figs. 1, 2), and can be classified as macroreticulation in the sense of Liebau (1971, 1977). Whether it is constant in the Amphissitidae to the same degree as the *Limburgina*-pattern is in modern Trachyleberididae, can only be decided after examination of much more material.

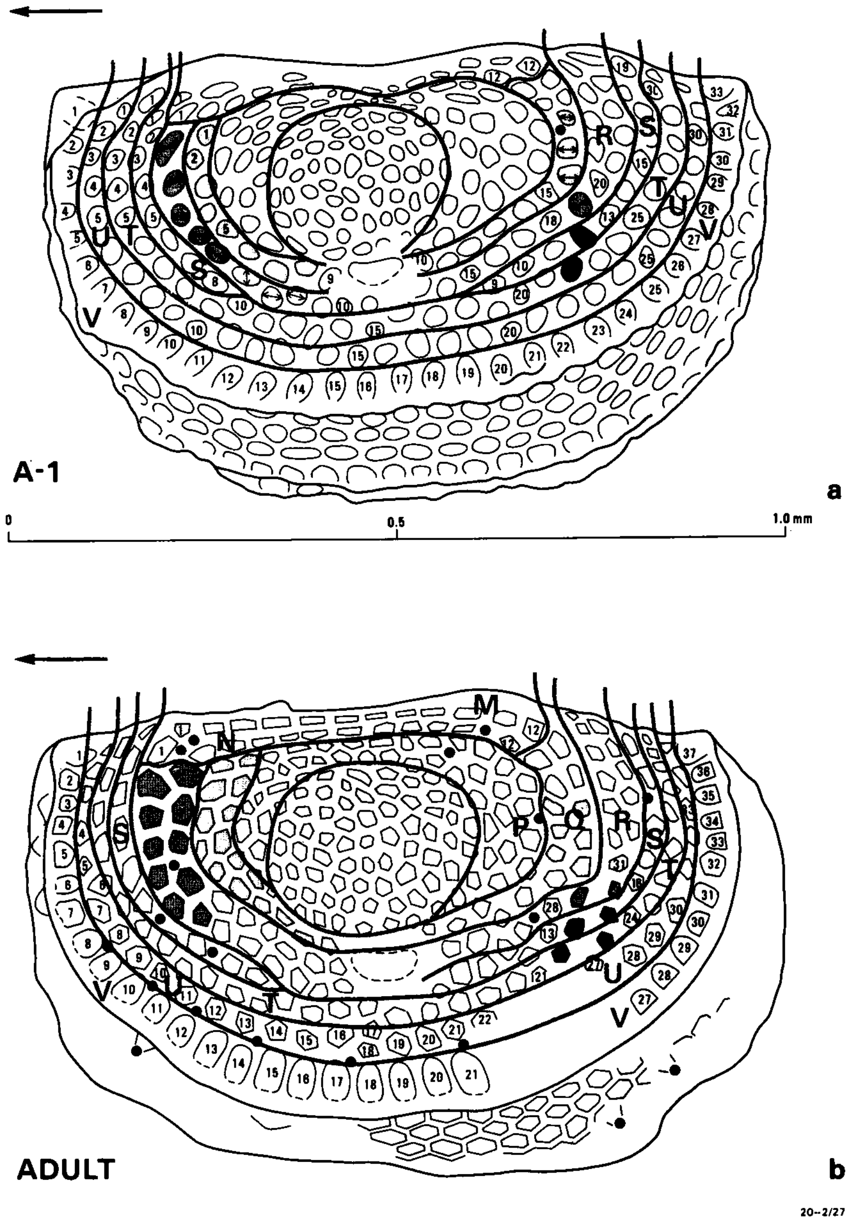
The basic pattern consists of 13 areas (designated alphabetically M to Z) that lie between the dorsal carina and the adventral structure (=outer marginal carina). It does not include the fossae on the dorsum (*e.g.*, see tilted carapace in Text-fig. 1b). Apart from two mesh rows (M, N) that lie parallel to the dorsal carina between the anterodorsal and posterodorsal ribs, the remaining 11 rows (P to Z; O is not used) are arranged in a U-shaped concentric pattern around the median node, which is microreticulate.

The macroreticulation situated between the outer and the inner marginal carinae consists of 4 mesh rows (W to Z). Z-meshes are closer to the outer marginal carina. Single meshes of the W to Z groups are difficult to distinguish near the anterior and posterior ends of valves, and therefore are not individually numbered. In some species of *Amphissites* (*e.g.*, *A. carinatus* Cooper, 1941) the W to Z groups cannot be seen in lateral view, because the inner marginal carina is declined ventrally (*i.e.*, in cross-section; Henningsmoen, 1965, p. 337, fig. 5B) and obscures the outer marginal carina. Individual carapaces in which this adventral structure is destroyed by dorsally applied compression (*e.g.*, *Amphissites* aff. *centronotus;* Text-fig. 1b, Pl. 1, fig. 5), also hide the W to Z meshes in lateral view.

Macroreticulation situated between the inner marginal carina and the dorsal carina can be individualized by the mesh row and number. The V-mesh row, situated closest to the inner marginal carina is perhaps the most distinctive, even when this structure is damaged (*e.g.*, Pl. 2, fig. 1).



TEXT-FIG. 1a, b.—Mesh rows of the lateral reticulation, of (a) *Amphissites centronotus* (Ulrich and Bassler, 1906); adult left valve, CPC 16641, Upper Pennsylvanian, Texas, USA; and (b) *Amphissites* aff. *A. centronotus*; adult carapace CPC 16647, left lateral view, Lower Carboniferous, Visean, Bonaparte Basin, Western Australia.



TEXT-FIG. 2a, b.—Mesh rows of the lateral reticulation, and sites of pore cones in *Amphissites* sp. *B*; Lower Carboniferous, Visean, Bonaparte Basin, Western Australia: (a) (A-1) right valve; CPC 16645; (b) Adult right valve (CPC 16643); both illustrations are reversed for comparisons with left valves. The epidermal cells in rows Q to T of the A-1 stage are divided in the presumed adult stage. Particular cells (R19, S12, and T22) of the A-1 stage are responsible for the ventral growth of the posterodorsal rib in the presumed adult stage. Others are responsible for shell growth in the anterior (*e.g.*, R1 to 9; Q1 to 9) and the posterior (Q16 to 18) parts of the carapace.

TABLE 1—NUMBER OF FOSSAE PER ROW FOR *Amphissites centronotus* (ULRICH and BASSLER, 1906) AND ALLIED SPECIES.

	Length	M	N	P	Q	R	S	T	U	V	Total
Amphissites sp. *B (A - 1)*	0.93	12	12	35	22	29	19	31	32	33	225
A sp. *B* Adult	0.98	12	12	39	35	42	20	32	35	37	264
A. centronotus	0.80	11	11	12	18	26	11	24	25	28	166
A. aff *centronotus*	0.86	13	13	38	c.18	c.28	8	>32	>40	35	>225

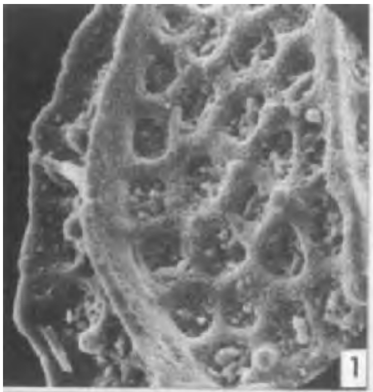
20–2/30

In this example, an A-1 instar of *Amphissites.* sp. *B,* there are 33 V-cells, as compared with the 37 in the adult specimen (Table 1). The V mesh-row probably played an important role in the construction of the inner marginal carina, which appears as a calcified extension along the outer sides of muri and of the intramural pores (Pl. 2, fig. 4). The epidermal cells, which the V-fossae now represent, probably contained the genetic code that controlled the optimum amount of calcite necessary for the construction of the inner marginal carina. The intramural pores may have functioned as tegmental ducts to facilitate this celation process.

Both the T and U meshes are aligned in continuous rows that are parallel to the V-row. The S mesh-row is discontinuous in the area below the "kirkbyan pit", where it is displaced by the R-mesh row. There is a gradual reduction in the number of fossae per row from the V-group to the S-group (Table 1). The sharp increase in the number of fossae in the R-row reflects the important role that this mesh-row plays in cell-division from the (A-1) to the adult stage. This increase is already apparent in the (A-1) stage of *Amphissites* sp. *B,* where the R-row develops from a single to a double row of cells (following R20), immediately behind the posterodorsal rib (Text-fig. 2a, Table 1). Eight R-meshes (R1-8) arranged in a single row immediately behind the incipient anterodorsal rib in the (A-1) stage are divided in the adult stage. A similiar development of cell division takes place in the Q-mesh row (Q1-6, 16–18), where the net gain in fossae between the (A-1) and adult stages is 13 (as it is the R group). Cell division is not apparent within the P-meshes, but I have not studied this group in detail.

Comparative studies of the reticulation patterns in the (A-1) and adult specimens of *Amphissites* sp.*B* show that the development of the posterodorsal rib is due to cell-division. The posterodorsal rib in the (A-1) specimen extends as far as the R19 cell (Text-fig. 2a). It is the division of this cell, and of the S12 and T22 cells below it, that permits the posterodorsal rib to extend as far as the U row in the adult specimen. Thus, cells R19, S12, and T22 of the (A-1) stage divide, and respectively become cells R29, 30, S14, 15 and T22, 23 in the adult stage (Text-fig. 2b). It would appear then, that the posterodorsal rib is developed by the fusion of adjacent parts of the muri of twin fossae.

PLATE 1—Figs. 1–4, 7. *Amphissites centronotus* (Ulrich and Bassler, 1906); Upper Pennsylvanian, Virgilian, Graham, Texas, U.S.A. Adult left valve (CPC 16641); 1. Details of anterior end, showing pore cones B1, 2 and 3, C3 and 4, and E3 (×240); 2. Lateral view. (×95); 3. Details of anterodorsal area of median node, showing pore cones G1, and 2 (×240); 4. Details of posterodorsal area of median node, showing pore cones E13, 14, F13, 14, G13, H11, 12, I11 (×240); 7. Details of posteroventral area showing pore cones B10, 11 and 12 (×280). Figs. 5, 6, 8. *Amphissites* aff. *A. centronotus* (Ulrich and Bassler, 1906); Lower Carboniferous, Visean, Bonaparte Basin, Western Australia. Adult carapace (CPC 16647); 5. Left view (×60); 6. Ventral view, with perforate conuli near the free margin (×60); 8. Details of anterodorsal area of median node, showing pore cones H10, 12 and G13; cf. fig. 4 (×230).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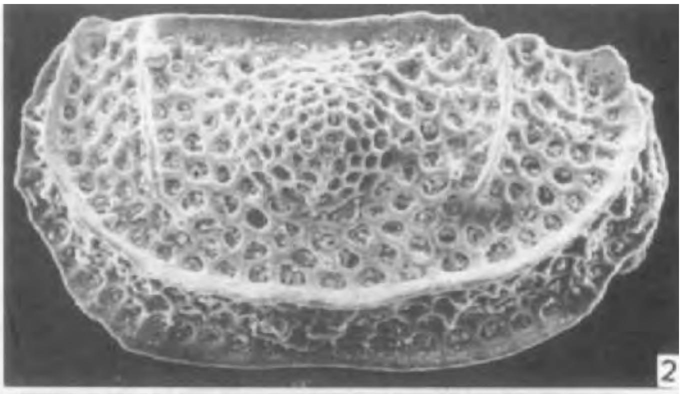
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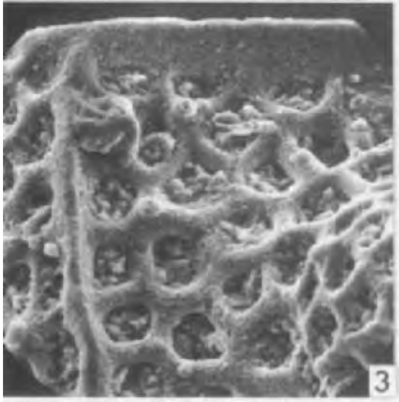
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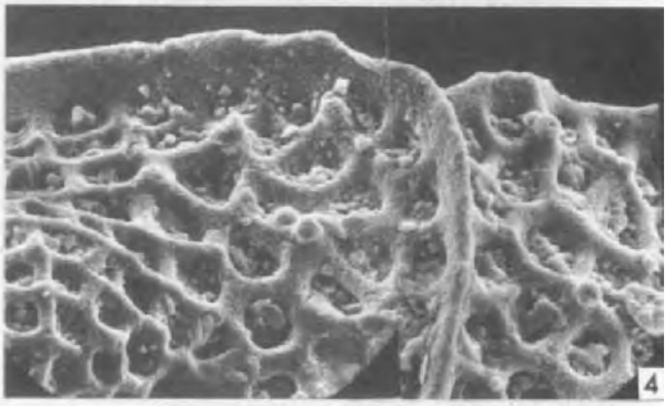
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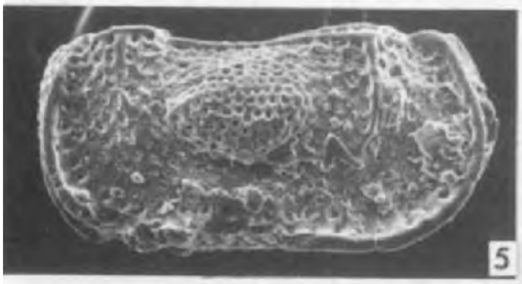
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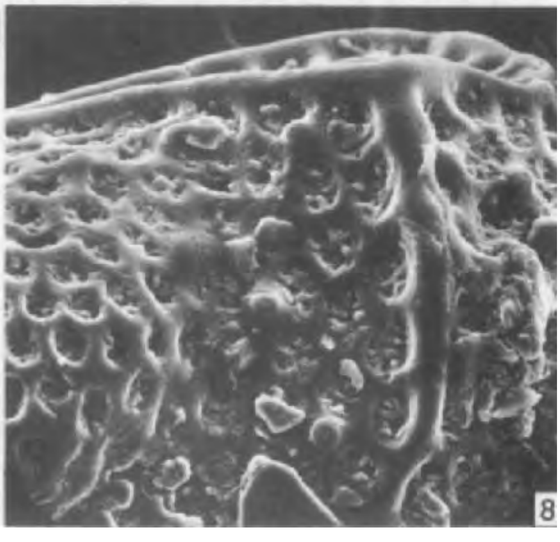
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PORE DISTRIBUTION

Normal pore canals—both simple and sieve types—are present in the three species examined here. The simple types occur as short pore cones, and the sieve types occupy the solae within fossae. The distribution of pore cones (macrocones sensu Liebau, 1977) appears to be fairly constant in all three species (Table 2; Text-figs. 3a, b; 4a,b).

TABLE 2—DISTRIBUTION OF PORE CONES IN *Amphissites centronotus* (Ulrich and Bassler, 1906) AND ALLIED SPECIES. AREAS SHADED ARE THOSE OCCUPIED BY THE MEDIAN NODE AND THE 9 H-POINTS SELECTED FOR THE CONSTRUCTION OF TEXT-FIGS. 4a AND b.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
I	+										+ ×			
H							MEDIAN			●○	+ ×□	+ ● ×		
G	+ ×	+ ○	●○ ×	●○			NODE						+ ●	
F				+		+				+ ○ ×			+ ● ×	+
E			+	+ ×	×								+	+
D					+ ○	●				+				
C			+	+ ×	+ ×	×	+ ×	+ ×	+ ×					
B	+	+	+	+	+ ×	+	+	+	+	+	+	+	+	+

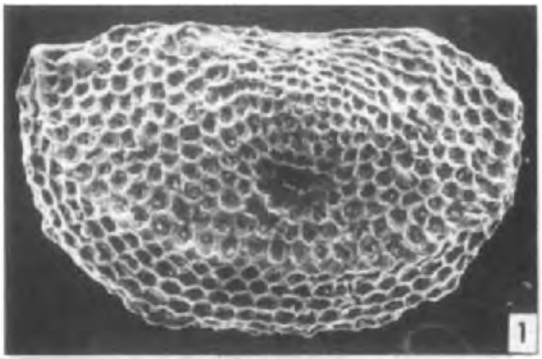
\+ *A. centronotus* (left valve) ● *A.* aff *centronotus* (left valve) ○ *A.* aff *centronotus* (right valve)
× *A.* sp. *B* (right valve; adult) □ *A.* sp. *B* (right valve; A-1 stage)

20-2/31

Pore cones

Pore cones are best seen in *Amphissites centronotus* where 24 are confined to the macroreticulation between the dorsal and the inner marginal carina, and 14 (plus at least 10 intramural pores) are situated between the inner and outer marginal carinae (Text-fig. 3a). There are no pore cones on the microreticulate median node. The pore cones are distributed in concentric rows that approximately conform to the pattern made by the boundaries between mesh rows. These rows of pore cones are designated here alphabetically A to I. A linear row of perforate conuli along the concave

PLATE 2—Figs. 1-10. *Amphissites* sp. *B*; Lower Carboniferous, late Visean, Bonaparte Basin, Western Australia. 1, 2, Right valve, A-1 (CPC 16645); 1, lateral view, showing mesh rows (W-Z) between the inner and outer carinae (×65); 2, detail of posterodorsal shoulder, showing one row of mesh between the H11 pore-cone and the posterolateral carina (×115); 3-10, right valve, adult (CPC 16643); 3, lateral view (×60); 4, detail of anterodorsal shoulder, showing twin (G1) pore-cores (×385); 5, detail of posterolateral carina, separated from the H11 pore-core by two rows of Q-mesh (×385); 6, detail of ventral part of inner marginal carina and V-mesh near the (C9) porecone-note the carina is constructed from the muri, which contains intramural pores (tegmental ducts?) (×385); 7, detail of internal view showing anterior terminal tooth, sieve-pores and the internal openings of the twin (G1) porecones (×125); 8, detail of posterior part of inner marginal carina, showing some sieve pores exposed in fossa V33 (×385); 9, detail of anteroventral part of outer marginal carina, showing a B-row pore cones (B5) behind a broken part of the inner marginal carina (×385); 10, detail of fig. 7, showing sieve pore pattern, and the internal openings of twin pore cones G1. (×385).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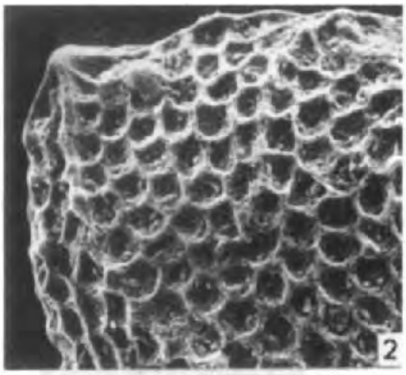
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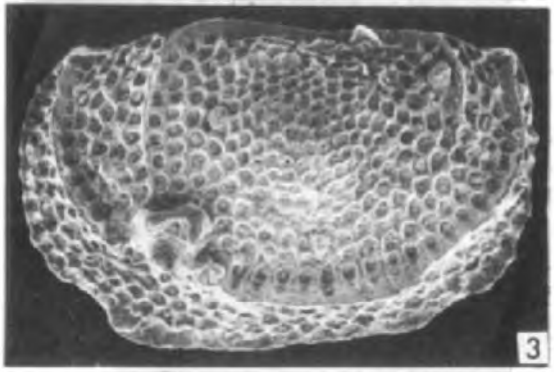
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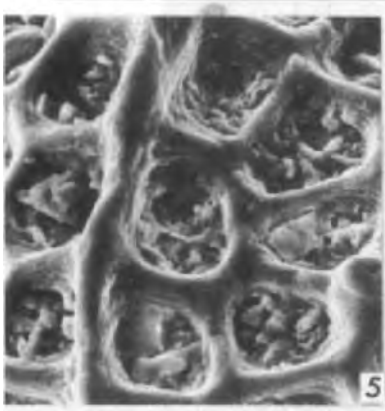
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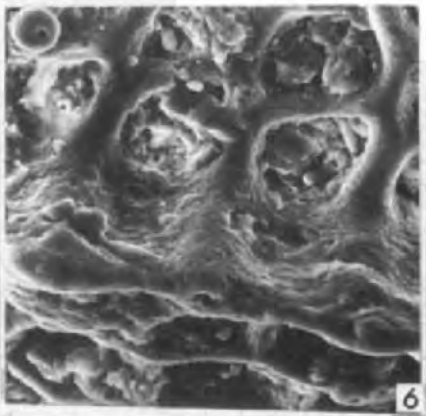
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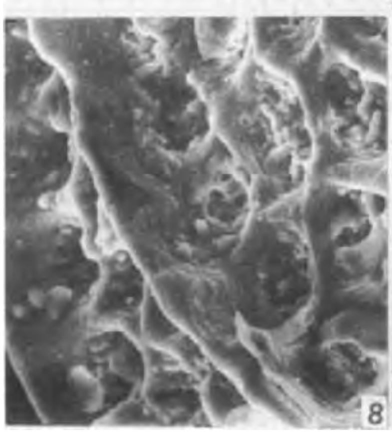
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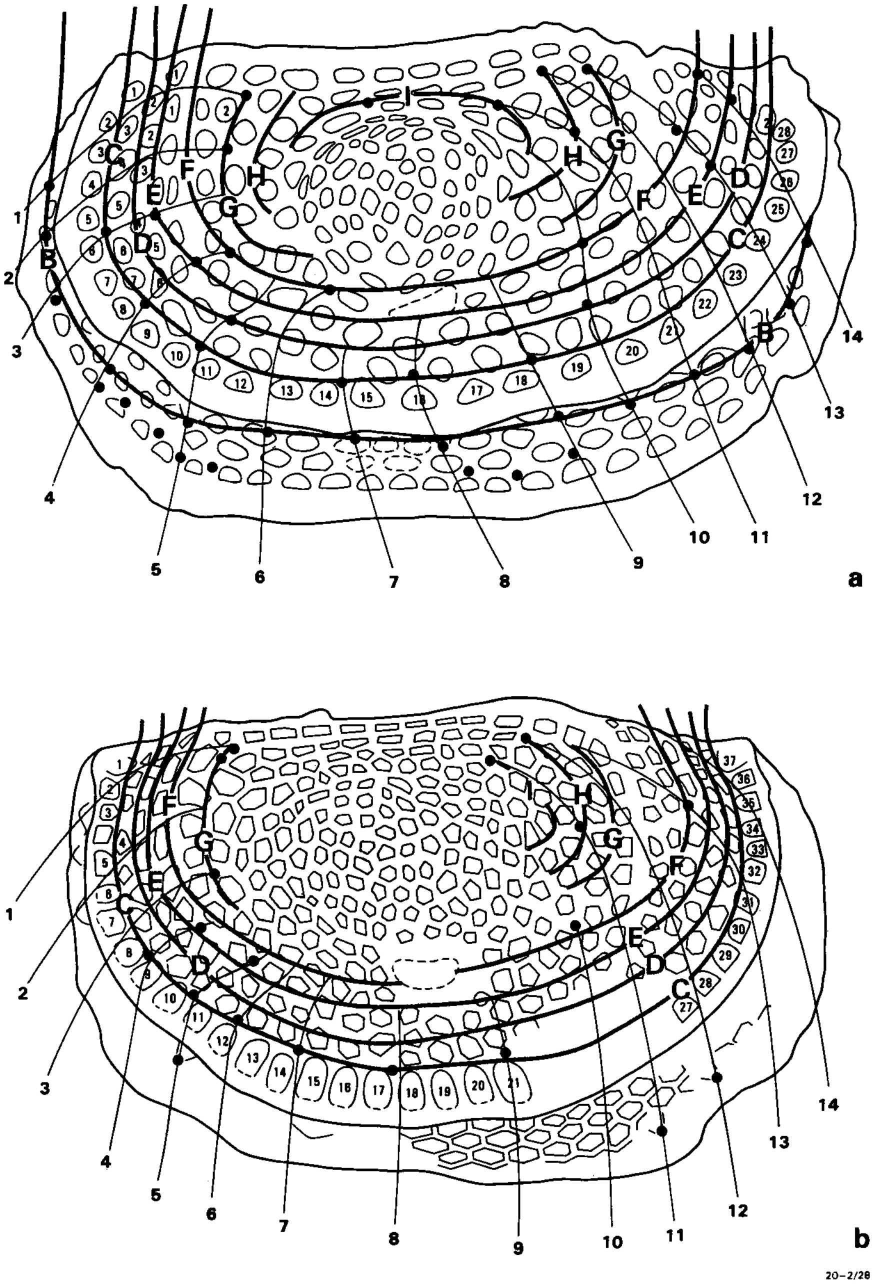
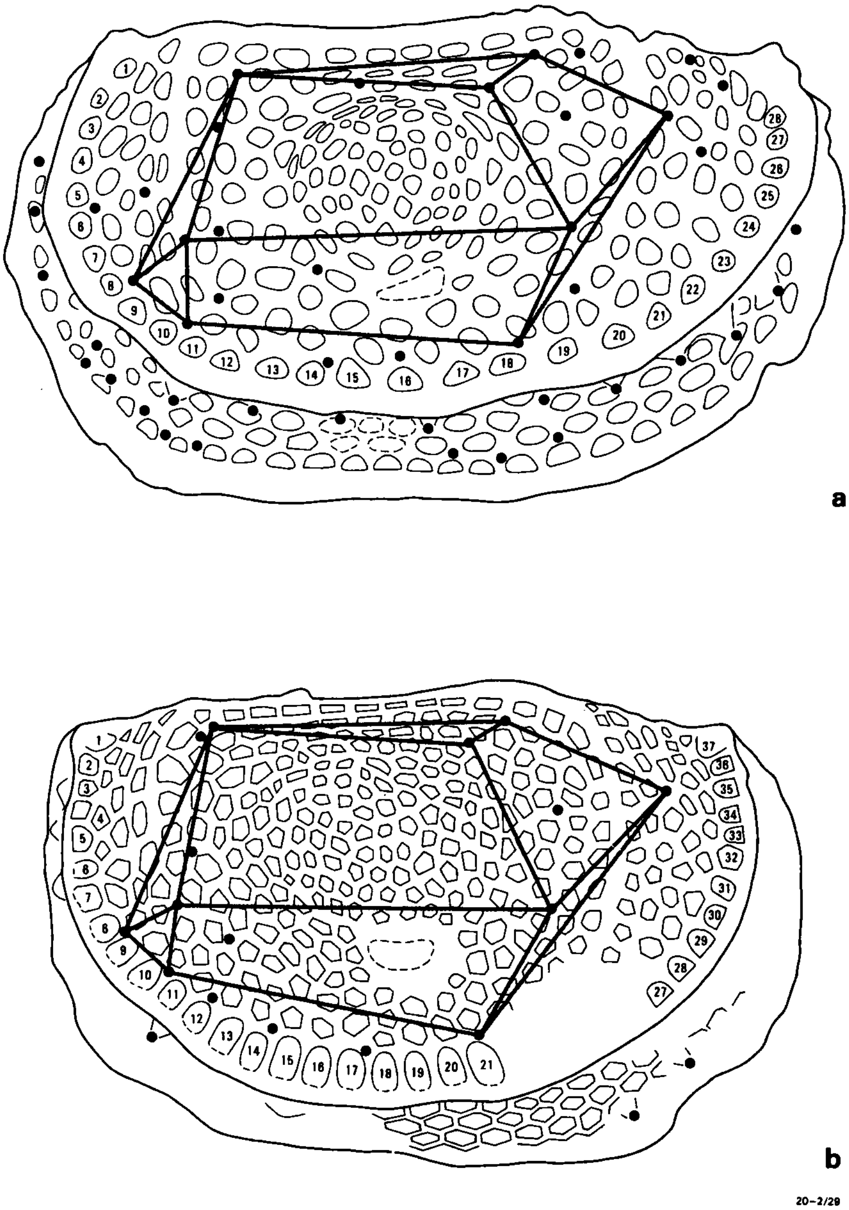


Text-fig 3a, b.—Coordinate-systems for the identification of homologous pore cones in *Amphissites*: (a) *A. centronotus* (Ulrich and Bassler, 1906) and (b) *A.* sp. *B.*



TEXT-FIG. 4a, b.—Polygon and triangle system fitted on nine common H-points for (a) *Amphissites centronotus* (Ulrich and Bassler, 1906) and (b) *Amphissites* sp. *B*.

area between the free margin and the outer marginal carina is referred to as row A. It is not seen in external lateral view, and is not considered further.

The first row of distinct pore cones lies immediately under the inner marginal carina; this is row B. Row C pore cones conform to the junction between the V and U meshes. Row D pore cones conform to the U/T junction; and the positions of successive rows of pore cones (Rows E to I) are shown in Text-fig. 3a.

The positions of individual pore cones that are along these rows can be located by a coordinate system that consists of 14 curved lines that radiate from a point near the dorsal part of the median node. These lines connect the 14 B-cones with the cones of other rows, by logically following the constraints of the mesh pattern (Text-figs. 3a,b).

By this coordinate system, homologous pore cones can be identified by notations *e.g.*, C4, E4, H11 and H12, which are common to both *Amphissites centronotus*, and *A.* sp. *B.* Text-fig. 4 shows all such homologous points, (H-points; Benson, 1982) on the carapaces of the three species of *Amphissites* studied here. Consideration of 9 of the H-points in the Late Pennsylvanian *A. centronotus* and the Late Visean *A.* sp. *B,* and of a grid composed of lines between these points, permits assessment of the changes in phyletic allometry in these species over some 40 million years. (Text-figs. 4a, b). The changes have been slight, and the present evidence shows that the distribution of normal pore canals in these species of *Amphissites* is remarkably constant.

Sieve pores

In both *Amphissites centronotus* and *A.* sp. *B,* the sola areas of many fossae are obscured by detrital grains. However, some sola areas are sufficiently exposed to reveal sieve pores (Pl. 1, fig. 1; Pl. 2, fig. 8). Examination of the internal surface of *A.* sp. *B* shows definite sieve pores, and the internal openings of pore canals, corresponding to the position of the twin G1 pore cone (Pl. 2 fig. 10). Between the muri, the outline of which can be seen on the internal surface, the sola areas are perforated by sieve pores (1–2 μm diameter; about 20–25 puncta per solum).

CONCLUSIONS

1. A system that analyses the sculpture pattern of the genus *Amphissites* is proposed, in terms of the arrangment of fossae and the distribution of pore cones.
2. The constancy of the basic plan of the reticulation pattern, and of the distribution of normal pores is demonstrated for three species of this genus over a period of some 40 million years.
3. In *Amphissites* sp. *B,* the changes in the reticulation pattern between the A-1 stage and the adult stage, demonstrates the results of cell division in the formation of the posterodorsal rib, and the increase in size of the carapace.

ACKNOWLEDGEMENTS

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DISCUSSION

This paper was read by Dr. P. De Deckker; the author provided written replies to the written comments by Drs. R.L. Kaesler and P.N. Schweitzer, as follows:

Kaesler: This is a very interesting paper that suggests ways in which we can begin to understand the macroevolutionary origin of these Paleozoic species. It is important to realize, however, that the engineering analysis necessary to support or refute Benson's ideas on architecture of the ostracode carapace remains to be done. Specifically, some such ideas may be overly adaptationist. It is difficult to think of a set of morphological characters remaining optimally adaptive over 40 million years of evolutionary time, while environments to which the ostracodes must adapt change on a scale of ecological time.

Jones: I agree that Benson's (1974, 1975) structural analogies of the ostracod carapace, however well-founded in architectural and engineering theory, need to be tested experimentally. Some studies of the mechanical and biophysical properties of the ostracod carapace have been started (*e.g.,* Whatley, Trier, and Dingwall, 1982), but more specific tests need to be devised. I believe that the normal pore distribution and the reticulation pattern of the ostracod carapace may best be interpreted in terms of constructional morphology (Seilacher, 1970; Reif, 1982, 1983) *i.e.,* a combination of the phylogenetic, the adaptational, and the architectural aspects in the analysis of a given structure. In modern ostracods, the distribution patterns of both normal pore canals and fossae appear to be controlled by a single inherited epigenetic (pleiotropic ?) program (Benson, 1976; Okada, 1983; Rosenfeld, 1982). I suggest that a similar epigenetic mechanism is responsible for maintaining a constant bauplan in *Amphissites* over some 40 million years, despite the environmental changes over this time. This does not mean that these characters have remained optimally adaptive; some minor variation both between and within species would be expected (Liebau, 1971, 1975). Benson must have realized that the optimal solution could never be attained, when he wrote (Benson, 1981, p. 78), "it is unlikely that any one example of skeletal structure is ever completely in equilibrium with its contemporary environmental stresses".

Schweitzer: (1) When you assert that the positions of the pore canals don't change much over a 40 million year period, be sure that the pore canals you use are really biologically homologous, and not just geometrically similar. I'm concerned that your method of locating the pores might be influenced by their positions and not their biological origin, which would bias your pore-locations in favour of morphological stability.

(2) There are quantitative methods for describing the amount of shape change in a set of homologous landmarks, and you should use them when you extend your study to more individuals.

Jones: (1) The macrocones selected in my specimens are regarded as simple type normal pore canals because they are of uniform size, and each one is penetrated by a single duct. The precise biological functions of these ducts, whether sensory, exocrinal, tegmental or osmotic, would be difficult, and may even be impossible, to determine. However, the distribution pattern of the macrocones appears to be closely related to the mesh pattern, leading one to suspect that both were controlled by the same gene (pleiotropism?).

(2) Yes, I intend to use quantitative methods when I am in the position to broaden my study to include more individuals.

Evolution of *Amphicostella* from the Middle Devonian in Europe (Metacopa, Ostracoda)

FRANCISZEK J. ADAMCZAK
University of Stockholm, Sweden

ABSTRACT

Five species (of which three are presented in open nomenclature) of the reticulate metacope ostracode of *Amphicostella* from the Holy Cross Mountains in Poland have been examined by pattern analysis. The result indicates strong intraspecific fluctuations in the number of meshes in the posterior part of valves and quite stable relations in this respect in the adductorial and anterior parts of carapaces. Although this opinion coincides with the outcomes obtained from a Recent reticulate podocope of Japan, it is interpreted here in different terms. In addition, the reticular elements of the valves, coded with letters and Arabic and Roman numerals, are shown in a new form of record, making comparative studies of the reticulum easier and more perspicuous.

INTRODUCTION

The genus *Amphicostella* Adamczak 1968 appears suddenly in the lower Eifelian (Middle Devonian) in the Holy Cross Mountains of Poland, where it is represented by four species. In addition to the Holy Cross Mountains, the fifth form, a presumably lower Givetian member, occurs in the Rheinish Slate Mountains (Western Germany) and Czechoslovakia.

The distinct morphologic features, rapid evolutionary rate and wide geographic distribution make *Amphicostella* forms suitable and potential guide fossils. On the other hand, sparse abundance and quite obscure ecology make them less attractive for stratigraphic studies.

Amphicostella has previously been considered a member of the paleocopes (kirkbyaceans); however, judging from pictures of the interior of valves shown to the author by Dr. H. Grocs Uffenorde during the symposium in Shizuoka, the genus should be classified as a metacope (thlipsuraceans). It shows a completely separate, tripartite hinge margin and an interrupted (?) contact groove in the larger, left valve.

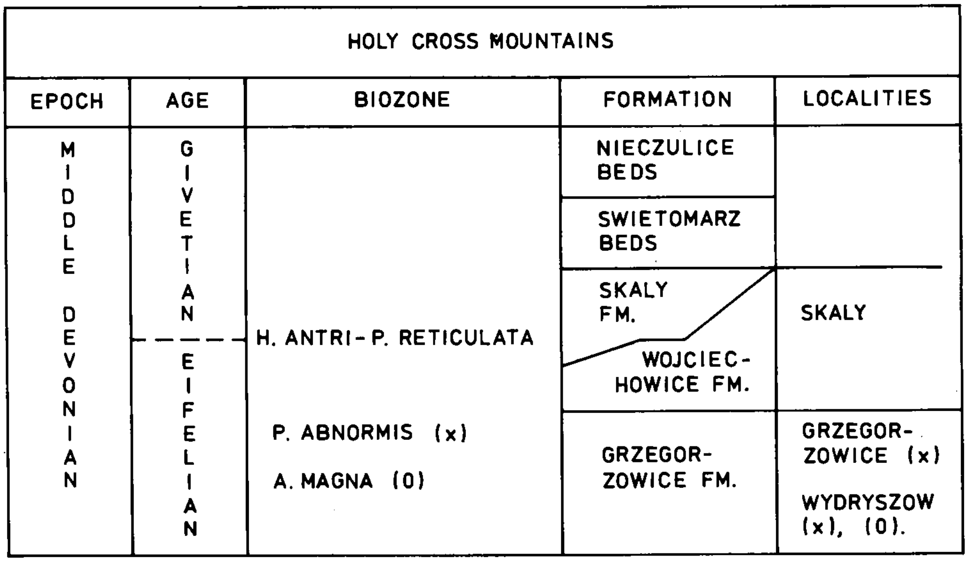
The *Amphicostella* forms are distinguished by their very small dimensions, reticulate ornamentation, ovål adductor muscle rosette and well developed longitudinal and vertical carinae. The ornamental features of the reticulation have been studied by the method of pattern analysis. The meshes (reticular elements) of the carapace were arbitrary, and for comparative purposes, codified with letters and Arabic and Roman numerals. This procedure also makes it possible to obtain a more perspicuous record of meshes, which simplifies comparisons of groups within a species and between the different taxa of *Amphicostella*.

It has been observed that morphologically very closely related *Amphicostella* species reveal analogous strategies in reduction of meshes and distribute the rest of them in long and regular rows. Although it is assumed that the decrease in number of meshes has been without any prearrangement in the different taxa, the site where this process took place was not coincidental. The change in number of meshes within a species occurs mainly in the posterior sector of the carapace. It is also responsible for the most important variation, which may be as high as 80%. Another aspect of this phenomenon seems to be related to the enlargement of meshes. Judging from the areal size of the reticulum, it seems that natural selection favoured individuals with large reticular elements. The arrangement of meshes in regular rows could have affected (1) the calcium carbonate economy of the animal and (2) reinforcement of the carapace wall.

STRATIGRAPHIC OCCURRENCE OF *Amphicostella* IN THE HOLY CROSS MOUNTAINS

The representatives of *Amphicostella* appear in calcareous clay rocks together with trilobites, brachiopods, small rugose corals and bryozoans. They are not numerous and make up less than one per cent of all ostracode forms in a sample. They have been found in three localities. At the first locality (Wydryszow), besides the type species, there are two other forms, designated as *Amphicostella* sp. 1 and *Amphicostella* sp. 2. At the second locality, there occurs *Amphicostella* sp. 3, which seems to be quite closely related to *A. prima* Adamczak. *Amphicostella* sp. 3 has been identified in only one sample (Text-fig. 1).

Although the four species appear suddenly in the Middle Devonian, it cannot be determined whether they originated in this region or migrated to it during the latter part of the Early Devonian transgression. The species mentioned above are presumably the earliest *Amphicostella* known from Europe. The fifth species, *A. sculpturata* (Pokorný), is represented in the Holy Cross Mountains by one specimen, which occurs in the lower Givetian.



HOLY CROSS MOUNTAINS				
EPOCH	AGE	BIOZONE	FORMATION	LOCALITIES
MIDDLE DEVONIAN	GIVETIAN	H. ANTRI-P. RETICULATA	NIECZULICE BEDS	
			SWIETOMARZ BEDS	
			SKALY FM.	SKALY
	EIFELIAN		WOJCIEC-HOWICE FM.	
		P. ABNORMIS (x) A. MAGNA (O)	GRZEGOR-ZOWICE FM.	GRZEGOR-ZOWICE (x) WYDRYSZOW (x), (O).

TEXT-FIG. 1—Stratigraphic and sampling localities of the Middle Devonian in the Holy Cross Mountains where *Amphicostella* has been found.

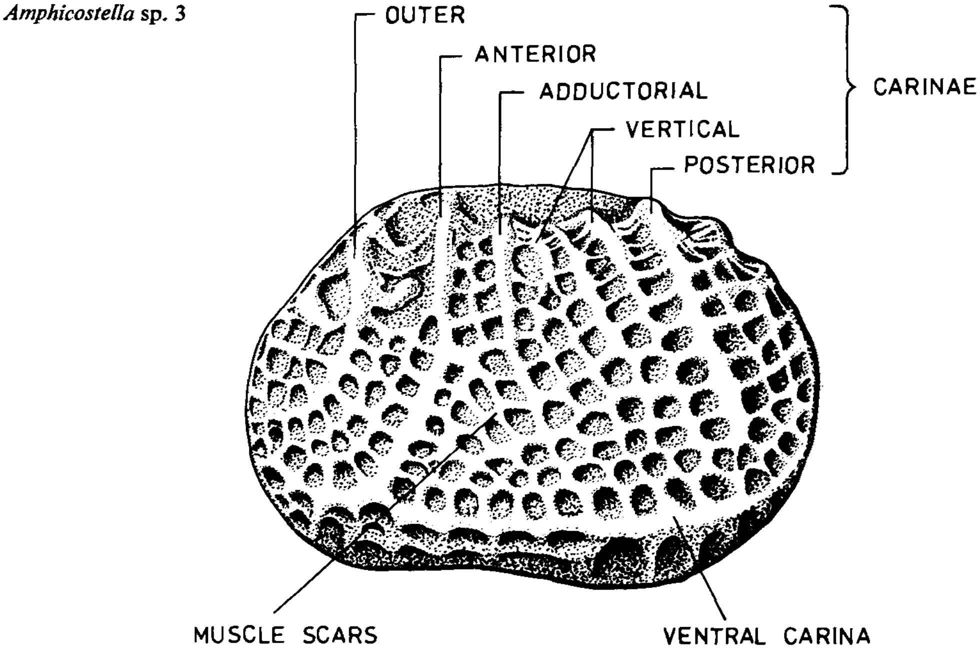
ORNAMENTAL PATTERN IN *Amphicostella*

The diagrams of *Amphicostella* forms shown in Text-figs. 2 and 3 indicate the presence of several sectors (outer, anterior, adductorial, posterior and caudal) which are parts of the ornamental pattern (meshes, carinae and the adductor muscle rosette) of the carapace and which have been examined in left aspect. From the sectors mentioned, anterior, adductorial and posterior have also been studied by pattern analysis (Pokorný, 1969; Liebau, 1969; Benson, 1972). The remaining sectors, because of the preservational state of the fossil material and the complexity of the valve ornamentation, have not been studied by this method.

The meshes of the analysed sectors have been coded in Arabic and Roman numerals and small and capital letters which are written below the reticular silhouette drawings of the different species in a characteristic record (Text-figs. 3, 5, 7, 8, 9 and 10). The records simplify the analysis of the reticulum and allow a particular pattern of meshes to be easily compared with the record of another individual of the same or different taxon. In other words, they are homologized.

It seems logical to begin the analysis of the various ornamental details with the more stable sculptural elements of the carapace, *i.e.* the rosette of the adductors and the major carinal (ridge) system.

The rosette. The rosette of the adductors is situated in the central part of the carapace. It consists of six "petals" which are presumably impressions of the adductors (Text-figs. 2, 4 and 6). Although the dimensions of the rosette are above the average, this does not mean that the adductors were abnormally large. The rosette seems to be a very stable feature in *Amphicostella.* It has greatly aided in the identification of most individuals of this genus and is suggested to be an important generic character.

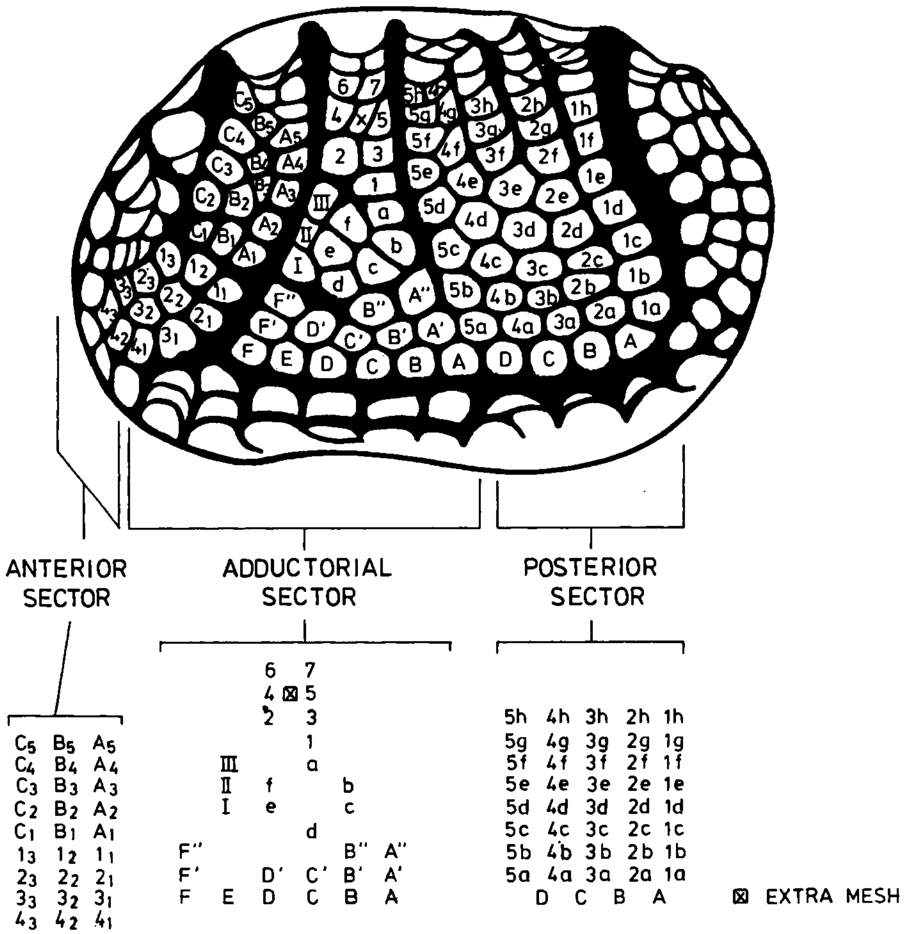


TEXT-FIG. 2—Basic morphological features in *Amphicostella* showing the mural and carinae systems as seen in the left valve (×140). Holy Cross Mountains, Grzegorzowice; Middle Devonian, Grzegorzowice Formation.

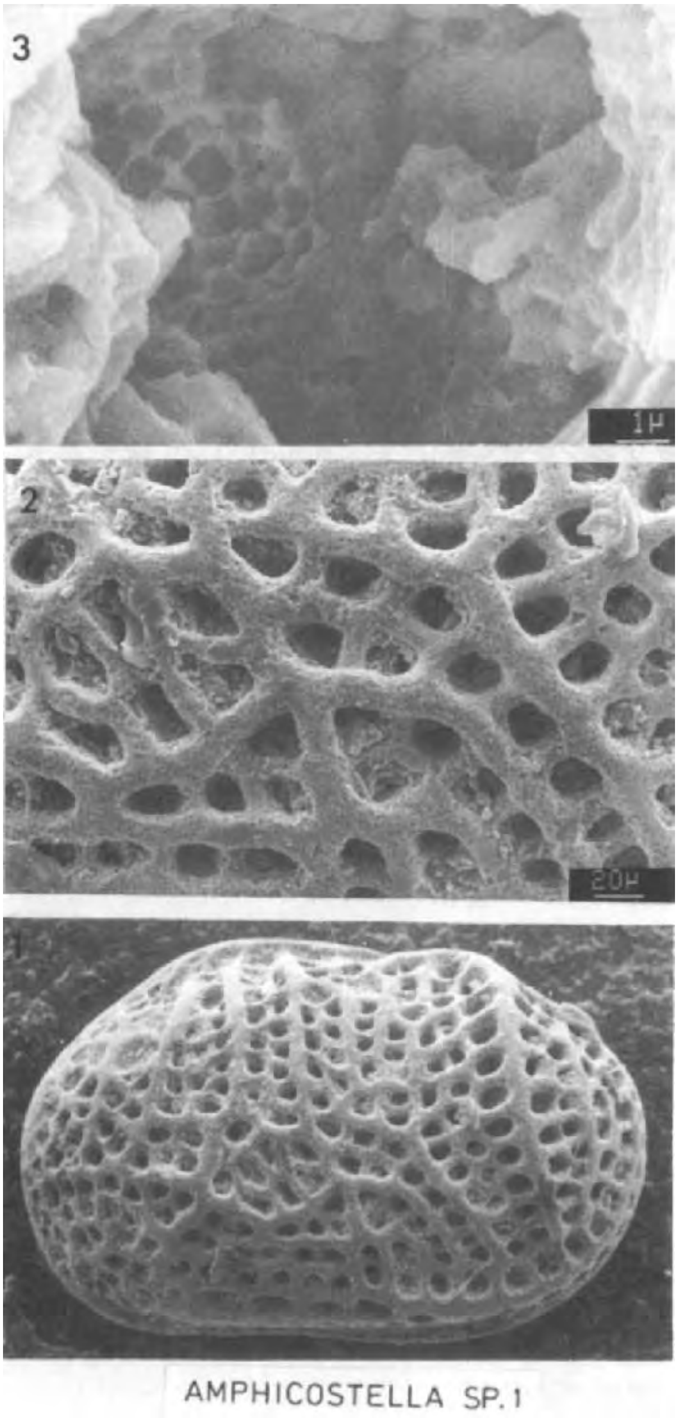
The carinal system. The major ridge (carinal) system, considered as an enlargement of the muri (Benson, 1977), consists of five carinae in the Eifelian forms (Text-fig. 2) and six ridges (carinae) in the Givetian species. From the five ridges identifiable in the Eifelian forms, the ventral, outer and adductorial ridges are less massive in *Amphicostella* sp. 1 and *Amphicostella* sp. 2 (Text-figs. 4, 6). The remaining ridge elements, *i.e.* the posterior and anterior carinae seem to be much more stable. Being massive and long, they connect the dorsal margin with the ventral carina. The sixth of the major ridges is present in the posterior sector of *A. sculpturata* (Text-figs. 9, 10). It is long and stable whereas its equivalents in the Eifelian forms are considered to be minor elements, which are less firm and one or two in number. They appear in *A. prima* and *Amphicostella*. sp. 3.

The reticulum. Although the pattern of meshes of a particular species of *Amphicostella* is quite distinct, the number of meshes, especially in the posterior sector, is considerably variable. A review of the different parts (sectors) of the valve given below begins with the anterior sector, which may be divided into dorsal and ventral sections. The dorsal part starts at the level of mesh I of the adductorial sector (Text-fig. 3). It may be biserial, coded: A_1, B_1; A_2, B_2, etc., which means that the meshes are arranged in two rows, as for example in *A. prima* (Text-fig. 8) or three rows (A_1, B_1, C_1;

Amphicostella sp. 3



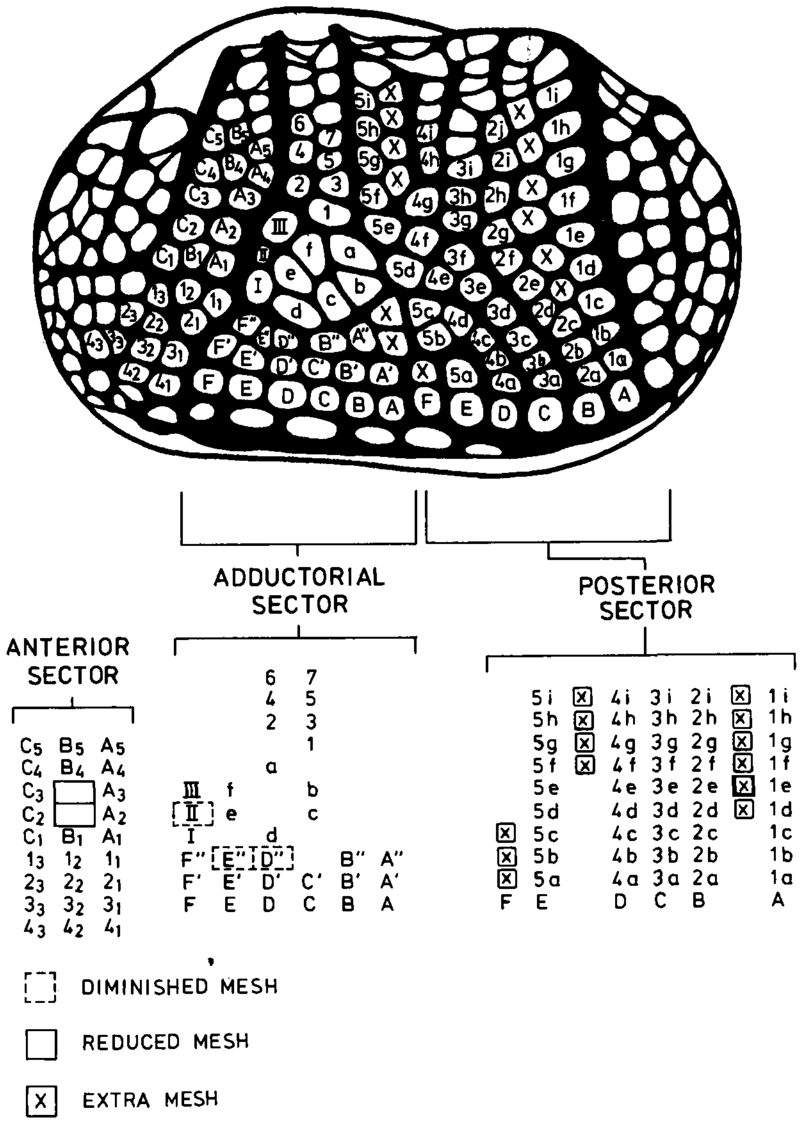
TEXT-FIG. 3—Schematic drawing of reticulation patterns traced from a SEM micrograph and record of meshes (×160). Holy Cross Mountains, Grzegorzowice; Middle Devonian, Grzegorzowice Formation.



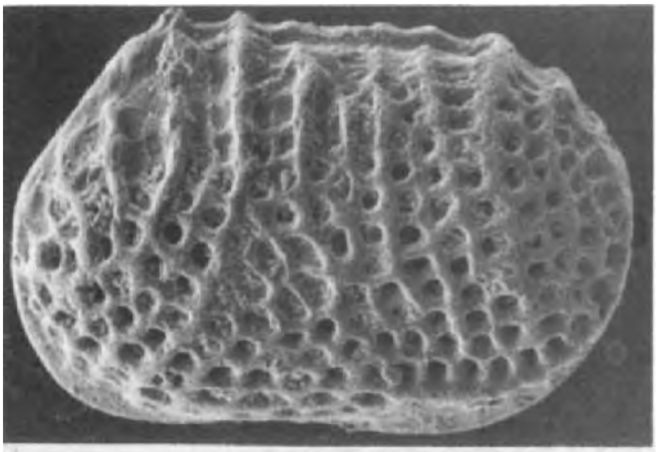
TEXT-FIG. 4—SEM micrographs. 1. Left lateral view of carapace (× 155). 2. Fragment of reticulation with adductor muscle rosette (to the left) and mural system. 3. Inside view of a mesh showing a surface of sieve-type pores(?) Holy Cross Mountains, Wydryszow; Middle Devonian, Grzegorzowice Formation.

A_2, B_2, C_2; A_3, etc.) as in *Amphicostella* sp. 2, *Amphicostella* sp. 3 and *A. sculpturata* (Text-figs. 3, 7, 9). Often the triserial arrangement of meshes can dorsally pass into a biserial one, similar to that visible in *A. prima*. In *Amphicostella* sp. 1 (Text-figs. 4 and 5), this part of the sector shows an intermediate character indicating that it starts at the height of mesh I with three meshes (A_1, B_1, C_1) and passes into a biserial design (A_2, C_2; A_3, C_3), and again demonstrates a triserial arrangement with the reticular elements coded A_4, B_4, C_4; A_5, etc. The ventral part of the anterior sector of the

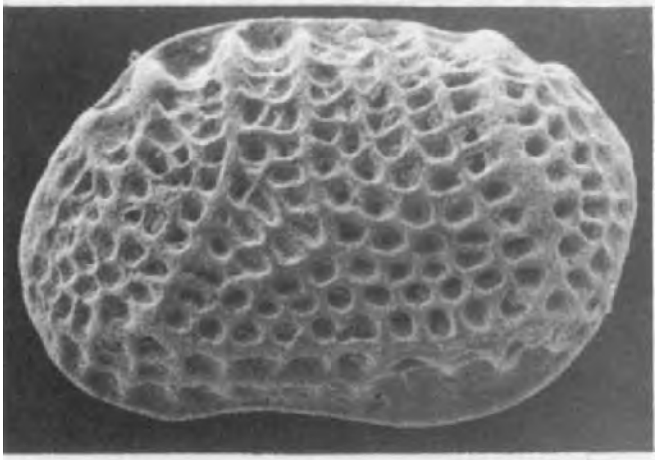
Amphicostella sp. 1



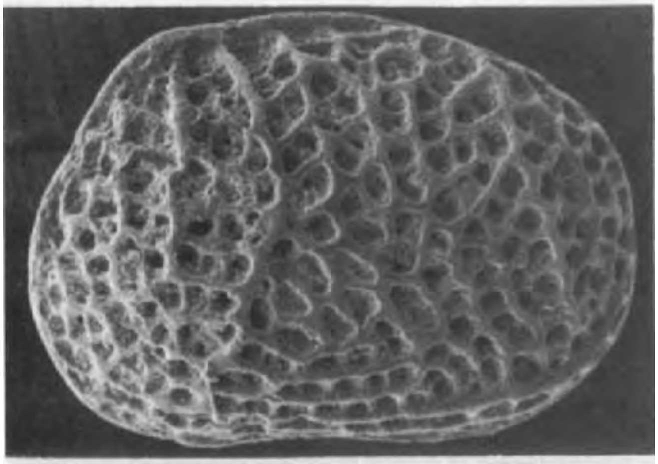
TEXT-FIG. 5—Schematic drawing of reticulation patterns traced from a SEM micrograph and record of meshes (×185). Holy Cross Mountains, Wyoryszow; Middle Devonian, Grzegorzowice Formation.



AMPHICOSTELLA PRIMA ADAMCZAK



AMPHICOSTELLA SP. 3



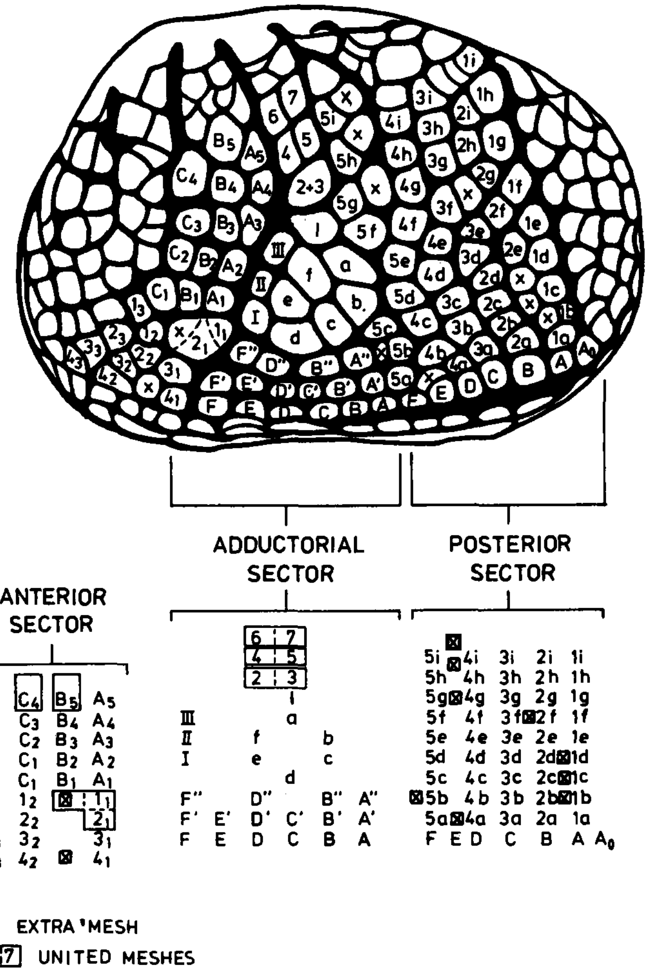
AMPHICOSTELLA SP. 2

Text-fig. 6—SEM micrographs of *Amphicostella* as seen in left lateral view (×155). Holy Cross Mountains, Wydryszow; (*Amphicostella* sp. 2, *A. prima*), Grzegorzowice (*Amphicostella* sp. 3); Middle Devonian, Grzegorzowice Formation.

Eifelian forms is as a rule triserial (1_1, 1_2, 1_3; 2_1, 2_2, 2_3; 3_1, 3_2, etc.), whereas in the Givetian species it begins biserially and terminates with one mesh. In *Amphicostella* sp. 2 the lower part of the anterior sector shows a large and united mesh coded in 1_1, 2_1, X* and the presence of another mesh of X situated between the meshes, 4_1 and 4_2 (Text-fig. 7).

Although the adductorial sector may show a quite differentiated pattern of meshes, the number of meshes remains quite stable within species. In the dorsal part of this sector, *i.e.* above the adductor muscle rosette which has been coded with small letters (a, b, c, d, e, f), there are 1–9 or

Amphicostella sp. 2



TEXT-FIG. 7—Schematic drawing of reticulation patterns traced from a SEM micrograph and record of meshes (×190). The same specimen is pictured in Text-fig. 6.

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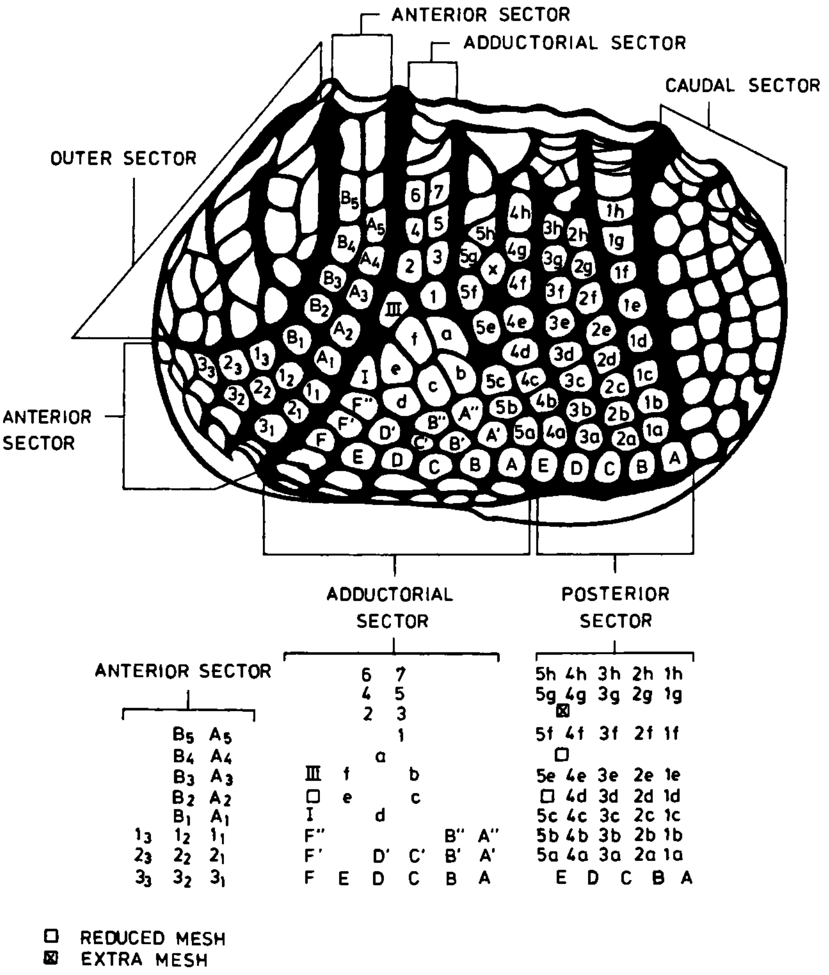
* Mesh X, as interpreted in the present paper, is an element which does not fit very well in the record in question.

more meshes. They are biserially arranged with distinct horizontal muri and less massive vertical elements. Occasionally, a mesh X may appear in this part of the valve (*Amphicostella* sp. 3, Text-fig. 3). In front of the adductor muscle rosette there are two (I, III) or three (I, II, III) meshes. Mesh II is often smaller, or very small.

The ventral part of the adductorial sector is coded with capital letters from A, A′, A″ to F″. It has a maximum of seventeen (*Amphicostella* sp. 1, Text-fig. 5) and a minimum of twelve meshes (*A. sculpturata*, Text-fig. 10). In the latter species, which comes from Czechoslovakia and shows the right valve, reticular elements A′, B, D″, E′ and E″ have disappeared. The posterior sector demonstrates not only the largest diversity in the pattern of meshes, their number, dimensions

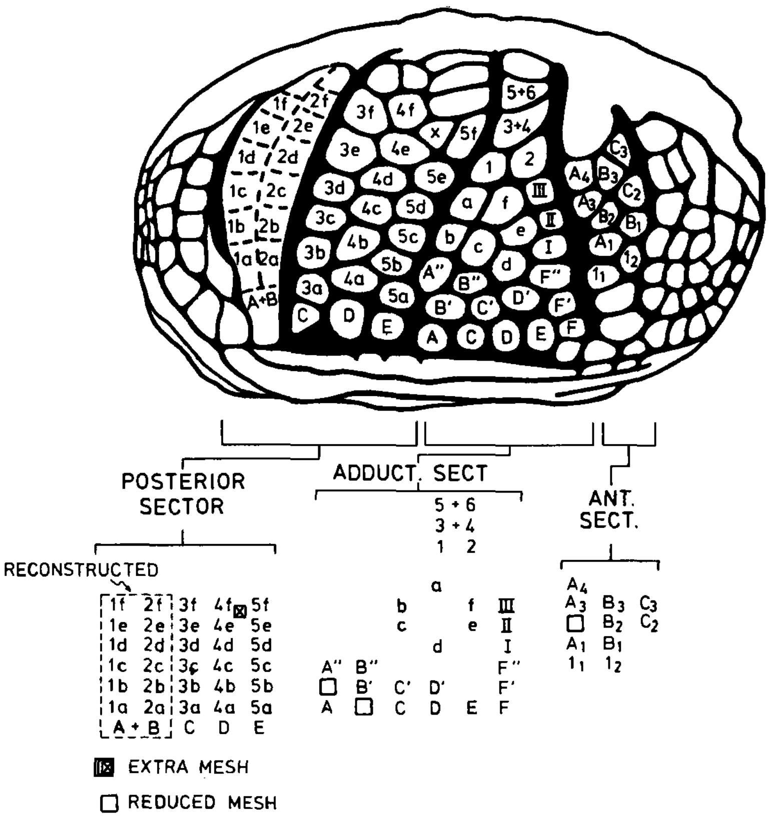
Amphicostella prima Adamczak



TEXT-FIG. 8—Schematic drawing of reticulation patterns traced from a SEM micrograph and record of meshes (×190). The same specimen is pictured in Text-fig. 6.

and size among the different species of *Amphicostella*, but it also reveals an immense individual variability. There are, at the base of this sector, just above the ventral carina, up to seven meshes coded A_0, A, B, C, D, E, F, as in *Amphicostella* sp. 2 (Text-fig. 7) or six meshes A, B, C, D, E, F, as in *Amphicostella* sp. 1 (Text-fig. 5). In *A. prima* four meshes occur, coded: A, B, C, D, whereas *Amphicostella* sp. 3 and *A. sculpturata* (Text-figs. 9, 10) have five meshes (A, B, C, D, E) in this part of the valve. Besides the mentioned reticular elements, the majority of species of *Amphicostella* have five, more or less vertically arranged, rows of meshes which are, beginning from behind, coded: 1a, 1b, 1c, 1d, 1e, 1f, etc. to 5a, 5b, 5c, etc. In *Amphicostella* sp. 1 and *Amphicostella* sp. 2 there occur some additional but incomplete rows of meshes coded as X-es. These are situated between rows 1 and 2, 4 and 5, and in front of row 5. The mentioned species have as many as over ten X meshes present in the posterior sector of the carapace (Text-figs. 5, 7). Furthermore, in *A. prima* the number of X meshes is also important though not to such a degree as in the previous species. The largest number of X meshes found in the form mentioned is five. Generally, *A. prima, Amphicostella* sp. 3 and *A. sculpturata* have only one X mesh, which may be situated any place in the posterior sector of the valve, or none. Moreover, specimens provided with several X meshes frequently show that

Amphicostella sculpturata (Pokorný)



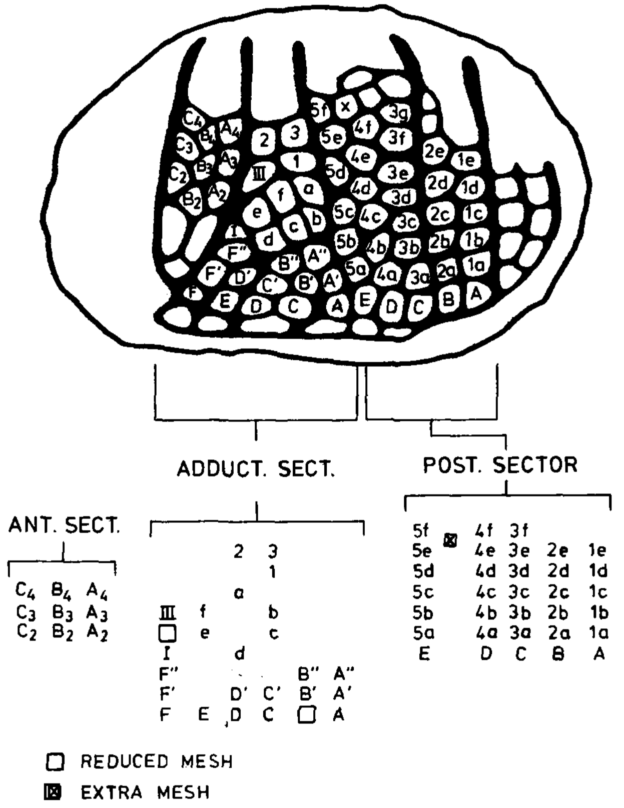
TEXT-FIG. 9—Schematic drawing of reticulation patterns traced from a SEM micrograph and record of meshes (×190). Holy Cross Mountains, Skaly; Middle Devonian, Skaly Formation.

rows, 2, 3 and 4 are slightly curved anteriorly (Text-figs. 5, 7) whereas forms lacking such meshes are straighter (cf. Text-fig. 8).

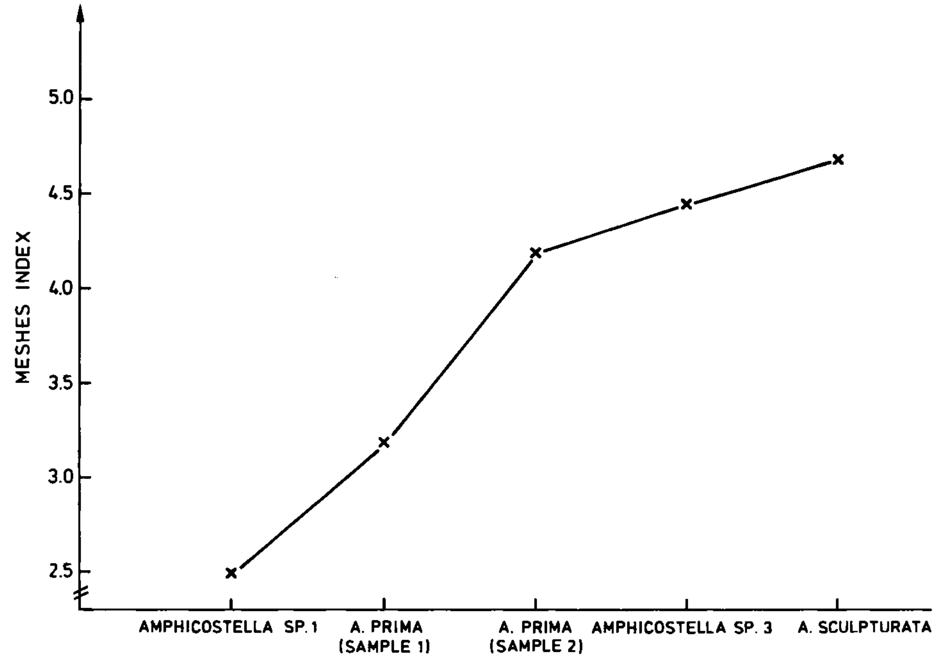
Another aspect of the appearance of meshes in the posterior sector is the occurrence, particularly in row 5 and between rows 5 and 4, of increased muri. Often, these acquire the shape and size of a mesh and are interpreted here as vestiges to them (Text-fig. 8).

A further set of features, which are worthy of mention, concern the size of meshes. These disclose a wide spectrum of dimensions among species and important variability on an intra-species level in space and time (Text-fig. 11). They are round to polygonal in shape. Their shape is also a function of size. It seems that it is the size of meshes which has had a significant selective value, as indicated in the diagram of Text-fig. 11. On the other hand, changes in mesh size also influence the size of the reticulum, which has been analysed with help of a bild analyser. The reticulum becomes smaller (Text-fig. 12). This probably resulted in a more economical management of calcium carbonate for the animal and, perhaps, some behavioral advantage in which the valve wall becomes strengthened, *i.e.* more resistant to wave action.

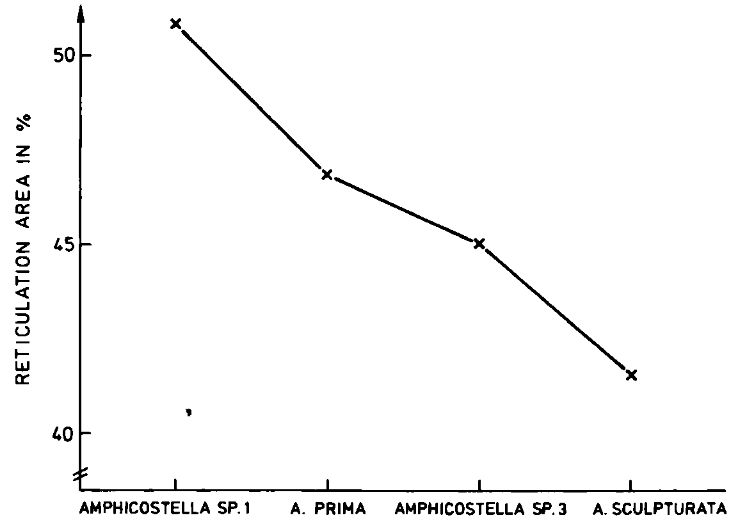
Amphicostella sculpturata (Pokorný)



TEXT-FIG. 10—Schematic drawing of reticulation patterns traced from a SEM micrograph and record of meshes (×160). Czechoslovakia; Middle Devonian.



TEXT-FIG. 11—Diagram of mesh indices (mesh diameter/valve length × 100) in *Amphicostella*.



TEXT-FIG. 12—Dimensions of reticulation area in % in adductorial and posterior sectors in *Amphicostella*.

CONCLUSIONS DRAWN FROM THE PATTERN ANALYSIS OF *Amphicostella*

The changes in pattern of meshes and other ornamental details are very clearly differentiated into two groups. The first concerns transformations of the characters gathered from the several units treated as species. The other affects changes within these units.

Generic characters include reticulation, the adductorial rosette and the five carinae (outer, anterior, adductorial, posterior and ventral) separating the different sectors. The species were separated on the basis of the number of meshes (the rows of meshes) in the various sectors and the number and shape (short, long, massive) of the vertical ridges (carinae) in the posterior sector. This point is summarized in Text-fig. 13.

Changes within the species show a very low level of innovation. These include appearance and distribution of the X meshes, reduction of meshes and changes in size of meshes. The last mentioned may also be considered a result of the other two changes. From the observations made on the intraspecific level, the following conclusions can be drawn:

1. Changes in the posterior sector appear to be isolated, *i.e.* there is no visible connection between them and the other parts of the carapace. They seem to be a product, which appeared very late during the ontogenetic development. Since growth of new segments proceeds from behind, *i.e.* from furca, and the thoracic elements are the last to occur, it therefore seems quite obvious to suggest that the immense variability of the posterior sector reflects the process of growth of the thoracic region and not environmental changes, as has been suggested by Abe (1983).
2. The observed changes have a very low level (microevolution). They do not exceed the limits outlined here for the species.
3. The examined species of *Amphicostella,* which appear to be very closely related, do not demonstrate the presence of any morphologically transitional form. Although there occur individuals in which some parts of the carapace (adductorial sector) exhibit such qualities, this is an isolated phenomenon.
4. It is assumed that natural selection favoured individuals with larger meshes and that reduction in the size of meshes was a direct response to this process.

	Anterior sector (upper section)	Adductorial sector	Posterior sector	
			Meshes	Ridges
Amphicostella sp. 1	3 rows	I–III; 17	5 rows + 13x ABCDEF	0
Amphicostella sp. 2	3 rows + 2x	I–III; 16	5 rows + 8x A_0 ABCDEF	0–1
Amphicostella sp. 3	3 rows	I–III; 14	5 rows + 1x–1 ABCD	2
A. prima	2 rows	I, III, 14	5 rows + 1x–1 ABCDE	3
A. sculpturata	2 rows	I–III, 13 (I, III)	5 rows + 1x–1(?) ABCD	1

TEXT-FIG. 13—Specification of number of rows, meshes and carinae (ridges) in *Amphicostella.*

ACKNOWLEDGEMENTS

Gratitude is expressed to Drs. B. Becker (Frankfurt/Main), H. Groos Uffenorde (Göttingen) and V. Pokorný (Praha), for comparative material of *Amphicostella.* I am also indebted to Dr. D. Guy Ohlson and Dr. R. Russel who read the manuscript and made improvements. J. Arnstrom and S. Jeval prepared the text-figures.

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DISCUSSION

Lundin: It would be interesting to evaluate the ontogenetic development of the pattern. Have you been able to do that?

It is not surprising that the main variation in the reticulation pattern occurs in the posterior sector. It is in the posterior part of the ostracod that the soft part of the morphology is most variable.

Adamczak: I have only some doubtful pre-adult forms in my material and therefore any evaluation of the pattern (reticular) from this point of view would not be easy question.

Your second comment: Yes, I agree but we have very few examples of such a connection in the fossil material. On the other hand, the reticulation has a direct connection with the epithelium and therefore the study of it in Paleozoic ostracods appears to me to be important.

Schweitzer: It seems that the subjective assignment of some fossae to the X category might cause your pattern analysis to be unstable. Perhaps the use of homologous landmarks to construct D'Arcy Thompson's transformation grids would generate more reliable and simpler displays. Methods for calculating these grids have recently been developed by Bookstein. These methods allow you to quantify the changes you see within and among species.

Adamczak: I'm much obliged for your suggestions.

Schweitzer: I'd shy away from plots of quantitative character vs species name; the apparent trend is questionable.

Adamczak: It is an experiment!

Helga Uffenorde: You have demonstrated the variation of fossae, but do you have any variation within the vertical or horizontal ribs or carinae? (Do they always show the same length and distinctness?)

Adamczak: There is some variation in the carinal system, but this concerns the small carinae in the posterior sector. They may fluctuate from right to left and vice versa, *i.e.* from row 1 to 2, etc. They are also different in length and weight. These fluctuations are very small and are presumably environmentally controlled.

IV

Biology

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Cytogenetic Studies on Marine Myodocopid Ostracoda: the karyotypes of *Gigantocypris dracontovalis* Cannon, 1940 and *Macrocypridina castanea* (Brady, 1897)

ALICIA MOGUILEVSKY AND ROBIN C. WHATLEY
University College of Wales, Aberystwyth, Wales

ABSTRACT

The number and morphology of the chromosomes of two species of a meso- and bathypelagic genus (*Gigantocypris*) and a mesopelagic species (*Macrocypridina castanea*), all belonging to the same superfamily of the Cypridinacea, are analysed and compared. The karyotype of these 3 bisexual species consists of $2n = 18$ (16A+XX) for the female and $2n = 17$ (16A+XO) for the male. Although the species share the same number of chromosomes, the morphology and size of their chromosomes are very different. A brief report on a preliminary study on the karyotype of species of Halocypridacea and on chromosome banding is also given.

INTRODUCTION

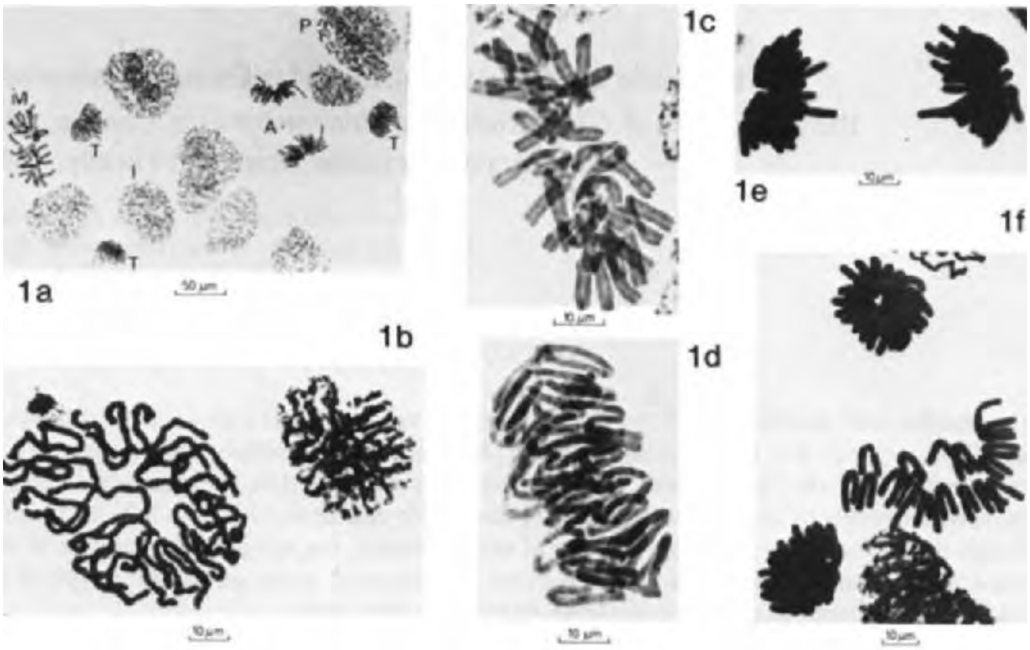
Following an initial study of the karyotype of *Gigantocypris muelleri* (Moguilevsky, 1985), a further two species of Myodocopina have been analysed. These are *G. dracontovalis* Cannon, 1940 and *Macrocypridina castanea* (Brady, 1897). The aim of the present research is to test the extent to which the karyotype of *G. muelleri* is typical or characteristic of the Cypridinacea, the superfamily to which all three species belong. The similarities and differences between the karyotypes of the three species will be outlined below.

The material used for this paper was collected by one of us (A.M.) during *Cruise* 148 of the RRS *Discovery* in the N.E. Atlantic in May–June 1984. Full station data can be obtained from the Cruise Report (Roe *et al.*, 1984). A description of the procedures adopted, from the capture by net to the culturing in a Colchicine solution, fixing and preserving, etc. is given in detail in Moguilevsky (1985).

The present study forms part of a much wider projected work on the cytotaxonomy of Ostracoda which is being carried out by A.M. at Aberystwyth with the aim of providing basic data on the karyotypes, DNA amounts, genetic distance, etc. of all extant ostracod groups. It is also part of a wider study of the distribution, biology, trophic relationships and role in the pelagic ecosystem of Atlantic and Southern Ocean Myodocopida. A number of other publications are currently in preparation (A.M.).

MATERIAL AND METHODS

Gigantocypris dracontovalis Cannon, 1940 is a bisexual, deep bathypelagic species belonging to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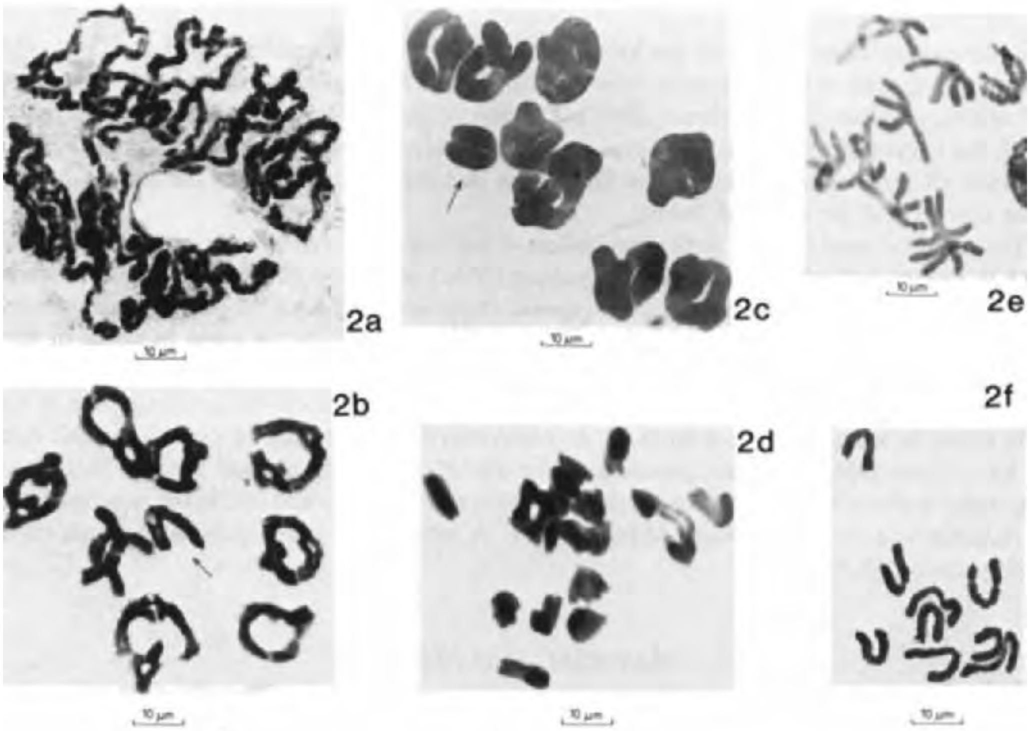
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the Cypridinacea within the Myodocopina. It is probably cosmopolitan in its distribution (Angel, 1981). The material on which this work is based was recovered from samples taken in the N.E. Atlantic. Although the majority of the specimens were obtained from hauls taken between 3,640 and 3,465 m, a few others occurred in near bottom samples at 4,031 m. *G. dracontovalis* is one of the largest living ostracod species (only slightly smaller than *G. muelleri*). Females are larger than males. The size of N.E. Atlantic specimens ranges between 8–10 mm for the female and 7–9 mm for the male (A.M. in prep.).

Macrocypridina castanea (Brady, 1897) which also belongs to the Cypridinacea is a species of cosmopolitan distribution. Its adults are deep mesopelagic in habit. The specimens studied in this paper were recovered from hauls taken between 1,530 and 350 m. *M. castanea* is also a large ostracod, although smaller than *Gigantocypris*. The size range of the female is between 4.6–7.6 mm and for males, 4.8–6.4 mm.

As is the case with many cypridinaceans, the females of both *G. dracontovalis* and *M. castanea* retain the eggs in a brood chamber where they develop before being released into the water as free swimming juveniles.

Embryos as well as testes of both species were used for analysis of mitotic and meiotic stages (Pl. 1; Pl. 2, figs. 1a–e). These tissues proved to give the best results for the study of karyotypes, as already demonstrated in the study of *G. muelleri* (Moguilevsky, 1985). Due probably to the great depths at which *G. dracontovalis* lives, added to the extremely bad weather conditions experienced during 'Cruise 148', none of the specimens were recovered alive. Therefore, all specimens were fixed and preserved immediately in a 3:1 absolute alcohol/acetic acid solution.

To best study chromosomes, one must encounter cells at the right stage of division. The method employed is based on the blocking effect on mitotic divisions obtained when Colchicine is added to the water of the medium in which the ostracods live. This produces an accumulation of cells at metaphase stage, thus rendering the study of the number and morphology of the chromosomes easier. This Colchicine treatment was carried out on the few live specimens of *M. castanea* recovered. The fact that no specimens of *G. dracontovalis* were found alive precluded their being cultured in this way. Fortunately, however, enough cells were found to provide sufficient information on the number and morphology of their chromosomes. All photographs were taken by one of us (A.M.) using a Leitz Laborlux 12 compound microscope with a Wild Photoautomat MPS 45 camera attachment. It was found that the best results were obtained by using a Kodak Image capture ZAHU microfilm 5460.

RESULTS

The study of cells from testes and young embryos of *G. dracontovalis* reveals a karyotype composed of a diploid number of 18 for the female and 17 for the male. The complement is made up of 16 autosomes and 2 X chromosomes in the female and 16 autosomes and one unpaired X chromosome in the male (XO).

Although the karyotype of *G. dracontovalis* appears to be highly symmetrical and uniform, two distinct groups of chromosomes can be distinguished. The first group is composed of three pairs

PLATE 1—Figs. 1a–f. *Gigantocypris dracontovalis*, Mitosis in an embryo squash.

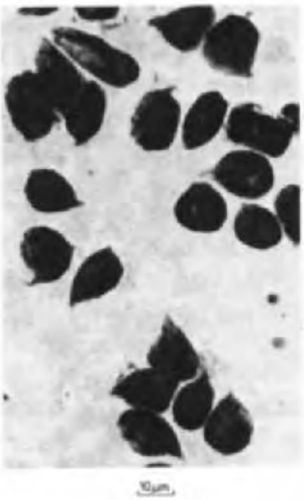
1a. Low power field of view showing: Interphase (I); Prophase (P); Metaphase (M); Anaphase (A) and Telophase (T) stages. 1b. Prophase and interphase. 1c. Metaphase. 1d. Early anaphase. 1e. Late anaphase. 1f. Anaphase and teleophase.

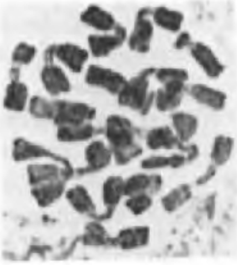
Figs. 2a–f. *Gigantocypris dracontovalis*, Meiosis in testis tissue. 2a. Zygotene. 2b. Diplotene, showing 8 bivalents and a single unpaired ×(arrowed). 2c. Diakinesis (Metaphase I); single unpaired ×(arrowed). 2d. Anaphase I. 2e. Prophase II. 2f. Anaphase II.

1a

1c

1e





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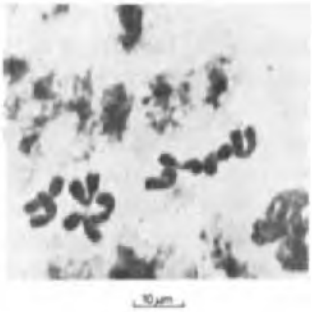

2a

2b

2c

of very similarly sized submetacentric chromosomes. The second group is made up of 6 pairs of metacentric or very slightly submetacentric chromosomes which are fractionally smaller than those of the first group. Between the largest and the smallest chromosomes there is a very gradual size gradient thus rendering difficult the identification of individual chromosomes exclusively on the basis of size (Pl. 2, fig. 2b).

The same type of tissue was used to study the karyotype of *M. castanea*. This shows a similar complement to that of *G. dracontovalis;* 18 chromosomes for the female (16A+XX) and 17 for the male 16A+XO). Although the number of chromosomes is the same in both species, their morphology is very different.

Taking into account their size and morphology, the chromosomes of *M. castanea* can be divided into three clear groups. The first group, composed of the largest chromosomes, includes 8 which are submetacentric, 4 of which show a secondary constriction in their long arm. The second group includes 8 metacentric chromosomes, smaller than the submetacentric ones. The remaining 2 chromosomes (3rd group) are smaller than all the others and clearly acrocentric. Their size ranges between 9 and 19 μm (Pl. 2, fig. 2c). The original study of *G. muelleri* revealed a karyotype comprising 18 chromosomes for the female (16+XX) and 17 for the male (16A+XO), all being metacentric (Moguilevsky, 1985).

DISCUSSION

Present Material

Three species of cypridinacean Myodocopida have been studied to date. These are: *Gigantocypris muelleri,* a bathypelagic species which lives between 700–1500 m depth in the N.E. Atlantic (Moguilevsky and Gooday, 1977); *G. dracontovalis,* a deep bathypelagic species which occurs at much deeper levels (around 400 m) with no overlap in its vertical distribution with *G. muelleri,* and *Macrocypridina castanea* which is meso- to bathypelagic in its vertical distribution.

All three species share the same number of chromosomes, their complement being 18 chromosomes for the female (16A+XX) and 17 for the male (16A+XO). The results of the research carried out so far on these 3 species indicate some clear similarities and differences between their karyotypes. These are outlined below:

The karyotype of *G. muelleri* is highly symmetrical, presenting a great uniformity in both the morphology and size of the chromosomes. All chromosomes are metacentric and their size ranges between 19 and 24μm. The size gradient between the largest and smallest chromosomes is so gradual as to render difficult the identification of individual chromosomes (Pl. 2, fig. 2a).

G. dracontovalis presents 6 chromosomes which are clearly submetacentric and the remaining 12 are metacentric or very sightly submetacentric and fractionally smaller than the others. Their size varies gradually between 16 and 22μm (Pl. 2, fig. 2b).

Macrocypridina castanea presents 8 chromosomes which are both submetacentric and the largest; four of these 8 show a secondary constriction in their long arm. Of the remaining 10 chromosomes, 8 are metacentric and 2 clearly acrocentric. Their size ranges between 9 and 19 μm (Pl. 2, fig. 2c).

Although the number of chromosomes is the same, there are some differences in morphology

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PLATE 2—Figs. 1a–e. *Macrocypridina castanea.* 1a. Prophase (C-mitosis in embryo squash). 1b. Metaphase (C-mitosis in embryo squash). 1c. Diakinesis (Meiosis in ovary tissue). 1d. Anaphase II (Meiosis in testis tissue). 1e. Sperms (testis).

Fig. 2a. *Gigantocypris muelleri*; karyotype (female). Fig. 2b. *Gigantocypris dracontovalis*; karyotype (female). Fig. 2c. *Macrocypridina castanea*; karyotype (female).

and size. The two species of *Gigantocypris* are more similar to each other than either is to *M. castanea* due to the presence of acrocentric elements in the latter species. When comparing the overall appearance of chromosomes at metaphase stage, those of the first two species are similar and 'baton'-like whereas those of *M. castanea* appear stouter, with some of them resembling a "bow-tie". (Pl. 2, figs. 2a–c).

As shown in Table 1, the largest chromosomes are found in *G. muelleri* followed by *G. dracontovalis;* the smallest chromosomes occur in *M. castanea.* This is in exact relation to the overall size of the 3 species. The significance of their relationship is not as yet clearly understood.

Hinegardner (1976) reports a positive correlation between adult body size and DNA content in certain animal species. Further study on both the karyotypes and DNA contents of many more species of Ostracoda is required in order to test to what extent this theory applies to this group.

TABLE 1—COMPARISON OF THE DIPLOID COMPLEMENT, SIZE RANGE AND MORPHOLOGY OF THE CHROMOSOMES OF 3 SPECIES OF CYPRIDINACEA (MYODOCOPINA)

Species	Diploid Chromosome Numbers			Size Range
Chromosome Type	Metacentric	Submetacentric	Acrocentric	(μm)
Gigantocypris muelleri	18	—	—	19–24
Gigantocypris dracontovalis	12	6	—	16–22
Macrocypridina castanea	8	8	2	9–19

Comparison with the Podocopina

Tetart (1978) analysed the karyotypes of 24 species of freshwater podocopid Ostracoda. Of these, 22 belong to the Cypridacea, 1 to the Cytheracea and 1 to the Darwinulacea. He found that the differences between the karyotype of the Cytheracea and that of the Cypridacea are mainly numerical, whereas the Darwinulacea differ also in the morphology of their chromosomes. *Darwinula stevensoni* Brady and Robertson (1870) has a peculiar karyotype composed of 22 chromosomes all of which are 'acrocentric' and very uniform in size. As can be seen in Table 2, the morphology of the chromosomes of the cyprids varies. Tetart suggests that the more 'primitive' karyotypes are composed of only 'acrocentric' chromosomes while more evolved karyotypes have less 'acrocentric' and more metacentric chromosomes.

Although the number of chromosomes of the Myodocopina studied to date seems to fall within the range of most podocopid species, their morphology and size are very different since the majority (or all) are of a metacentric of submetacentric type. The chromosomes of the former are also very much larger.

TABLE 2—DISTRIBUTION OF TYPES, DIPLOID NUMBER AND SIZE RANGE OF CHROMOSOMES WITHIN THE PODOCOPINA [BASED ON DATA TAKEN FROM TETART (1978)].

Superfamily	Diploid Chromosome Numbers				Size Range (μm)
	Total (2n)	Metacentric	Submetacentric	Acrocentric	
Cytheracea [*Limnocythere* (*L.*) *inopinata*] bisexual	14	2	—	12	3
Darwinulacea (*Darwinula stevensoni*) parthenogenetic	22	—	—	22	0.5–1
Cypridacea (various species) bisexual + parthenogenetic	15–35	1–14	—	7–30	0.5–6

The karyotypes of the 3 species of Myodocopina studied to date revealed some clear features which set the group apart from the Podocopina. Following Tetart's reasoning, the Myodocopina may prove to be a highly specialized group with a highly developed karyotype. However, other species of Cypridinacea as well as Halocypridacea need to be studied before any firm conclusions can be drawn regarding the position of the Myodocopina in the evolutionary plexus of the Ostracoda.

Some 15 species of Halocypridacea have been analysed to date (A.M. in prep.); unfortunately, the results have been somewhat unsatisfactory possibly due to the inadequacy of the material. Some modifications to the methods of culturing and fixing specimens of this particular group have already been introduced. The results, which will be published in due course, might throw some light onto the status of Halocypridacea within the Myodocopida and its comparison with the Podocopida.

Potential implication of future studies in the cytotaxonomy of Ostracoda

As explained above, Tetart in his work on freshwater podocopids suggested that evolution of the karyotype in ostracods involves a reduction in the number of chromosomes with centromere in a distal position which fuse to form chromosomes with the centromere in a median position or metacentric. These Robertsonian fusions are found to be one of the processes by which a reduction in the number of chromosomes occurs in closely related species in the animal kingdom.

The evolution of the karyotype of many species has been studied using chromosome banding techniques. One of the most important applications of chromosome banding is the unequivocal identification of the chromosomes in a karyotype, especially when these are of very similar size and shape, as well as small parts of the chromosomes which may have undergone rearrangements. In many cases the karyotypes of related species are remarkably similar. As a direct result of chromosome banding, karyotype changes have been shown to arise by several mechanisms such as Robertsonian fusion. Protocols for banding involve the pre-treatment of the chromosomes in such a way as to cause their structure to collapse. During subsequent staining certain regions of the chromosome reconstitute to produce darkly staining bands.

With a view to testing Tetart's ideas on the evolution of ostracod karyotypes, three different chromosome banding procedures were tried on the species of Myodocopina studied herein. These were, C-banding after barium hydroxide; Acetic acid-Saline-Giemsa (ASG) banding and R-banding by high temperature treatment, as described by Macgregor and Varley (1983).

To the authors' knowledge, these techniques have not been previously applied to Ostracoda. Chromosome banding was first developed for mammalian species, and although the results on Myodocopina are so far somewhat disappointing, the potential is very promising. These not very satisfactory results are due mainly to the overlapping of the large chromosomes and a certain inadequacy of the techniques. Modification of these protocols is expected to produce better results in the future.

Conventional taxonomic studies on Ostracoda are based on the analysis of a wide spectrum of characters of both carapace and appendages. Similarly, cytotaxonomy covers all aspects of taxonomy at the cellular level. Cytotaxonomic studies deal not only with the number of chromosomes, but also with their morphology and behaviour. Cytochemical information is now also being used. The study of genetic variability by means of gel electrophoresis provides the opportunity for understanding the interrelations between genetics and ecology.

The study of evolution at the DNA level entails the study of DNA gain and loss as well as of nucleotide changes. Hinegardner (1976) suggests that "animals and plants that are considered to represent primitive or ancient and relatively slowly evolving lineages often have more or much more DNA than the average of their particular taxon".

The authors are convinced of the potential importance of cytotaxonomic studies in Ostracoda.

The analysis of the karyotypes of all major groups is projected and in the near future it is also intended to begin a study of DNA amounts and gel electrophoresis of enzymes.

The overall results obtained to date are encouraging enough to consider the cytogenetical characteristics of the Ostracoda as a useful tool in the understanding of their evolution.

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V

Ecology

Morphological and Ethological Adaptations of Ostracoda to Microhabitats in *Zostera* Beds

TAKAHIRO KAMIYA
Kanazawa University, Japan

ABSTRACT

Detailed sampling of Ostracoda in *Zostera* beds revealed that two ostracod faunas are living in two distinct microhabitats, namely the leaves of *Zostera* and the surface of the sand bottom. Common morphological characters are seen among the constituent species of each fauna. The phytal species have round carapaces with a convex ventral area. Conversely, the sand bottom species have elongated carapaces with a flat ventral plane. Through the observation of their behaviour, it has been found that the differences in morphology are related to their mode of life, especially to their copulatory behaviour, which has adapted differently to their respective microhabitats. The functions of other morphological characters of the ostracod soft parts have also been estimated on the basis of their mode of life.

INTRODUCTION

Adaptation is generally reflected in the morphology of animals as its functional aspects which are attributed to evolution. An adequate functional appreciation of morphology should be based on the study of the mode of life of the animals.

Little has been known about the mode of life of Ostracoda themselves. Previous works have revealed the relationships between habitats and faunal compositions of Ostracoda. This is exemplified by the works of Williams (1969) and Whatley and Wall (1975) on phytal fauna in relation to microhabitats, its faunal composition being controlled by the species of algae. While carapace shapes have been mainly described for ostracod taxonomy, some work has dealt with functional aspects. Benson (1970, 1975) stressed the necessity of biomechanical interpretation of the carapace shape. McGregor and Kesling (1969) discussed the functional morphology of ostracod carapaces and soft parts in relation to their copulatory behaviour.

The aim of this work is to combine the characteristic features of the microhabitats, mode of life and morphology of Ostracoda living in the sea grass *Zostera* beds of the shallow subtidal zone. The *Zostera* beds may offer several kinds of microhabitats for Ostracoda, though it can be regarded as a single habitat in a broad sense. We can consider the surface of the *Zostera* leaves, the surface of the bottom sediments, the interstices of the sediment particles, etc., as possible microhabitats for Ostracoda. The first step in this work is to investigate what kind of species are living in those microhabitats in the *Zostera* beds. The second step is to comprehend the relationships between the morphologies and microhabitats through observation of the modes of life and to estimate the functional characters of ostracod morphology, especially that of carapace shape.

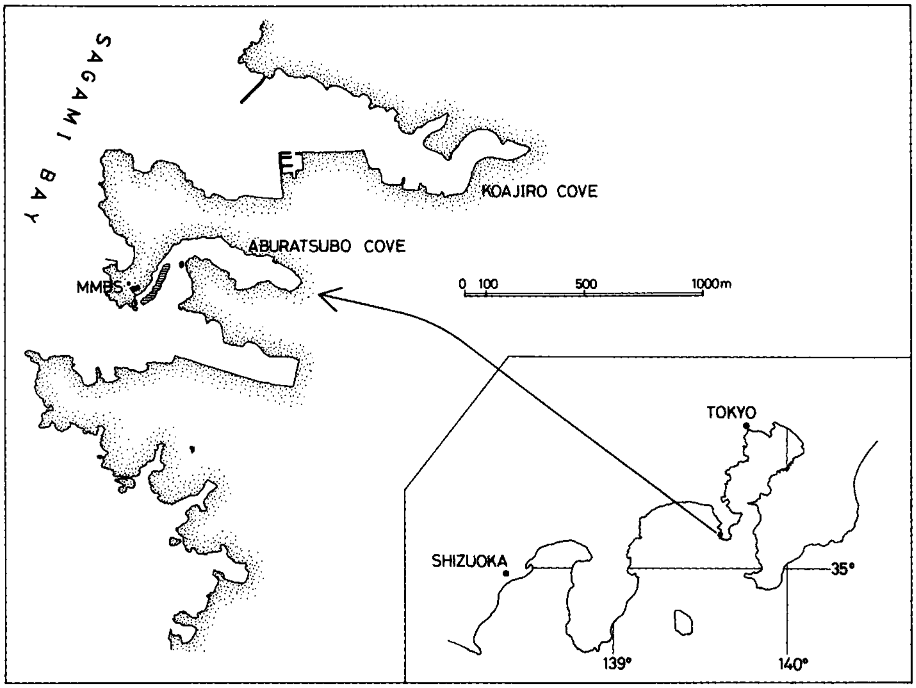
THE ENVIRONMENT OF *Zostera* BEDS

The eel grass, *Zostera marina* is one of the most popular and abundant sea grasses throughout the world. The plant, consisting of several thin leaves, 50–100 cm in length and about 1 cm in width, is joined to other plants by subsurface stems and grows in stock to form *Zostera* beds. A leaf has a short life, falling off within about two months and being swept away from the beds. There is an obvious seasonal vicissitude in the *Zostera* beds. The leaves grow thickly from spring to early summer and decline from late summer to winter.

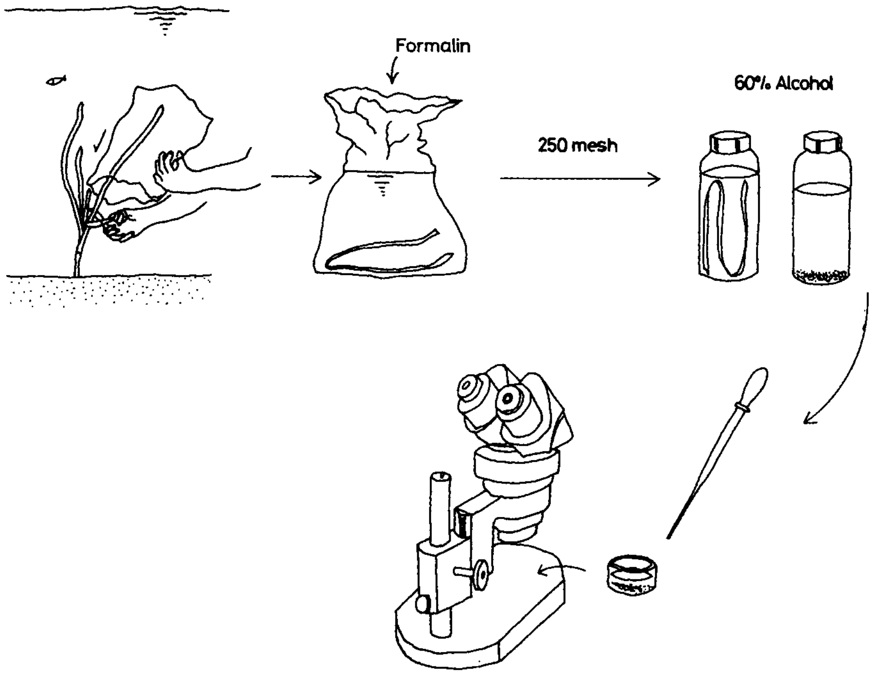
Samples were collected from the *Zostera* beds in Aburatsubo Cove which is located near the southern tip of the Miura peninsula, Pacific coast of central Japan (Text-fig. 1). Aburatsubo Marine Biological Station of the University of Tokyo is located on shore. The water temperature in the cove ranges from about 27 °C (Aug.) to 8 °C (Feb.).

Here, *Zostera marina* grows rankly in shallow water, 30 cm to 2 m deep during spring low tide, along the shore near the mouth of the cove (Text-fig. 1). The substratum in the *Zostera* beds is composed of medium- to coarse-grained sand. The surface is covered with a soupy flocculent layer less than about three millimeters thick.

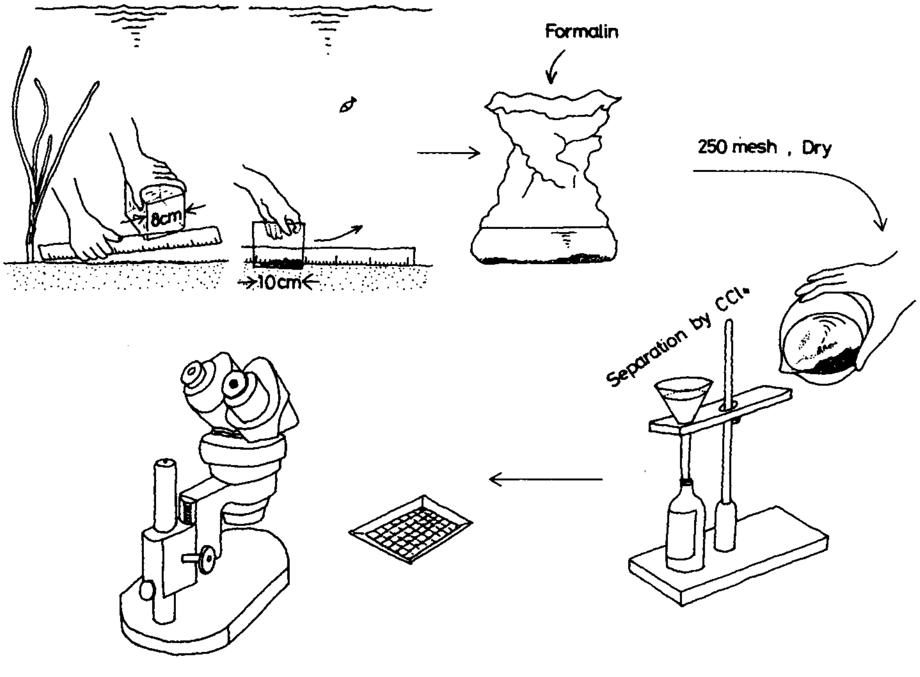
Three micro-environments were postulated in these *Zostera* beds where the benthonic Ostracoda might live. They are the surface of *Zostera* leaves, the surface of the sand bottom, *i.e.* in and on the surface of the flocculent layer, and the subsurface interstices between the sand grains. The *Zostera* leaves, which have smooth, flat surfaces, stand upright from the bottom because they hold air



TEXT-FIG. 1—Location of Aburatsubo Cove. Hatched area in the cove shows the distribution of *Zostera* beds. MMBS: Misaki Marine Biological Station of the University of Tokyo.



TEXT-FIG. 2—Sampling and preparation procedures of *Zostera* phytal fauna.



TEXT-FIG. 3—Sampling and preparation procedures of sand bottom fauna.

bubbles in cavities within the leaves. Because of these features, the habitat formed by the surface of the *Zostera* leaves may contrast strikingly with that of the sand bottom surface for Ostracoda.

SAMPLING AND PREPARATION

Three kinds of samples, *Zostera* leaves, sand bottom surface and subsurface sand, were first collected separately. However, no Ostracoda were found living in the subsurface samples, and thus later seasonal and periodic samplings were made from leaves and surface sediments alone.

To collect Ostracoda on *Zostera* leaves, a *Zostera* leaf was covered with a plastic bag, and cut off from the plant with a scissors (Text-fig. 2). The phytal fauna on the leaves was fixed with formalin, then dipped into 60% alcohol and the Ostracoda were picked up under the microscope. The *Zostera* leaves could be subdivided into old and young leaves or tip and base of the leaves. However, as there proved to be no difference in ostracod composition among the subdivided samples, they were then treated collectively.

The surface of the sand bottom was sampled quantitatively by using a small plastic sampler of box-type (Text-fig. 3). After fixing with formalin, the surface materials were washed through a 250 mesh/inch sieve and dried. They were then separated into light and heavy grains by CCl_4, and the separations were repeated twice for the sunken residues. Ostracoda were picked up from the light grains under the microscope. Test samplings were made separately for the bottom samples according to the thickness of the flocculent layer, but no difference in Ostracoda could be found in these samples.

Subsurface sand was dug out from a horizon about 1–20 cm below the surface, but no living Ostracoda were found in it.

Specimens with perfect soft parts were regarded as living individuals and others, such as those with only the epidermis and some of the appendages remaining, were treated as dead individuals. Only living individuals were used for later analyses.

Samples were collected once or twice a month from September 1983 to February 1985 around a fixed point at the centre of the *Zostera* beds.

OSTRACODA IN THE *Zostera* BEDS

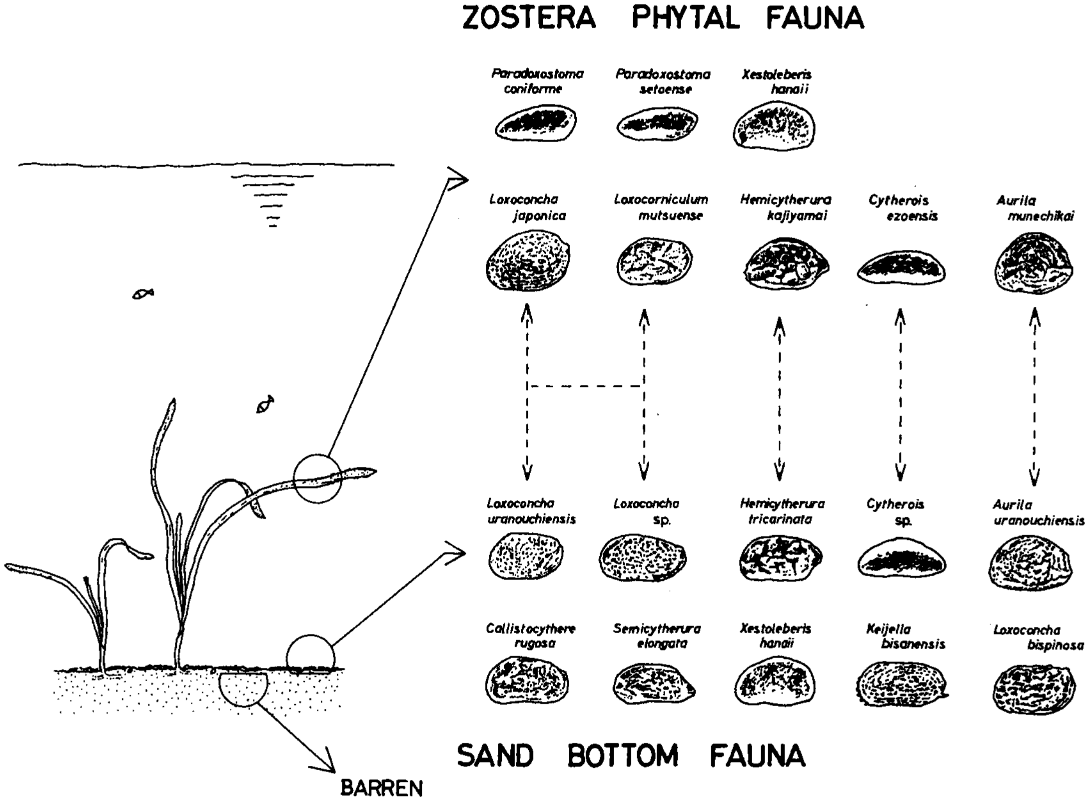
As a result of precise samplings, two ostracod faunas were found, one living on the *Zostera* leaves and the other on the surface of the sand bottom (Text-fig. 4).

Eight species are found to be living on the leaves of *Zostera* and constitute the *Zostera* phytal fauna. In this fauna, *Loxoconcha japonica* is predominant from early summer to early autumn, making up 94–99% of all individuals. *Paradoxostoma coniforme, P. setoense* and *Cytherois ezoensis* are equally dominant from winter to spring, altogether accounting for 80–95% of the whole population. *Xestoleberis hanaii, Hemicytherura kajiyamai, Loxocorniculum mutsuense,* and *Aurila munechikai* are rare throughout the year.

The surface of the sand bottom is inhabited by ten species which are here referred to as the sand bottom fauna. The dominant species, *Loxoconcha uranouchiensis,* is particularly abundant from autumn to winter. *Aurila uranouchiensis, Callistocythere rugosa, Cytherois* sp. and *Loxoconcha* sp. are the main associate species which are commonly found in most seasons. *Xestoleberis hanaii* is rare, but consistently found. Several individuals of *Hemicytherura tricarinata, Semicytherura elongata, Keijella bisanensis,* and *Loxoconcha bispinosa* are occasionally found. *Xestoleberis hanaii* is the only species common to both faunas, although the number of individuals is always small.

Distribution of these species in other environments was checked in the area surrounding the *Zostera* beds. The dominant species of the phytal fauna, *Loxoconcha japonica,* lives exclusively on the leaves of *Zostera. Paradoxostoma setoense* was found to live abundantly not only on the *Zostera* leaves, but also on the green alga *Ulva* in tide pools on the rocky shore. *Xestoleberis hanaii, Hemicytherura kajiyamai* and *Loxocorniculum mutsuense* have their main habitat in the bushy, calcareous alga *Corallina* in tide pools. *Aurila munechikai* lives mainly on the *Sargassum* and *Zostera* which grow along the mouth of the cove. The dominant species of the sand bottom fauna, *Loxoconcha uranouchiensis,* lives on the sand bottom in and around the *Zostera* beds. *Aurila uranounchiensis, Callistocythere rugosa, Cytherois* sp. and *Loxoconcha* sp. are also abundant on the sand bottom in and around the beds, but the last has a tendency to be more abundant in the deeper parts. *Hemicytherura tricarinata* is common on muddy sand bottoms with poor circulation as, for example, in the *Zostera* beds in the inner part of Koajiro cove (Text-fig. 1). *Keijella bisanensis* and *Loxoconcha bispinosa* live chiefly on the mud bottom at the centre of the cove.

Several pairs of congeneric species were recognised between the phytal and the sand bottom fauna (Text-fig. 4). *Loxoconcha japonica,* the dominant species of the *Zostera* phytal fauna has its counterpart *Loxoconcha uranouchiensis* in the sand bottom fauna. Other examples are *Hemicytherura kajiyamai* in the phytal fauna and *H. tricarinata* in the sand bottom fauna. *Cytherois ezoensis* and *C.* sp., and *Aurila munechikai* and *A. uranouchiensis.* A parallel relationship in species composition is recognised between the two faunas which live in two adjacent, but distinctly different microhabitats. This relationship will aid analysis of the functional and adaptive morphology of the ostracod carapace.

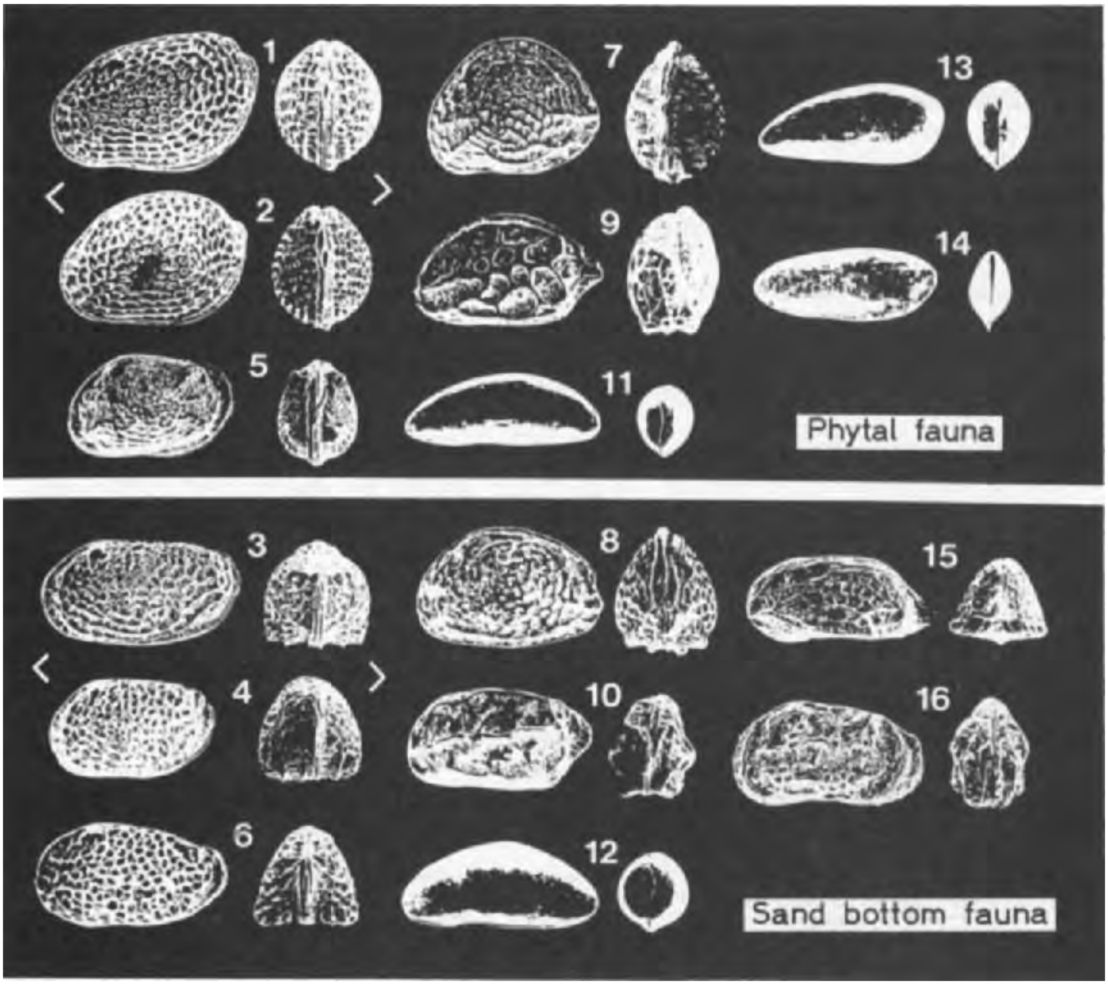


TEXT-FIG. 4—The two ostracod faunas in the *Zostera* beds. Dashed arrows show pairs of congeneric species between the phytal and the sand bottom faunas.

CARAPACE SHAPE OF OSTRACODA IN THE *Zostera* BEDS

The species in each fauna have their own common characters of carapace shape (Text-fig. 5). The carapace shapes of the phytal species are circular or oval in lateral view and rounded, rugby-ball-shaped, in posterior view. The carapace shapes of *Loxoconcha japonica* (Text-figs. 5-1, 5-2), *Loxocorniculum mutsuense* (Text-fig. 5-5) and *Aurila munechikai* (Text-fig. 5-7) are typical examples. *Paradoxostoma* spp. (Text-figs. 5-13, 5-14) and *Cytherois ezoensis* (Text-fig. 5-11) have shapes which are somewhat elongated in the anterior-posterior direction, with a ventral contact margin sharper than is typical.

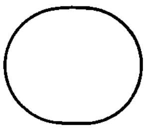
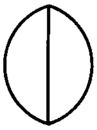
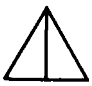
Conversely, the carapace shapes of the sand bottom species are rectangular in lateral view and triangular or circular with a flat "ventral plane" in posterior view. The typical representatives with



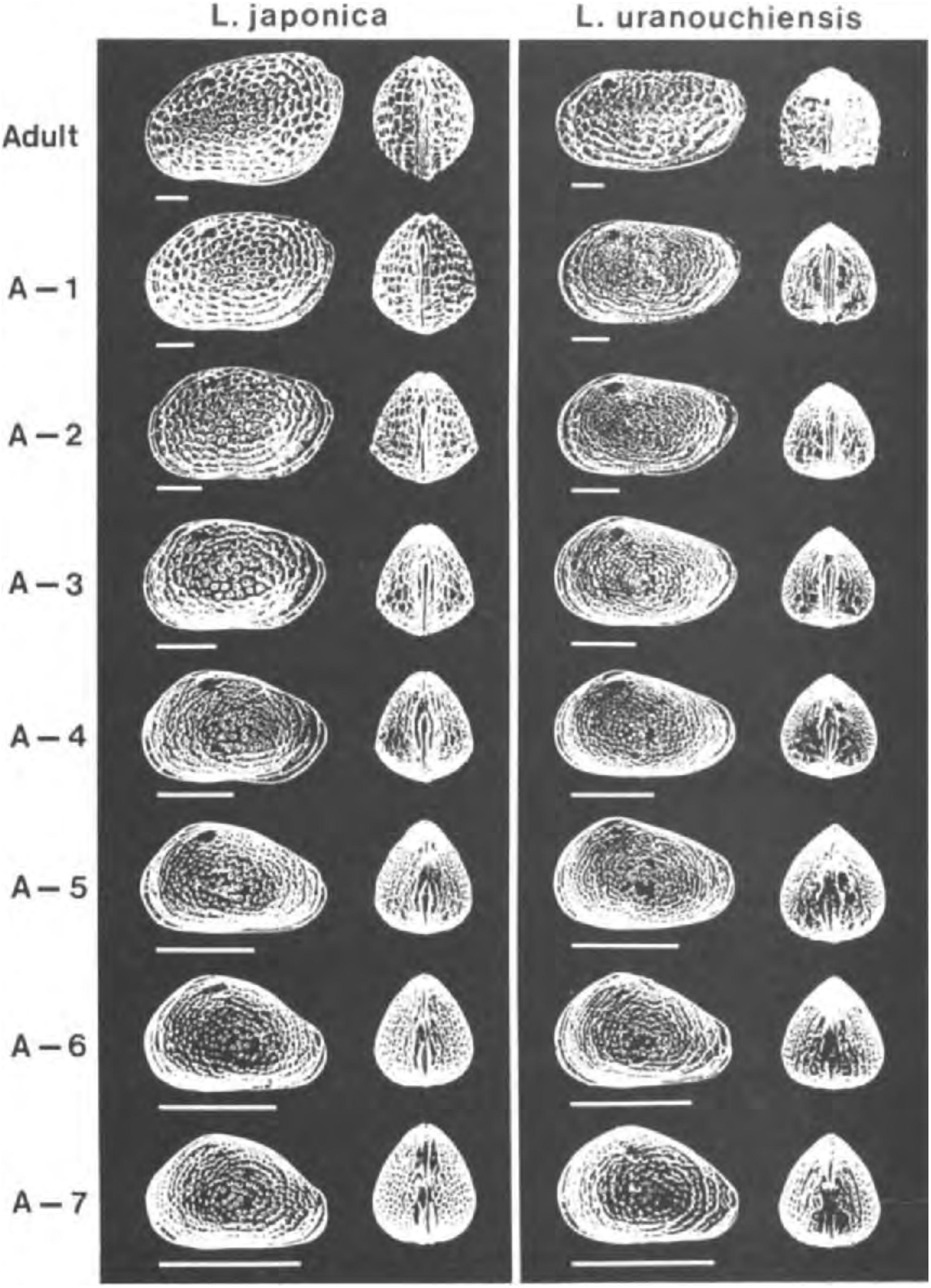
TEXT-FIG. 5—Carapace shapes (lateral and posterior views) of Ostracoda in the *Zostera* beds. 1. *Loxoconcha japonica* (male). 2. *L. japonica* (female). 3. *L. uranouchiensis* (male). 4. *L. uranouchiensis* (female). 5. *Loxocorniculum mutsuense*. 6. *Loxoconcha* sp. 7. *Aurila munechikai*. 8. *A. uranouchiensis*. 9. *Hemicytherura kajiyamai*. 10. *H. tricarinata*. 11. *Cytherois ezoensis*. 12. *C.* sp. 13. *Paradoxostoma coniforme*. 14. *P. setoense*. 15. *Semicytherura elongata*. 16. *Callistocythere rugosa*.

a triangular posterior view are *Loxoconcha uranouchiensis* (Text-figs. 5-3, 5-4), *L.* sp. (Text-fig. 5-6), *Aurila uranouchiensis* (Text-fig. 5-8) and *Semicytherura elongata* (Text-fig. 5-15). They have a distinct edge along the ventral part of the carapace, where the carapace bends inward and makes a flat ventral plane. *Cytherois* sp. and *Keijella bisanensis* are examples of a circular outline in posterior view. These carapace shapes are shown schematically in Text-fig. 6.

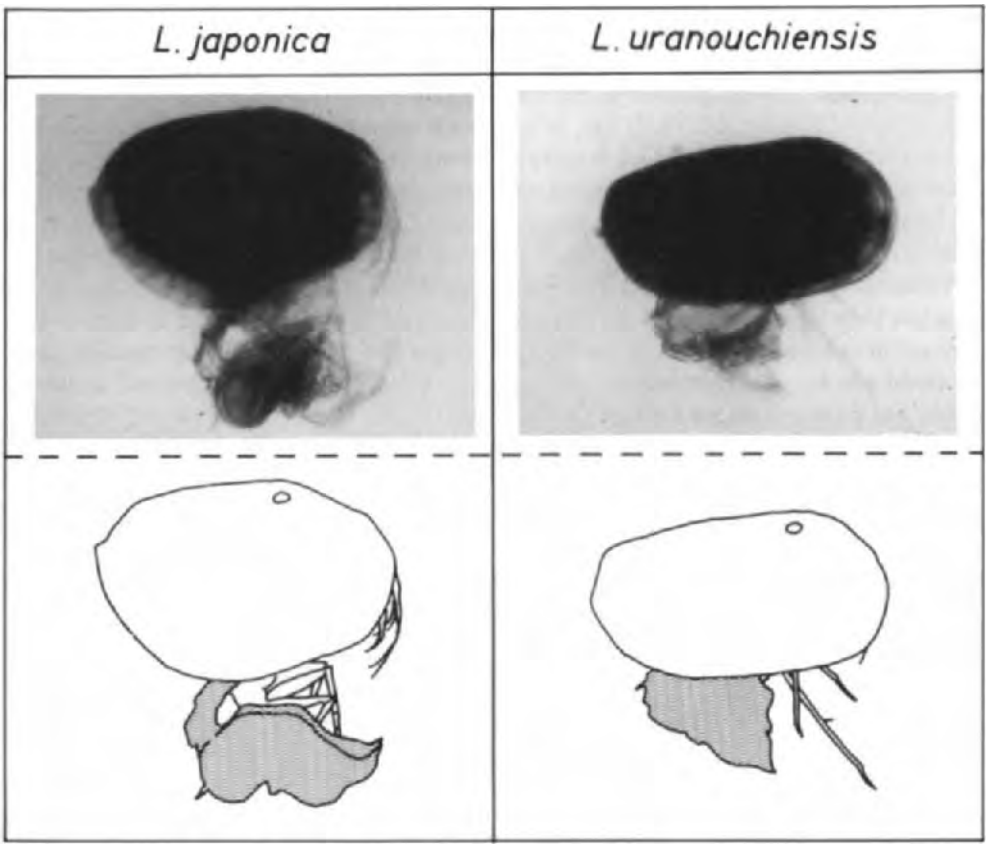
These morphological characteristics common among taxonomically diverse species are thought to be most probably a consequence of adaptations to life on *Zostera* leaves or, for the other fauna, on the sandy bottom. A pair of *Loxoconcha* species, *Loxoconcha japonica* (Text-figs. 5-1, 5-2), the proper *Zostera* species and *L. uranouchiensis* (Text-figs. 5-3,5-4), the proper sand bottom species, are ideal for comparison because both species are most abundant and characteristic of their respective microhabitats. The male of the phytal *L. japonica* has an inflated posterior part and a truncated ventral margin, apparently different from the rectangular lateral view and distinct ventral plane of the sand bottom *L. uranouchiensis.* This contrast in ventral shape was pursued back to the early developmental stages (Text-fig. 7). Juveniles of both species grow through seven ecdyses before the adult stage. At the first stage, they closely resemble each other being distinguishable only by the shape of their dorsal margins. The differences in the ventral area and the posterior part become clearer as they grow and complete at the final adult stage. The anatomy of the soft parts revealed that the swollen and inflated posterior part of the phytal species provides space to accommodate the enormous penis with its long stem (Text-fig. 8). On the contrary, the sand bottom species with a slender posterior part has a short sexual organ without a long stem (Text-fig. 8).

	Shape of carapace		species
	lateral view	posterior view	
phytal sp.	circle 	rugby-ball shape 	*Loxoconcha japonica* *Loxocorniculum mutsuense* *Paradoxostoma coniforme* *P. setoense* *Cytherois ezoensis* *Hemicytherura kajiyamai* *Aurila munechikai* *(Xestoleberis hanaii)*
sand bottom sp.	rectangle 	triangle 	*Loxoconcha uranouchiensis* *L. bispinosa* *L.* sp. *Aurila uranouchiensis* *Hemicytherura tricarinata* *Semicytherura elongata*
	elongate rectangle 	circle 	*Cytherois* sp. *Keijella bisanensis* *Callistocythere rugosa* *(Xestoleberis hanaii)*

TEXT-FIG. 6—Schematic comparison of carapace shapes of phytal and sand bottom Ostracoda.



TEXT–FIG. 7—Morphological changes during development of the carapaces of the phytal and the sand bottom species of *Loxoconcha*. Scale bar 100 μm.



TEXT-FIG. 8—Male sexual organs of the phytal and the sand bottom species of *Loxoconcha.*

The fact that the differences in carapace shape between the two species become apparent at the adult stage and are related to the morphology of the sexual organs, suggests a causal relationship between carapace morphologies and reproductive behaviour.

RELATIONSHIP BETWEEN MORPHOLOGY AND ETHOLOGY

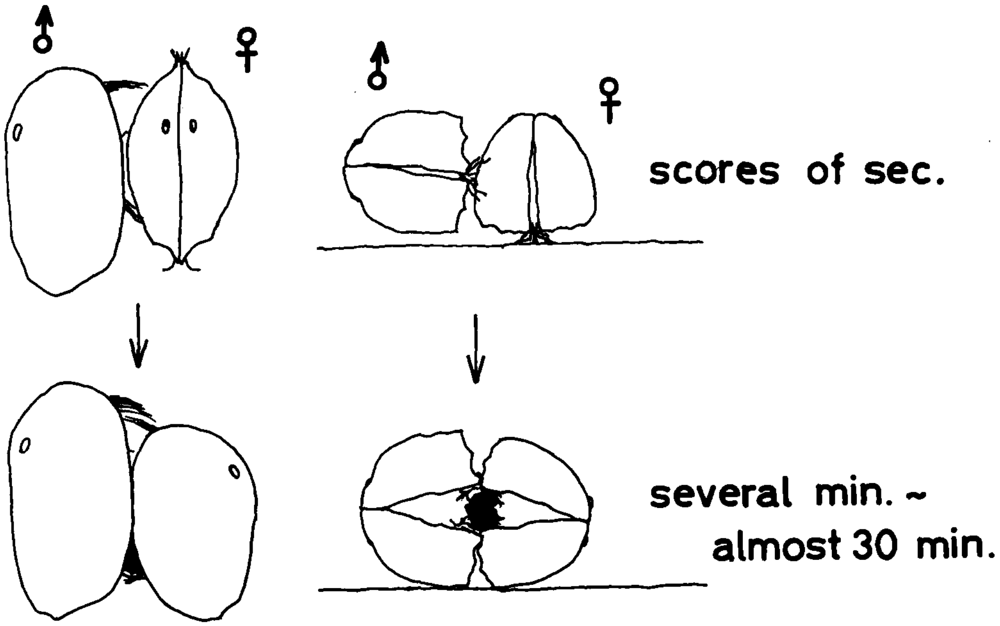
Ostracoda generally reproduce through copulation. There are three known couplatory positions–ventral to dorsal, ventral to posterodorsal, and ventral to ventral (Elofson, 1951; McGregor and Kesling, 1969). Little is known of the relationship between the copulatory positions and their life habits or habitat characteistics.

Carapace Morphology and Copulatory Behaviour

According to the writer's observation in petri-dishes in the laboratory, the sand bottom species, *Loxoconcha uranouchiensis* copulates in the ventral to ventral position (Text-fig. 9. Pl. 1, figs. 8-11). In the dish, a male actively looks for females and then comes to meet one of them. It climbs on to the carapace of a favourite female, clings to the lateral side of the female in what is probably courtship behavior and then, if the female opens the carapace, slowly makes the ventral to ventral contact. They copulate lying down or standing on their heads on the substrate, holding on to each other, with their appendages, for more than twenty minutes. In both males and females of this species the carapace has a flat ventral plane which is suitable for copulation in the ventral-to-ventral position in terms of geometry.

On the other hand, the congeneric phytal species, *Loxoconcha japonica* copulates in the ventral-to-lateral position (Text-fig. 10. Pl. 1, figs. 1-7). A male aggressively looks for females and tries to step on the carapace of a female which is creeping along. If a stepped-on female stops creeping, the male clings to the lateral side of the female (courtship behaviour). The moment the male quickly stretches its penis, the female opens the carapace, and firmly clings to the surface of the leaves to support the male and herself, and the male copulates with the inclining female keeping the same clinging position. To complete this series of steps usually takes only a few seconds, and copulation itself lasts less than three seconds. If the phytal species were to copulate in the complete ventral-to-ventral position holding on to each other by appendages like the sand bottom species, the coupling pair could not support themselves, but would slip down from the *Zostera* leaf to the bottom. This would not be comfortable for them.

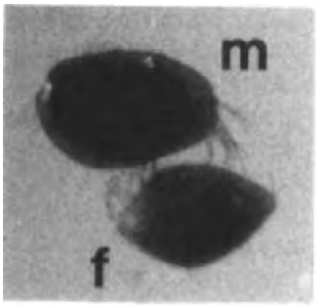
The rounded carapace of this species makes such a copulatory position possible. When a female clings to a *Zostera* leaf in an upright position, the rounded ventral margin leaves space between the leaf for the penis to pass through and be inserted into the opened carapace of the female. A gentle inflation of the carapace along the ventral margin allows the carapace edges of both sexes to touch diagonally. Even though the carapace shape is ideal for the ventral-to-lateral position, in



TEXT-FIG. 9—Copulation of the sand bottom species, *Loxoconcha uranouchiensis*. Left: view from above. Right: side view.

PLATE 1—Copulatory behaviour of the phytal and the sand bottom species.

Figs. 1-7. Phytal *Loxoconcha japonica*. 1-4, 5-7. Respective steps in copulation by two pairs of same individuals. 1, 2, 5. Courtship behaviour. 6. The moment of extension of the hemipenis. 3, 4, 7. Coupling. Owing to the strong light and the slippery surface of the petri-dish, they got tired and were steeply inclined or slipped off. Figs. 8-11. Sand bottom *Loxoconcha uranouchiensis*. 9-10. Successive behaviour of same individuals. 8. Courtship behaviour. 9-11. Coupling. (m: male; f: female; p: penis).



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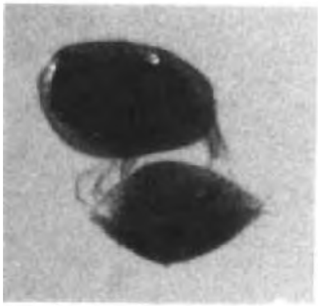

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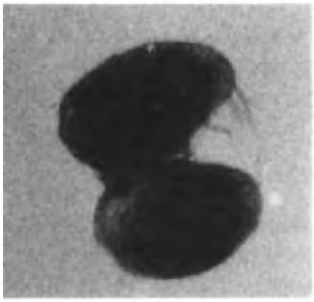

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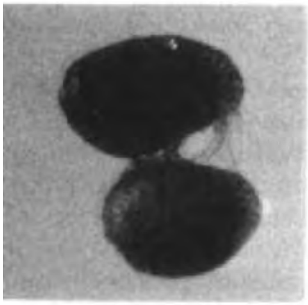

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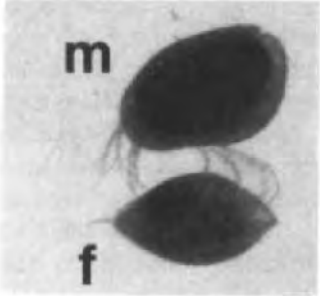

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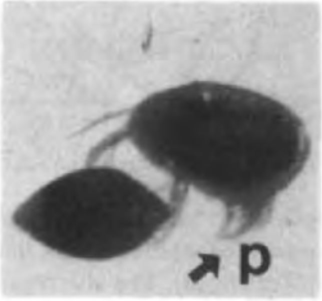

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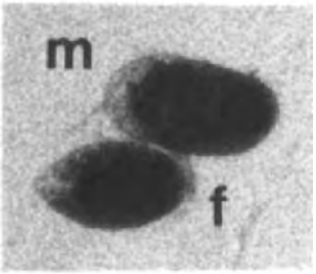

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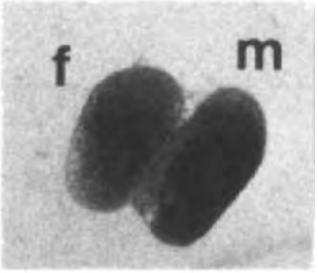

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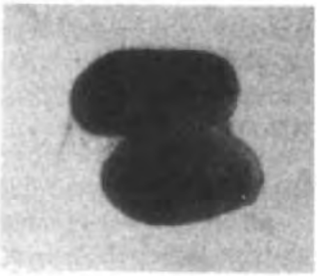

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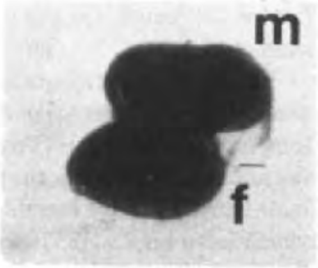

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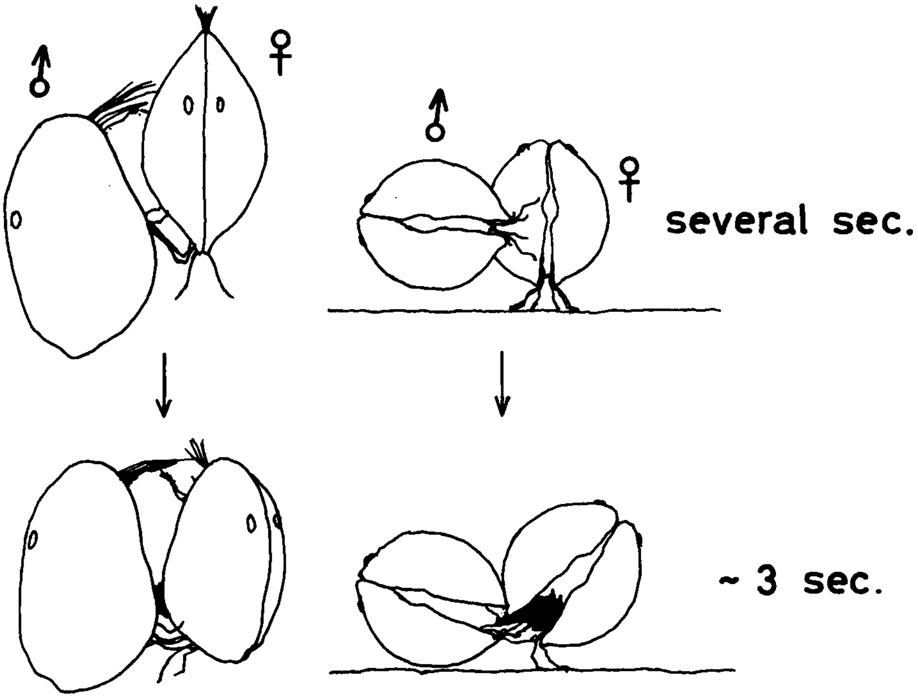


TEXT-FIG. 10—Copulation of the phytal species, *Loxoconcha japonica*. Left: view from above. Right: side view.

this position the sexual organs of both sexes are still some distance apart from each other in an oblique position. Thus it is quite reasonable that the penis of this phytal species is large with a long flexible stem which can bend easily (Text-fig. 8). The shortness of the mating time is also advantageous in this habitat.

Other Morphological and Ethological Characters

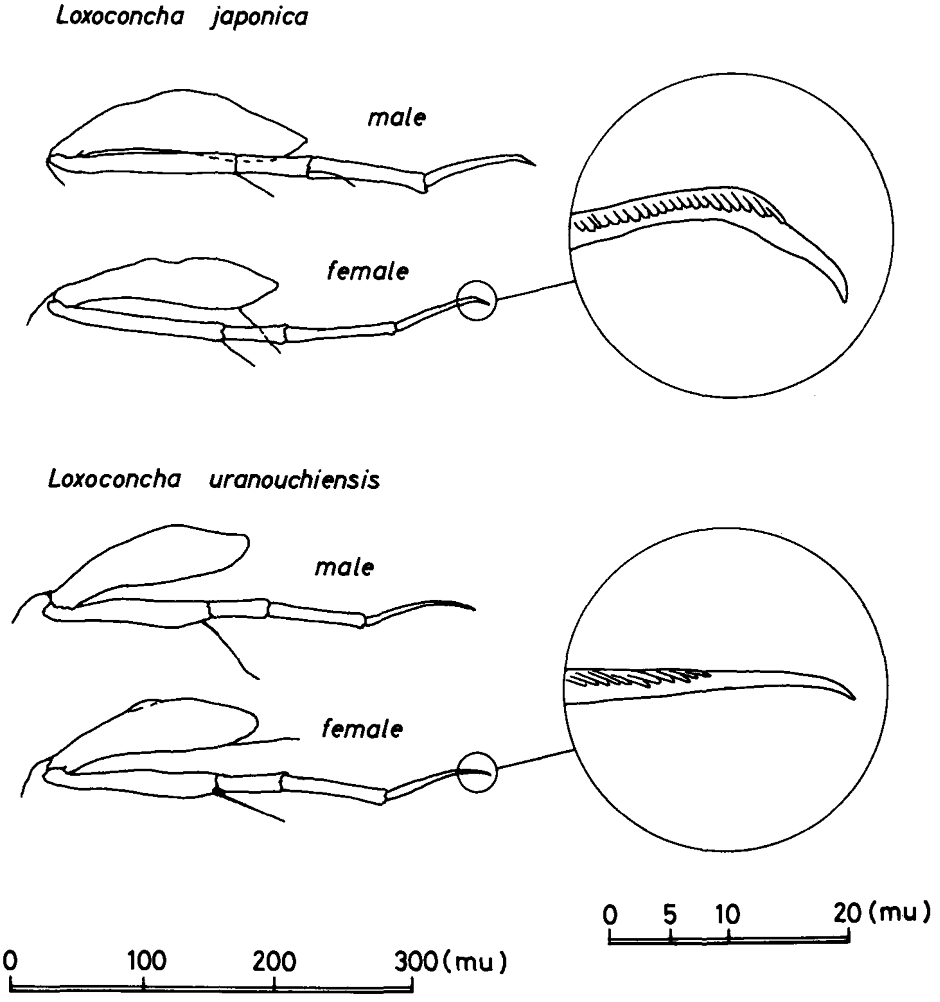
All phytal species generally have rapid and active behaviour. This seems essential for life on the unstable leaves of *Zostera*. Their morphology is suitable to such a habitat.

Paradoxostoma spp. and *Cytherois ezoensis* have thin carapaces to lessen body density. This can be seen when the specimens are dipped in 60% alcohol and sucked up with a syringe. They float up to the surface together with detritus and fine grains under the influence of a weak current. They can easily support their body on the inclined surface of the *Zostera* leaves and walk fast on the leaves. On the contrary, a swift current is needed to pick up *Loxoconcha japonica* and sand grains.

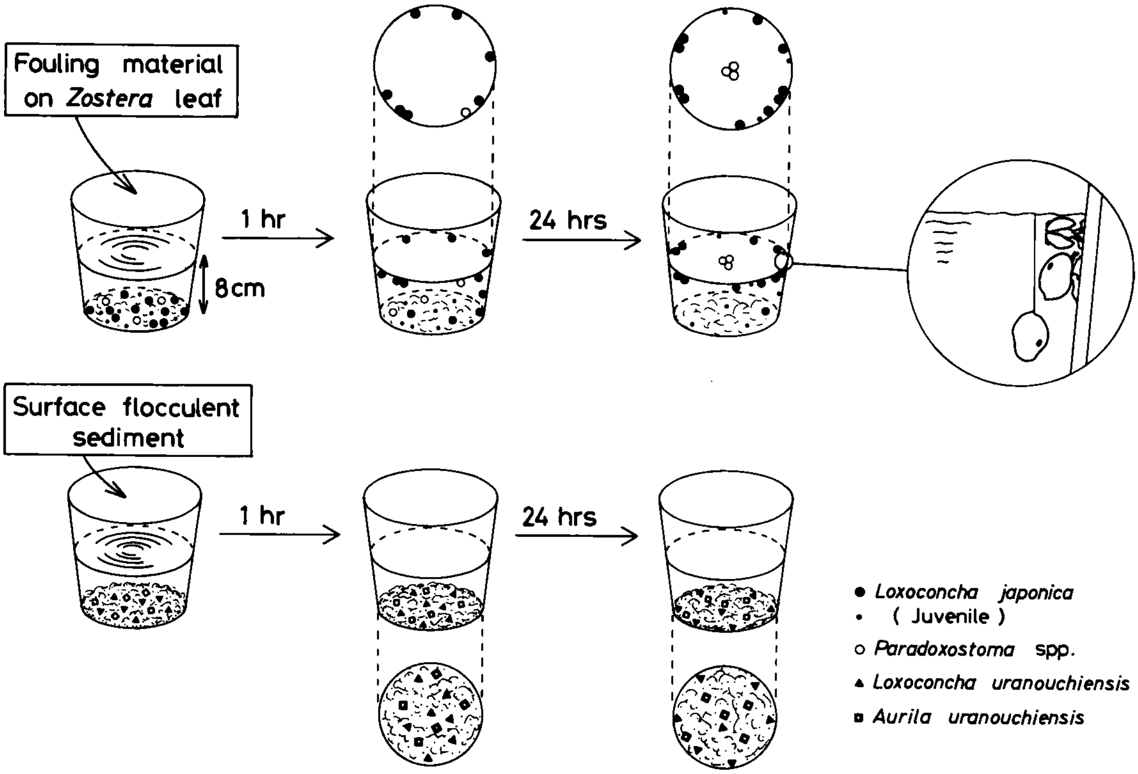
While *Paradoxostoma* and *Cytherois* adapt to the habitat on the *Zostera* leaves with their low body density, *Loxoconcha japonica*, whose carapace is thick and heavy, utilizes unique appendages with long hooks at their tips (Text-fig. 11). This hook structure is useful for supporting their bodies, creeping about and climbing the smoooth and perpendicular surfaces of the leaves. During copulation the male hangs on to the female by means of its antennae and first, second and third thoracic legs, all of which have hooks (Pl. 1, figs. 1-7). The female supports the male and herself with her hooks. Text-fig. 12 shows a difference in the behaviour of phytal and bottom species in a plastic bucket just after sampling. The adults of the phytal species *Loxoconcha japonica* never stay still, but creep around quickly and immediately start to climb up the perpendicular side wall. Many of them climb to the water's surface within an hour. After twenty-four hours, most of the adults and some of the juveniles climbed the side of the bucket up to the surface and stayed there or crept just below the water's surface. Some adults put out threads like a spider and hung down in the water. *Paradoxostoma* spp. are weak and easily die when they float on the surface.

No sand bottom species climbs the side of the bucket. After twenty-four hours, adults of *Loxoconcha uranouchiensis* tended to gather along the edge of the bottom, but *Aurila uranouchiensis* seems to have no tendency to show any particular distribution.

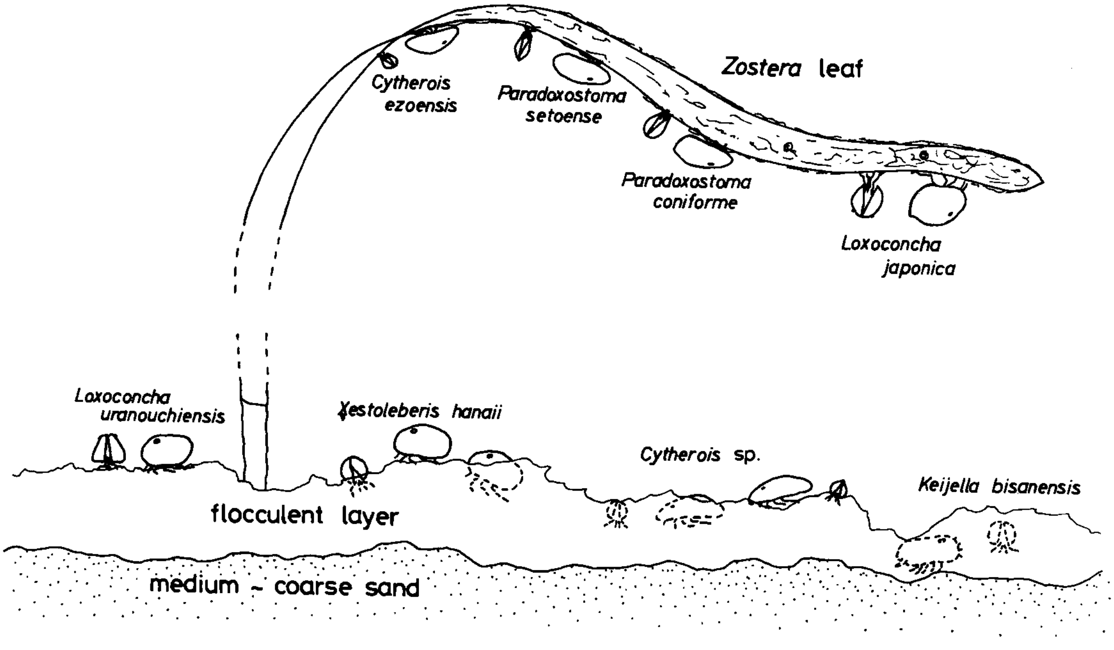
The activities of the sand bottom species were observed in detail under the microscope (Text-fig. 13). The species with elongated carapaces whose cross-sectional shape is circlar, such as *Cytherois* sp. and *Keijella bisanensis*, often crawl into the flocculent layer on the surface of the sand and move around in it. The streamlined shape of their carapace may be convenient for this mode of behaviour. Conversely, the species with triangular cross-sections, such as *Loxoconcha uranouchiensis*, tend to crawl on the surface of the flocuclent layer. Their broad and flat ventral plane seems to give them stability on the surface of the soupy flocculent layer.



Text-fig. 11—Morphology of appendages (third thoracic leg) of the phytal and the sand bottom species of *Loxoconcha*.



TEXT-FIG. 12—Behaviour of the phytal and the sand bottom species in the bucket.



TEXT-FIG. 13—Microscopic distributions of the sand bottom and the phytal species.

SUMMARY AND CONCLUSION

The study of Ostracoda in *Zostera* beds has revealed that congeneric but different species are living in two distinct microhabitats in the beds. Comparison between these congeneric species is advantageous for analysing adaptive morphology and behaviour. It makes it possible to reduce the effects induced by any phylogenetic differences. A causal relationship is recognised among the microhabitats, the mode of life, and the morphology of Ostracoda.

Species living on the surface of sea weeds, especially on the smooth surface of *Zostera* and *Ulva,* can support themselves only by their appendages in order not to slip down to the bottom. They copulate in an upright position clinging to the leaf and the time required is amazingly short. Their carapace shape, circular in lateral and rugby-ball-shaped in posterior view, is convenient for this copulatory position. The sexual organ of the male is large enough and flexible enough to fit this position. Individuals dropped to the bottom creep around to find an upright leaf and soon climb up it. To support themselves firmly and creep swiftly on the smooth surface, some species have thin carapaces which lessen their body density and another species possesses a hook at the tip of the appendages which functions as a clasping organ.

Species living on and in the flocculent layer on the surface of the bottom can support themselves not only by their appendages but also by their carapaces. They copulate for a long time with ventral-to-ventral contact holding on to each other with their appendages and lying down sideways on the bottom. The species crawling on the surface of the soupy flocculent layer have a flat and broad ventral plane to spread the weight and give them stability. The species crawling into the flocculent layer have streamlined carapaces to enable them to move smoothly.

Functional characters in morphology are exhibited in three different parts of the carapace and soft body. They are the shape of carapace, especially that of the ventral area, the length of the stem of the male sex organ, and the structure of the tips of the appendages. The morphology of these parts is dominantly adaptive, and differs between the congeneric species of *Loxoconcha.* The lateral view of the ostracod carapace has been used mainly for ostracod taxonomy and much less attention has been paid to the posterior view. The posterior view, however, clearly illustrates the shape of the ventral area, which may indicate the mode of behaviour and the habitat characteristics of the species. Differences in morphology of the appendages and sexual organs, which have been used largely for taxonomy, also contain characters not only determined by phylogeny but also resulting from adaptation to different habitats.

These conclusions on functional morphology were mainly drawn from observations on the mode of copulation. Males of Ostracoda seem to devote most of their time to looking for copulatory mates and are coupling all the time. Mode of copulation is proved to be related to the shapes of carapace and sexual organ as already shown by McGregor and Kesling (1969) for *Candona* and some other freshwater species. It is known that Ostracoda generally possess huge sexual organs which form a large proportion of the volume of their soft parts. The copulation of Ostracoda has an important role in their ethology and morphology, and the study of ostracod breeding is thought to be essential to the understanding of the Ostracoda themselves.

ACKNOWLEDGEMENTS

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DISCUSSION

Keyser: Did you find that larvae and adults live on different substrata, for instance, on *Zostera* and on the sandy bottom underneath?

Kamiya: No, I did not. The larvae and adults of phytal species were found living only on the leaves of *Zostera* and those of bottom dwelling species solely on the sand bottom.

Morphological Variations of *Cytheromorpha acupunctata* (Brady) in Continuous Populations at Hamana-ko Bay, Japan

NORIYUKI IKEYA AND HITOSHI UEDA
Shizuoka University, Japan

ABSTRACT

Continuous monthly populations of *Cytheromorpha acupunctata* (Brady, 1880) at a fixed station in Hamana-ko Bay, Pacific coast of central Japan, were examined to understand the morphological features of this species. From their population structures, reproduction is considered to take place throughout the year. Precocious sexual dimorphism is observed clearly in the A-1 stage and possibly in A-2, as suggested by biometrical analysis. The extent of reticulation on the carapace is found on a wide and continuous scale in different forms. Differences in size are also observed, in association with differences in ornamentation: well-developed reticulations tend to occur in small carapaces, less-ornamented carapaces are apt to be large. The morphological changes occur seasonally, *i.e.*, samples collected in summer contain more individuals with well-developed reticulation and a small carapace, whereas the reverse can be noticed in specimens collected in winter. Variation is presumably influenced by environmental factors, such as water temperature, along with genetic factors.

INTRODUCTION

Some morphological variations exist in any biological species, and the ostracods are no exception in this respect. It has remained a question for a long time, however, whether the morphological variations in ostracods are attributable to genetic causes or to environmental factors. We are now trying to see how far we can clarify these variations and their causes.

A population is the smallest unit of groups of individuals of any biological species and thus it is usually taken as the material for the study of morphological variations. However, it would certainly be hasty to assume that only genetic variations exist within the same population, and only environment-related variations are to be found between different populations. It is to be expected that there are morphological variations within the same population that are caused by seasonal changes in the environment and other things. It is also possible that between different populations the differences in the gene frequencies, as well as those in the environmental factors, exert a strong influence on morphological variations. In this research, we investigated the morphological variations in the ostracod species *Cytheromorpha acupunctata* (Brady) and their possible causes by periodical examination of continuous populations of this species over a year.

Cytheromorpha acupunctata was first described by Brady (1880) as *Cythere acupunctata* from a muddy bottom in the Inland Sea of Japan which lay on the route of the Challenger Voyage. He made such statements as "Surface of the shell thickly covered with small, impressed, circular puncta", as well as drawing fine punctation all over the surface of the carapace in his figures. Hanai (1961) noticed that the hinge morphology of this species is gongylodont, and transferred it to the genus *Cytheromorpha.* Later, Ishizaki (1968) reported *C. acupunctata* in his study of the Recent ostracod associations in Uranouchi Bay, Shikoku, Japan, and also proposed *C. japonica* as a new taxon. His description and figures suggest that the name *C. acupunctata* is applied to individuals with developed reticulation, and *C. japonica* to those that have only punctation. *C. japonica,* as referred to by Ishizaki, is very similar in morphology to *C. acupunctata* as described by Brady. Hanai *et al.* (1977) therefore concluded that *C. japonica* was a synonym of *C. acupunctata,* and *C. acupunctata* as described by Ishizaki (1968) is the same species as *C. acupunctata* as described by Brady (1880), although there is a considerable difference between these two forms. They also pointed out that "two forms differing in the coarseness of surface ornamentation" are found in the same sample.

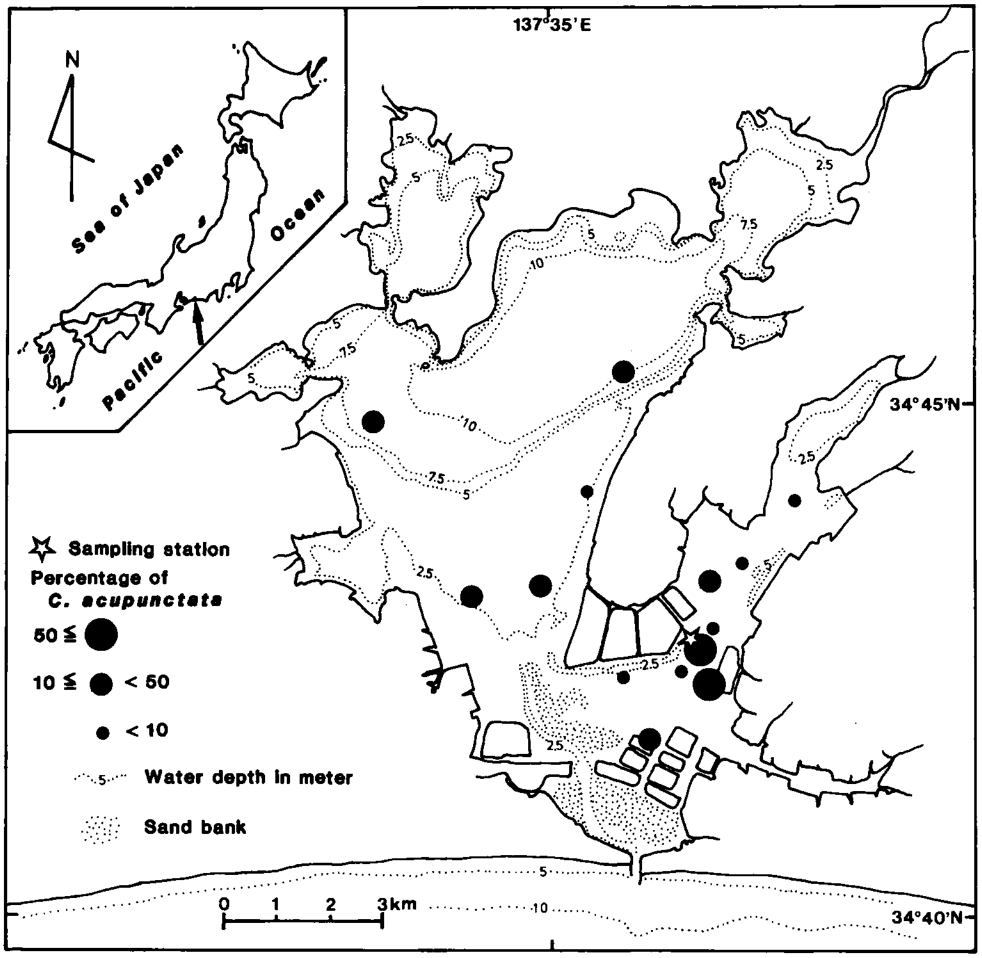
Okubo (1978) dissected specimens of this species from the Inland Sea of Japan, and described their soft parts. He also noticed that the outline of the carapace differs widely between males and females, and that there are two distinct morphological types in the males which differ in surface ornamentation. Occurrences of this species were also reported by several authors, from a number of other localities in Recent inner bays, and from inner bay sediments formed in the Pleistocene and later, in various parts of Japan. Ikeya and Hanai (1982) concluded, from their research on the ostracod assemblages in Hamana-ko Bay on the Pacific coast of central Japan, that this species is among those that are characteristic of silty bottom sediments of the inner bay biofacies.

Regarding intraspecific morphological variations in the genus *Cytheromorpha,* some differences have been observed in surface ornamentation between specimens of *C. paracasteana* (Swain) from different localities. In this species Sandberg (1964) reported that "from low salinities—[it] is thin shelled and weakly ornamented with faint to moderate reticulations. The same species from nearly marine salinities has a distinctly thicker shell and strong, high-walled reticulations." In *C. acupunctata,* however, both these morphological variants are often found together in the same sample, and thus these variants are not considered allopatric ones. Nor is this diversity an example of sexual dimorphism, generally conspicuous in the carapace of the *Cytheromorpha* species, as is shown by the fact that the different morphological variations are found among the males for this species.

In order to investigate the morphological variations and their possible causes in *C. acupunctata,* a fixed station in Hamana-ko Bay was chosen as a sampling locality. As this is not a very large bay and its mouth is rather narrow, and because there is also no other bay in the neighbourhood, it is unlikely that there will be any drastic change in the gene frequencies of the population at the sampling station caused by immigration from other populations. This makes it particularly suitable for examining the influence of changes in the environmental factors.

MATERIALS

The senior author has previously investigated the sediments and sedimentary environments of Hamana-ko Bay (Ikeya and Handa, 1972), as well as the ecology of the ostracod faunas (Ikeya and Hanai, 1982). The latter work has revealed that both the population density of *Cytheromorpha acupunctata* and the percentage of this species in the living ostracod assemblage is higher at 'Station 48' than at any other station. For this study, we selected a sampling station about 200 m northwest of this 'Station 48' (137°36′42″E, 34°42′40″N) (Text-fig. 1). Here the average water depth is around 2.5 m and the bottom sediment consists of moderately well-sorted sandy silt.



TEXT-FIG. 1—Location of the sampling station and the percentages of *Cytheromorpha acupunctata* in the living ostracod assemblages.

Between March 1977 and February 1978, twelve samples were collected at this station at intervals of about a month. Below, sampling methods and preparation are only briefly described. Details are given in Ikeya, Ohishi and Ueda (1986) which also records the seasonal changes in the ostracod faunas. Each monthly sample consisted of a quantitative sample collected by means of a Phleger-type core sample (3.6 cmϕ), and a non-quantitative sample by a modified Ockelmann-type bottom net sampler. The core sampler was dropped three times for each monthly sampling, and the top 1 cm layer of each core sample was taken for examination. In this research the samples taken from the three cores were combined and treated as a single sample with a surface area of 30.5 cm^2 and a volume of 30 cm^3. All the samples were fixed with 10% neutralized formalin, and washed with water through a 200-mesh sieve (opening 74μm). A part of each net sample was then preserved in 70% alcohol and the rest of the sample was dyed with Rose Bengal and then dried. Ostracods were picked from all the Phleger core samples, but not enough individuals of *C. acupunctata* were obtained for statistical analysis. Additional ostracods were therefore picked from the dried net sample to bring the total number of specimens of this species up to at least 100 each month. The dates of collection of the samples, the numbers of *C. acupunctata* individuals, and other relevant information are listed in Table 1.

Table 1—List of Sampling Dates and Numbers of *Cytheromorpha acupunctata* Specimens Collected by Means of Two Different Samples (Phleger-Type Core Sampler and Modified Ockelmann-Type Bottom Net Sampler).

Month	Sampling date	Number of specimens				
		Phleger core		Net		Total
		Living	Dead	Living	Dead	
Mar.	26, 1977	17	21	35	26	99
Apr.	27	32	37	36	31	136
May	31	14	2	60	25	101
Jun.	28	30	13	65	51	159
Jul.	21	12	25	23	43	103
Aug.	26	8	15	52	67	142
Sep.	26	11	21	30	40	102
Oct.	27	11	23	77	51	162
Nov.	2	13	30	58	28	129
Dec.	5, 1978	12	49	4	32	97
Jan.	3	11	25	61	113	210
Feb.	7	11	16	45	58	130

Study of the seasonal changes in the ostracod fauna using these Phleger core samples (Ikeya, Ohishi and Ueda, 1986) has revealed that the samples collected over the year contained 12 species with living specimens and 31 species in total. Among the living species, the four species of *Spinileberis quadriaculeata* (Brady, 1880), *Cytheromorpha acupunctata* (Brady, 1880), *Hemicytherura tricarinata* (Hanai, 1957), and *Semicytherura* sp. were dominant in this order. In any month the sum of these species made up more than 95% of the total living population. Except in May and June, the composition of the living population was relatively stable through the year. The June sample was markedly different from those of other months. This may in some way be related to the fact that the June sample was composed of silty sand, whilst in all other months the samples consisted of sandy silt. *C. acupunctata,* which was the second most common species in all other months, was the dominant species in June. These facts suggest that the June sample was collected from a subtly different environment, which is turn implies that either the sampling station of that month was slightly off the fixed station or a large amount of sandy sediment was brought in from neighbouring areas.

LIFE CYCLE

In order to understand the degree of intraspecific morphological variation within an ostracod population, it is essential to have some preliminary knowledge of the life cycle of that species, *i.e.*:

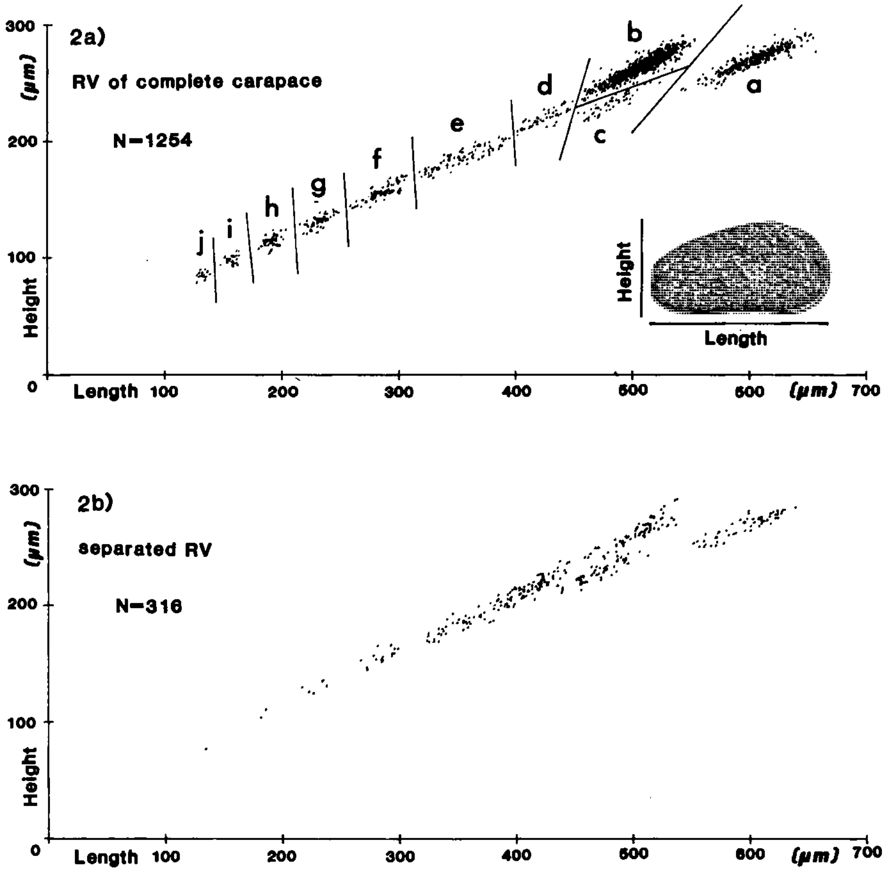
1) Clarification of the mode of growth is required because the morphology changes with moulting, and differs between the two sexes.

2) Knowledge of population dynamics is needed because the seasons of spawning and growth, providing different environmental elements, result in different morphologies.

Study methods: All the specimens found in the Phleger core and bottom net samples collected every month at the fixed station were measured. A preliminary investigation revealed that the right valve is slightly larger than the left, although the difference is almost negligible. It was decided to measure only the right valves. The length and height of each specimen was measured three times using a digital micrometer, and the mean values were calculated (Text-fig. 2). On the basis of these values, the moult stage of each specimen was determined and the relative growth formula was calculated. All complete carapaces were examined, and those specimens found to contain nearly complete appendages in their carapaces when observed in transmitted light were considered to have been alive when they were collected.

Mode of growth: The 1254 complete carapaces and 316 separated right valves measured were plotted as scatter diagrams (Text-fig. 2a, b). In the diagram for complete carapaces, the plotted points form ten separate groups (a–j) as shown in the figure, whereas in the diagram for separated right valves, the separation of groups b and c, and that of d and e, as seen in the diagram for complete carapaces, was not clear. This implies that some of the separated right valve specimens may have been distorted. In order to secure precision, therefore, we dealt only with specimens with complete carapaces.

Each group (a–j) of points represents a particular moult stage and a particular sex. Groups a and b all correspond to adult stages, whereas groups c to j represent juvenile forms. This was confirmed by observation of the duplicature, which is fully developed in groups a and b. Dissection of alcohol-preserved specimens of groups a, b, c, and d revealed that groups a and b are adult males and



Text-fig. 2—Length/Height diagrams for right valves of *Cytheromorpha acupunctata*. 2a: Measurements based on complete carapaces. Each moult stage and sex is shown as one of ten separate groups (a–j). 2b: Measurements based on separated valves. Distinction between two consecutive moulting stages is unclear at later moult stages.

Table 2—Ten Groups Representing Different Moult Stages and/or Sexes and Their Statistical Data (Means Standard Deviations and Pearson's Coefficients of Variation).

				Length			Height		
Group	N	stage	sex	mean	s.d.	c.v.	mean	s.d.	c.v.
a	282	Adult	male	604.0	21.8	3.6	271.1	9.8	3.6
b	588	Adult	female	506.8	20.3	4.0	264.6	10.9	4.1
c	44	A–1	male	480.4	15.7	3.3	232.3	8.5	3.6
d	46	A–1	female	423.2	12.7	3.0	220.0	6.9	3.1
e	87	A–2	mixture	353.0	20.7	5.9	186.5	9.1	4.9
f	69	A–3	—	285.6	12.0	4.2	157.1	7.1	4.5
g	52	A–4	—	231.4	7.3	3.2	131.7	5.1	3.9
h	46	A–5	—	191.5	5.0	2.6	114.7	4.5	3.9
i	24	A–6	—	157.2	4.0	2.5	98.8	3.6	3.6
j	16	A–7	—	132.2	3.3	2.5	85.6	2.9	3.4

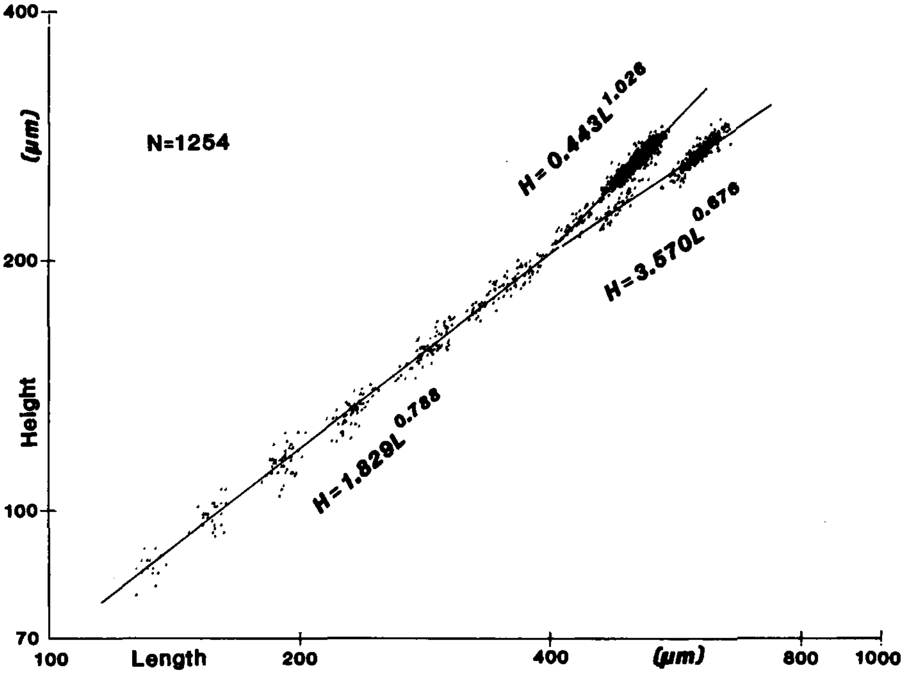
females, respectively, since the male copulatory organ and eggs were found in the corresponding specimens. Immature male copulatory organs were found in the specimens of group c, which is thus considered to represent males of the A-1 stage (Pl. 1, fig. l; Pl. 2, figs. l, m). Group d is considered to represent females of the A-1 stage (Pl. 1, fig. m; Pl. 2, figs. n, o), taking into account the carapace size of this group and the differences between adult males and females. Group e represents the A-2 stage, but spreads rather widely, suggesting that it may reflect the inclusion of both sexes at a time when sexual dimorphism is just beginning. In *C. acupunctata,* the eight moult stages from the A-7 to the adult stage were recognised relatively clearly by length/height measurements. Although the earliest moult stage recognised by observation of existing specimens was the A-7, the size of the probably mature eggs (approximately 75 μm, confirmed by dissection) indicates the possible existence of the A-8 stage.

In order to formulate the average mode of growth of *C. acupunctata* throughout the year, an allometry formula was applied on the length (L) and height (H) of the carapace.

$H = bL^a$; where a = relative growth coefficient, and b = relative growth constant.

The values of a and b were calculated by regression using the reduced major axis method, because L and H are independent of each other (Imbrie, 1956). Since the mode of growth differs between males and females in the advanced moult stages, growth formulas were determined separately for 1) males of A-1 and adult stages, 2) females of A-1 and adult stages, (in both of which obvious sexual dimorphism could be observed) and 3) individuals belonging to the A-2 stage or younger (Text-fig. 3). The mode of growth up to the A-2 stage is represented by groups of points corresponding to each moult stage aligned at regular intervals on the graph, suggesting that the growth rates of L and H are almost constant at every moulting (L: approximately ×1.22, H: approximately ×1.17). This regularity agrees with Dyar's law, which is often applicable to the mode of growth in arthropods.

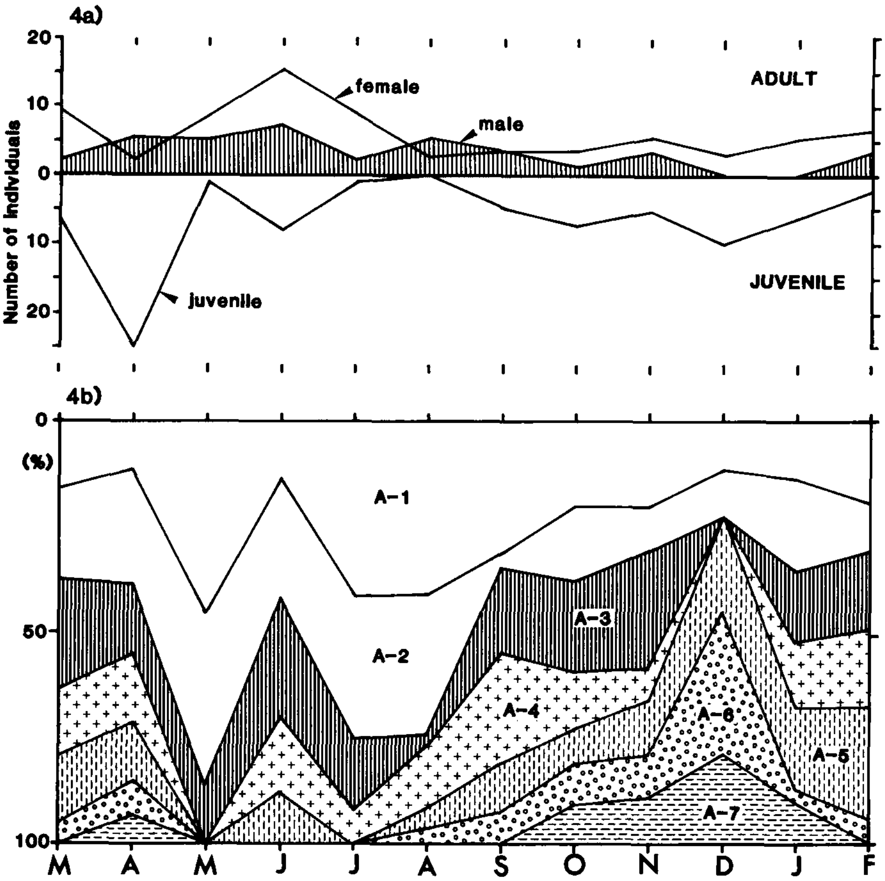
Population dynamics: Of the 1254 complete carapaces, 728 were judged to have been alive when they were collected. Among these, the living specimens in the Phleger quantitative samples totalled 182 individuals. Seasonal changes in the number of individuals of each moult stage in the quantitative samples were studied (Text-fig. 4a). Since living juvenile individuals were not abundant in the Phleger samples, juveniles of all stages were treated collectively. Whereas the numbers of adult individuals, both male and female, are relatively stable throughout the year, the number of juveniles shows marked changes with the season, increasing in April and decreasing in summer.



TEXT-FIG. 3—Length/Height diagram on logarithmic coordinates and allometry formulas for males, females and sexually undifferentiated juveniles.

Adult males were not observed alive in December and January. The relative stability of the adult population over the seasons in comparison with that of the juveniles probably indicates that the life span of the adult is considerably longer than the juvenile period. In the samples collected in June, both adults and juveniles were abundant, but, as stated in 'Materials', these samples may have been collected slightly off the fixed station, and the population is likely to have been smaller at the right station.

The percentage of individuals of each juvenile stage was examined every month (Text-fig. 4b). Since the juveniles in the Phleger core samples were not abundant, those from the bottom net samples were added. Individuals of the A-5 stage and older occur throughout the year, and no significant tendency was observed such as a particular moult stage being concentrated in any one month. Living specimens of the A-6 stage were not observed from May through July, and those of the A-7 stage were not found from February to March, or from May through September. However, a female adult was found carrying probably mature eggs, which, together with the numbers of individuals of the A-5 stage and older confirmed every month, implies that individuals of the A-7 stage also exist throughout the year, as well as those of the A-6 stage. It is inferred, therefore, that *C. acupunctata* spawns all year round, although the number of eggs produced may vary with the season and is less in summer. The length of time needed to grow from hatching to maturity and the life span after maturity are not yet exactly known. However, we estimate that the growth period, although we think it fluctuates with the seasons, takes around three months on the basis of the time lag between juvenile and adult peaks in Text-fig. 4a.



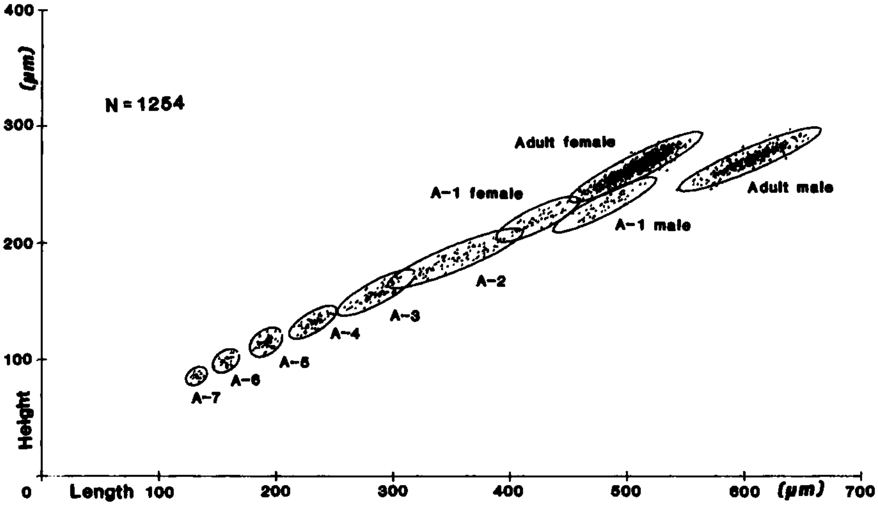
TEXT-FIG. 4—Seasonal distribution of living *Cytheromorpha acupunctata* individuals. 4a: Change in number of individuals in the Phleger quantitative samples. 4b: Change in the percentage of each juvenile stage in the total samples including net samples.

MORPHOLOGICAL VARIATION

The carapace of *C. acupunctata* varies widely from one individual to another in size and surface ornamentation. Particularly, it has already been pointed out that there are two morphotype patterns in their carapace sculpture.

Variation in size: Variation in carapace size was analysed using the measurements of all the samples from all months mentioned in the preceding chapter. The distributions of the two parameters L and H are nearly normal in nine of the ten groups of points in the graph described above (Text-fig. 2a) that were formed on the basis of the moult stage and the sex, the only exception being the group representing the A-2 stage. The rejection ellipse method was applied to each of these groups (Text-fig. 5). It will be seen that only the ellipse corresponding to the A-2 stage is rather stretched out and does not represent well the actual distribution of the points. This suggests that both males and females coexist in the group representing the A-2 stage, and thus the morphological characters of both sexes are reflected here.

Variation in surface ornamentation: Individuals with less developed reticulation have punc-



Text-fig. 5—Length/Height diagram with series of rejection ellipses of ten groups computed from five values (means and standard deviations of both Length and Height, and orientation of plotted distribution) with 99% confidence intervals.

tation all over their carapaces. About 500 puncta occur on each valve, and each punctum is roughly the same size (about 70 μm in diameter). Reticulation is formed by the development of muri surrounding several (two to five) puncta, and somewhat obscure puncta are often seen inside each fossa. The reticulation in this species, therefore, is an example of second-order reticulation (Sylvester-Bradley and Benson, 1971). The location, shape and size of each fossa is consistent among individuals of this species, probably because the number of muri included in each fossa is roughly constant (macroreticulation in Liebau, 1977). However, the degree of development of the muri of the corresponding fossa differs widely from one individual to another; a continuous variation was observed between weak and low muri that are not much different from puncta, and those that form high and steep projections surrounding faint puncta. It was also observed that the degree of development of the muri is not consistent all over the carapace; a mixture of puncta and fossae was found in a number of individuals. The area in which reticulation develops also varies from one individual to another. Generally, however, reticulation develops most often in the posterior third of the shell. These observations revealed that the surface ornamentation of the carapace in this species is not a character with two distinct forms but rather has a wide and continuous variation.

For convenience, we recognised three morphotypes based on the relative development of reticulation seen under the microscope. Those with reticulation covering almost the entire carapace (80% or more) were classified as Coarse Type, those with only punctation as Fine Type, and those between these two extremes as Middle Type. All 1570 specimens were placed in one of these three categories. It is to be remembered that these are only for convenience and do not represent distinct polymorphic features, because the development of reticulation is in fact a continuous character.

Observation of broken sections of adult male carapaces by SEM revealed a clear positive relationship between the degree of development of reticulation and the thickness of the carapace. In the posteromedian area, the carapace thickness of Fine Type specimens was about 2 μm on puncta and 4 to 5 μm around them, whereas that of Coarse Type specimens was 4 to 5 μm on puncta and up to 15 μm in muri parts. Moreover, the carapace thickness of each specimen is almost constant all over, except in the marginal zone. Even in Middle Type specimens, where reticulation and punctation exist together, there was no fluctuation in thickness associated with the degree of external surface ornamentation in any part of the carapace. In summary, the more reticulate the carapace, the thicker it is; a highly reticulated carapace becomes almost twice as thick as a carapace with only punctation.

Development of the surface reticulation: In order to know how the degree of carapace surface ornamentation changes with growth and how it is related to carapace size, rejection ellipses for all individuals of each ornamentation type, Coarse, Middle, and Fine, and the measurements of specimens of the corresponding type were drawn on the same graph (Text-figs. 6a, b, c). Fine Type specimens occur in all moult stages, whereas more coarsely reticulated specimens of the Middle and Coarse Types are found only in the advanced moult stages. Fine Type specimens, on the contrary, decrease significantly in the adult stage. This indicates that no individual of *C. acupunctata* is reticulated on hatching, and that individuals with developed reticulation increase with growth or moulting. The degree of surface ornamentation, therefore, may be considered to be a morphological variation associated with growth. Regarding sexual difference, a wide range of variation is observed in adult males from individuals with no reticulation at all to those that have reticulation all over the carapace. In females, on the other hand, individuals with only punctation are rarely seen, (*i.e.* ornamentation is generally coarser than in the male, as stated in Sandberg, 1964), and the range of variation is not so wide.

Some difference in surface ornamentation is seen to be associated with adult carapace size. The coarser the surface ornamentation, the smaller both L and H; the weaker the reticulation, the larger the size. This tendency is observed in both sexes in the adults, but is not very clear in juveniles. The measurements L and H in adults of both sexes were analysed statistically with respect to each type of surface ornamentation (Table 3).

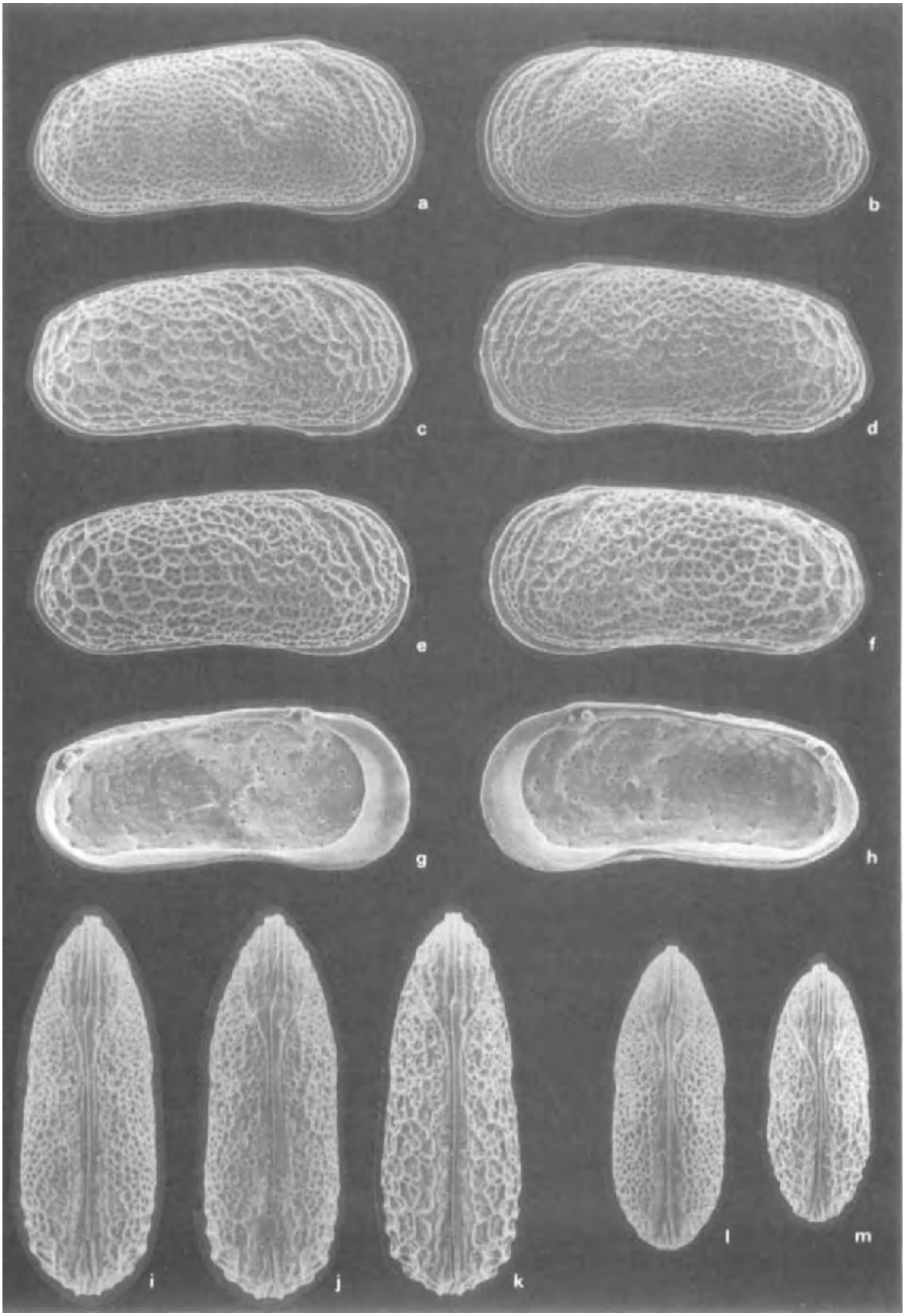
Seasonal change in morphological variations: The preceding sections show that there are two kinds of morphological variations in the carapace of *C. acupunctata,* namely carapace size, and degree of development of surface reticulation. It was also found that these two are likely to be related to each other. On the basis of these results, we then examined how these variations change with the season, using living specimens from the samples collected every month. The ratio of Coarse, Middle and Fine Types was calculated with respect to the adult individuals found in all the sam-

TABLE 3—STATISTICAL DATA (MEANS AND STANDARD DEVIATIONS) OF THREE MORPHOTYPES OF ADULT *Cytheromorpha acupunctata.*

	Ornam.			Length		Height	
Sex	Type	N	%	mean	s.d.	mean	s.d.
	Fine	91	32.3	614.9	17.9	276.0	7.9
Male	Middle	125	44.3	605.0	20.7	271.9	9.0
	Coarse	66	23.4	586.9	17.9	263.0	8.7
	Fine	4	0.7	524.3	5.1	271.0	5.5
Female	Middle	406	69.0	511.0	19.5	266.9	10.6
	Coarse	178	30.3	496.6	18.4	259.2	9.7

PLATE 1—*Cytheromorpha acupunctata* (Brady, 1880) (all figures ×100).

Figs. a, b. External lateral view of F-type male, right and left valve, IGSU-O-458.
Figs. c, d. External lateral view of M-type male, right and left valve, c: IGSU-O-460, d: IGSU-O-461.
Figs. e, f. External lateral view of C-type male, right and left valve, e: IGSU-O-463, f: IGSU-O-464.
Figs. g, h. Interior lateral view of M-type male, left and right valve, IGSU-O-466.
Fig. i. Dorsal view of F-type male carapace, IGSU-O-459.
Fig. j. Dorsal view of M-type male carapace, IGSU-O-462.
Fig. k. Dorsal view of C-type male carapace, IGSU-O-465.
Figs. l, m. Dorsal view of A-1 carapaces, l: male, IGSU-O-478, m: female IGSU-O-481.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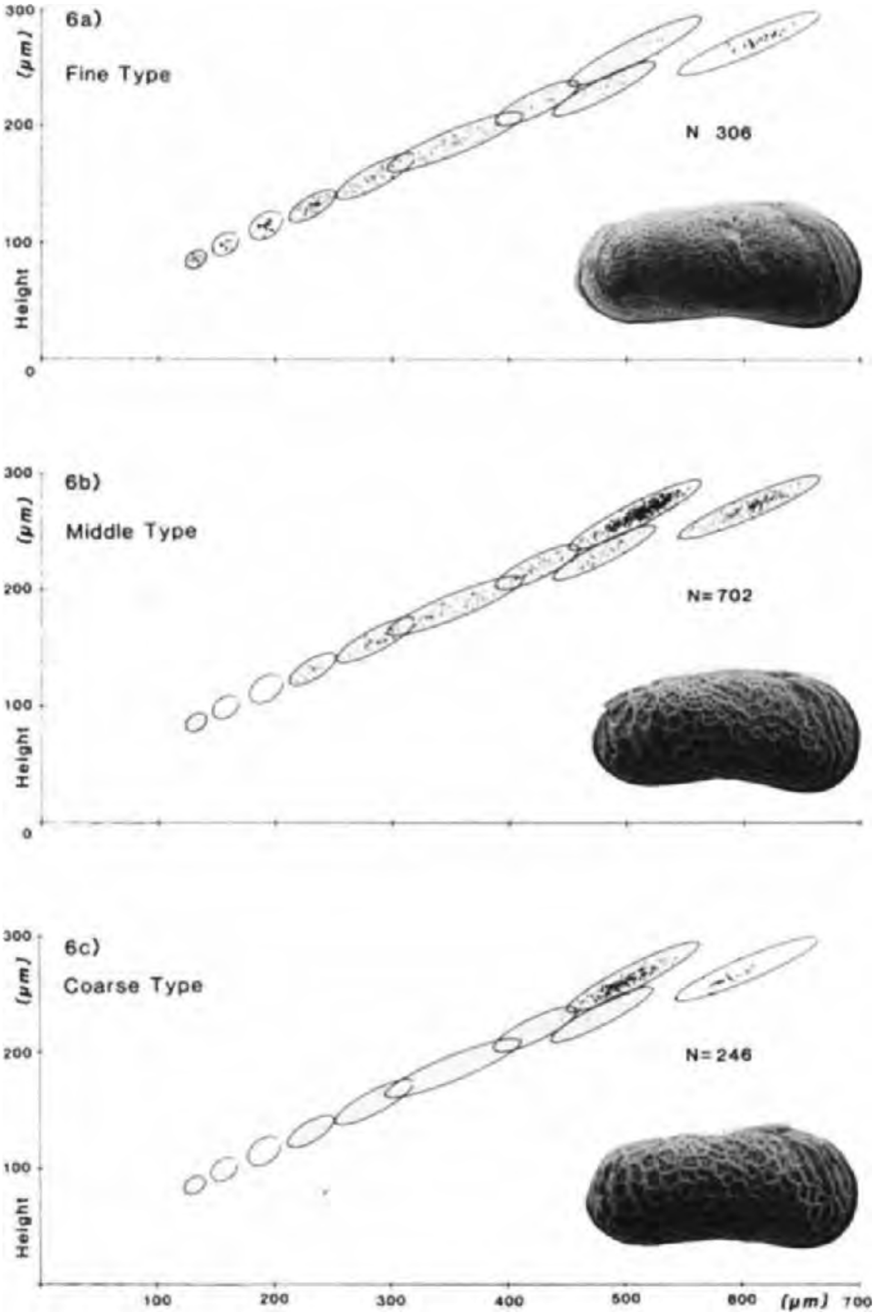
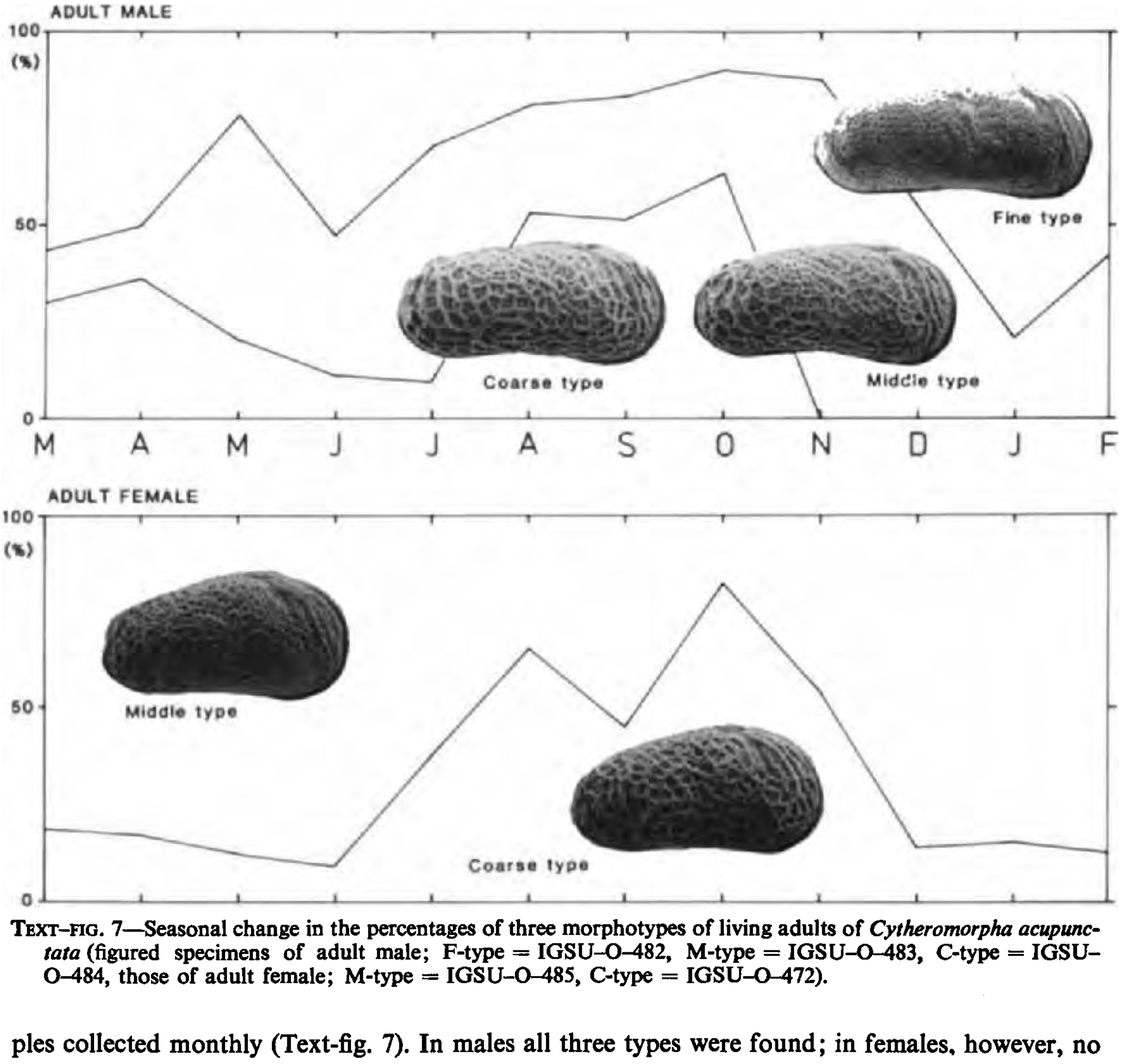


TEXT-FIG. 6—Length/Height diagrams with the same series of rejection ellipses as in Text-fig. 5. 6a: Measurements based on F-type specimens (figured specimen: right valve male, IGSU-O-482). 6b: M-type specimens (figured specimen: right valve male, IGSU-O-483). 6c: C-type specimens (figured specimen: right valve male, IGSU-O-484).

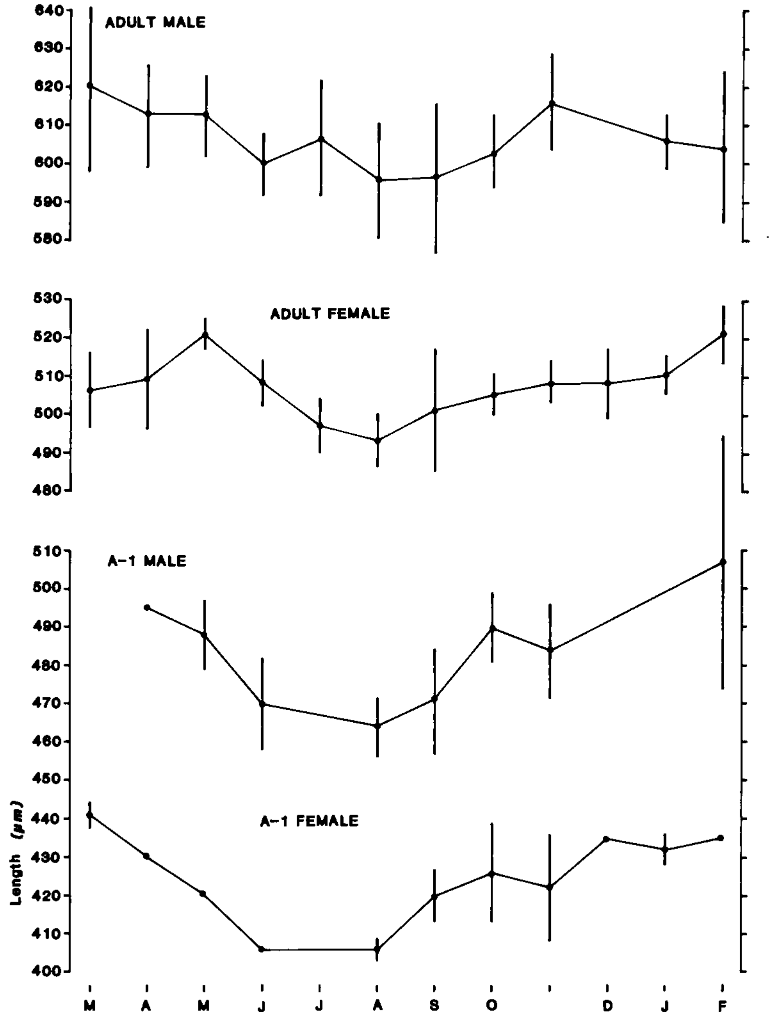


TEXT-FIG. 7—Seasonal change in the percentages of three morphotypes of living adults of *Cytheromorpha acupunctata* (figured specimens of adult male; F-type = IGSU-O-482, M-type = IGSU-O-483, C-type = IGSU-O-484, those of adult female; M-type = IGSU-O-485, C-type = IGSU-O-472).

ples collected monthly (Text-fig. 7). In males all three types were found; in females, however, no living specimen of Fine Type was found, and thus the ratio was figured for only two types. In both sexes the ratio of individuals with developed reticulation (*i.e.* coarser surface ornamentation) becomes higher from summer to autumn and both sexes show analogous tendencies throughout the year. Assuming that the adults survive for some period after the last moulting, the seasonal change in surface ornamentation of the individuals immediately after the last moulting may be even more remarkable.

In order to know how the carapace size changes seasonally, the mean values of the carapace length (L) of the four groups from A-1 to adult were plotted (Text-fig. 8). It was confirmed in all four groups that carapace size tends to become smaller over the summer. The carapace size of juveniles decreases a little earlier than that of adults, which is probably attributable to the intermoult period of each juvenile stage and the life span of the adults.

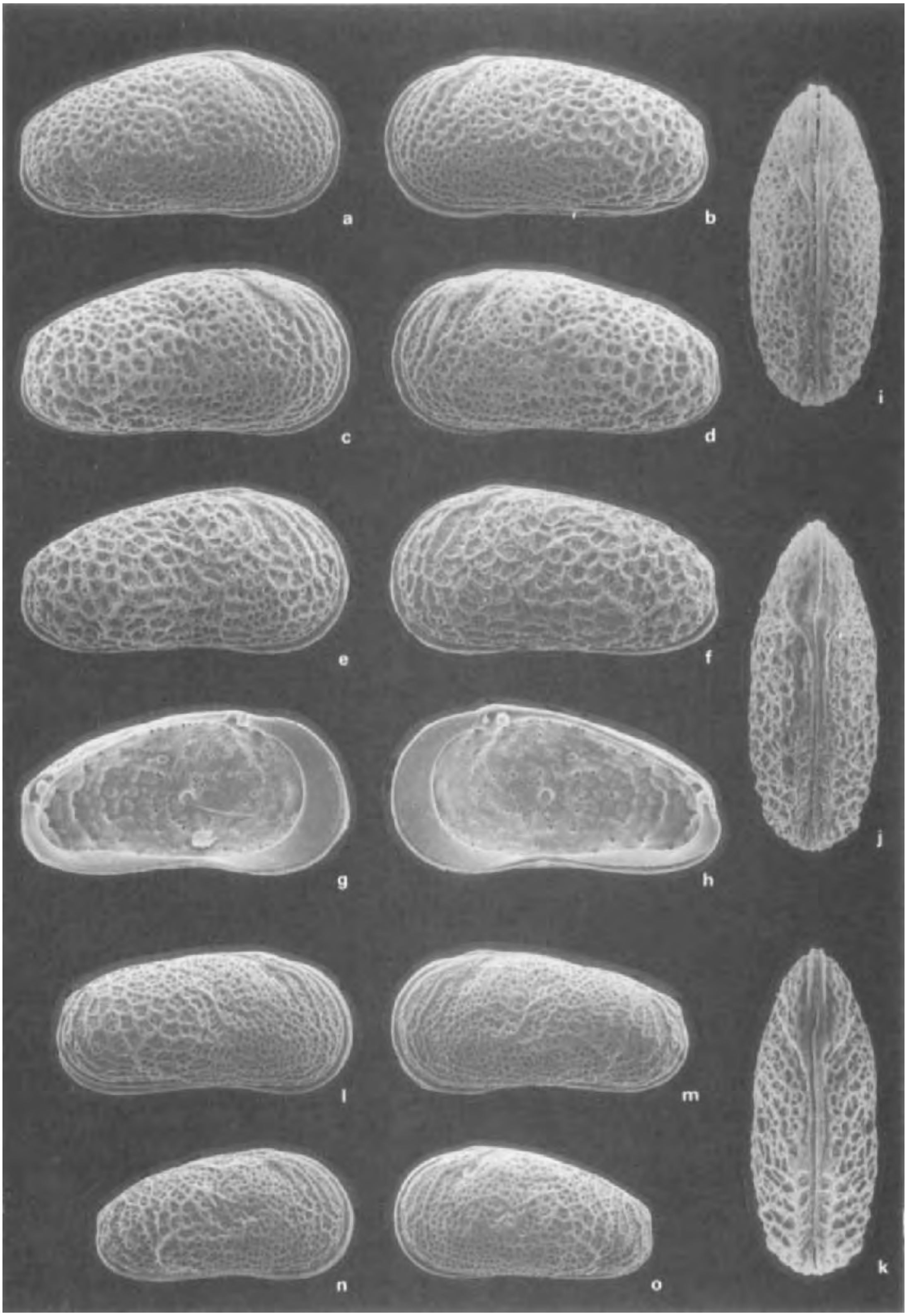
The two kinds of morphological variation, surface ornamentation and carapace size, show analogous tendencies. The number of individuals with coarse surface ornamentation increases from summer to autumn, and the carapace length decreases in summer. However, these two changes do not take place at exactly the same time and the decrease in size tends to occur slightly earlier.



Text-fig. 8—Seasonal change in size (Length) of living individuals of A-1 and adult stages. Vertical bars indicate 95% confidence intervals of mean values.

Plate 2—*Cytheromorpha acupunctata* (Brady, 1880) (all figures ×100).

Figs. a, b. External lateral view of F-type female, right and left valve, a: IGSU-O-467, b: IGSU-O-468.
Figs. c, d. External lateral view of M-type female, right and left valve, IGSU-O-470.
Figs. e, f. External lateral view of C-type female, right and left valve, e: IGSU-O-472, f: IGSU-O-473.
Figs. g, h. Interior lateral view of M-type female, left and right valve, IGSU-O-475.
Fig. i. Dorsal view of F-type female carapace, IGSU-O-469.
Fig. j. Dorsal view of M-type female carapace, IGSU-O-471.
Fig. k. Dorsal view of C-type female carapace, IGSU-O-474.
Figs. l, m. External lateral view of A-1 male, right and left valve, l: IGSU-O-480, m: IGSU-O-476.
Figs. n, o. External lateral view of A-1 female, right and left valve, n; IGSU-O-480, o: IGSU-O-479.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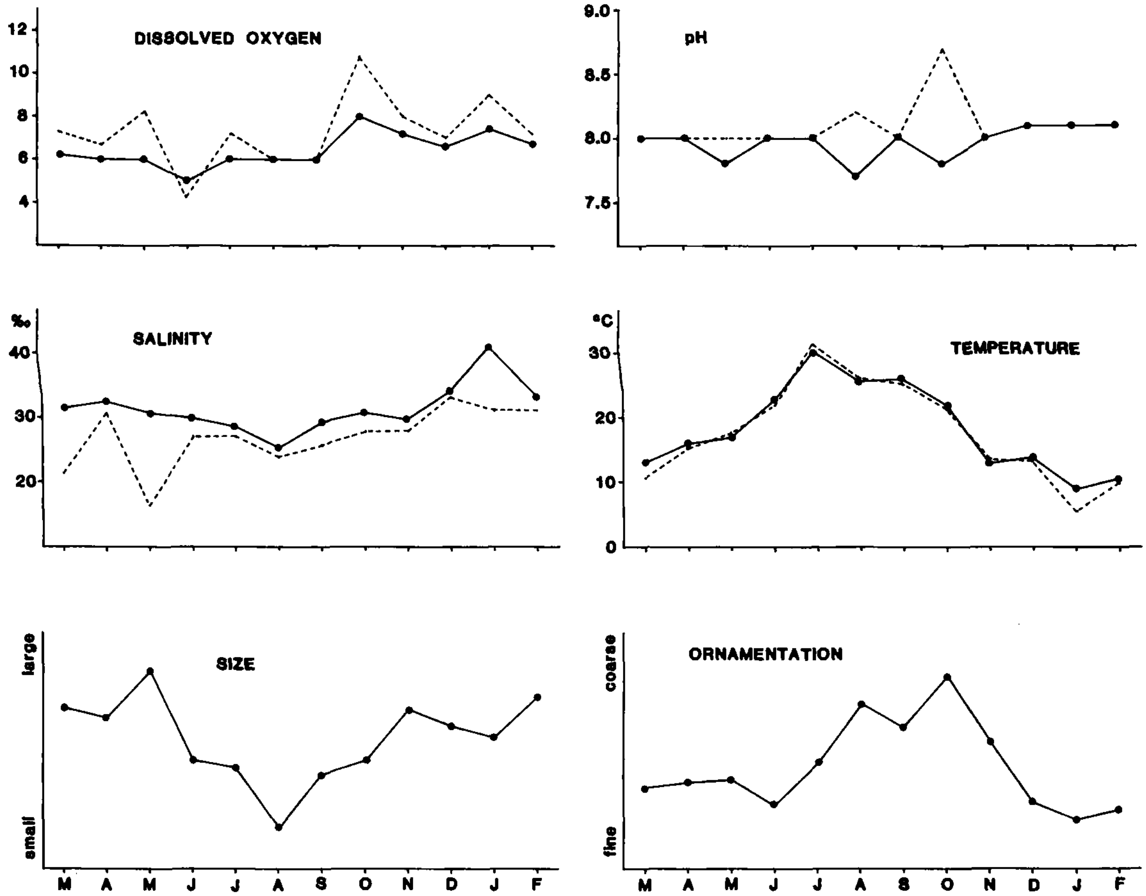

Text-fig. 9—Seasonal change in the hydrographical data at the sampling station and in morphological characters of *Cytheromorpha acupunctata* (average of both living adult males and females). In the graphs of the hydrographical data, solid lines represent bottom water, and broken lines represent surface water.

Discussion

Precocious Sexual Dimorphism

A quarter century ago, the sexual dimorphism in Myodocopid and Podocopid ostracods was believed to become apparent usually only after the last moulting, that is, in the adults, but not in the juveniles (Van Morkhoven, 1962, p. 90). Later, examples of sexual dimorphism were reported in a number of Myodocopid species (*e.g.* Kornicker, 1970), but no such report was made for a long time concerning any Podocopid species. Whatley and Stephens (1977) reviewed the information on sexual dimorphism in juveniles, and also reported that, amont the Bathonian fossils of six

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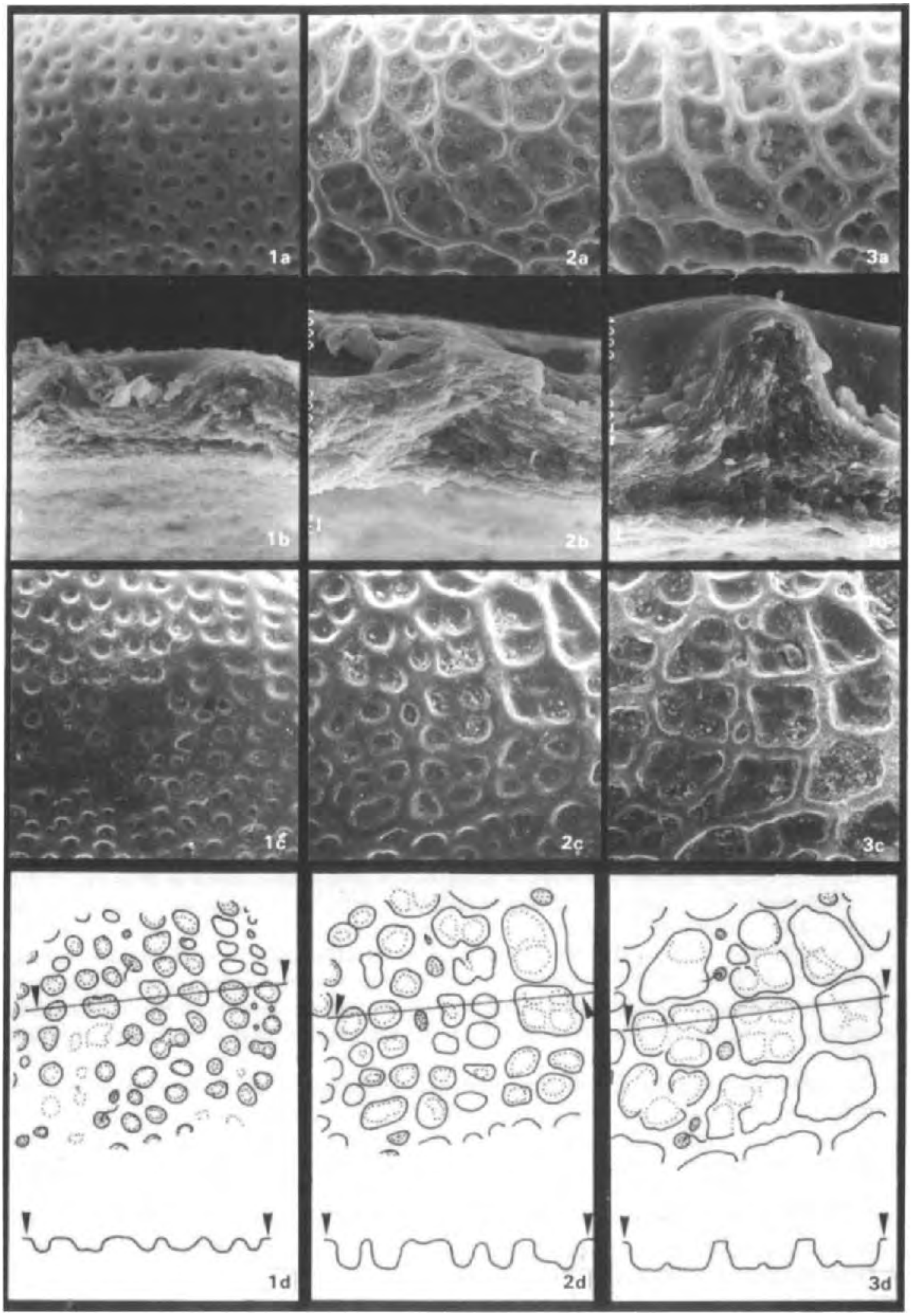
Plate 3—*Cytheromorpha acupunctata* (Brady, 1880).

Figs. 1a, 2a, 3a, Ornamentation on posteromedian surface of right valve male, ×300. 1a: F-type (IGSU-O-482), 2a: M-type (IGSU-O-483), 3a: C-type (IGSU-O-484). Figs. 1b, 2b, 3b. Broken section on posteromedian area of right valve adult male, ×4000. 1b: F-type, 2b: M-type, 3b: C-type. Figs. 1c, 2c, 3c. Ornamentation on posterior surface of left valve male, ×350. 1c: F-type (IGSU-O-81), 2c: M-type (IGSU-O-82), 3c: C-type (IGSU-O-83). Figs. 1d, 2d, 3d. Sketches of surface ornamentation and undulation on Figs. 1c, 2c, and 3c, ×350.


1a
2a
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3d

Podocopid species they studied, sexual dimorphism was recognized as early as in the A-5 stage in the most extreme example. However, they did not observe such a phenomenon in any Recent species. In Recent species, Rohr (1979) demonstrated through a biometrical study that sexual dimorphism in *Cyprideis torosa* (Jones), a brackish water species, becomes evident in the A-3 stage. Van Harten (1983) also reported the appearance of sexual dimorphism in *Cyprideis similis* (Brady) in the A-1 stage. Using fossil specimens, he also showed examples of sexual dimorphism appearing in the A-2 stage in three other species of *Cyprideis* (Van Harten, 1975b, 1980 and 1983).

In the Recent *Cytheromorpha acupunctata* studied here, morphological difference between the two sexes is evident by the A-1 stage. Biometrical data, in addition, suggests that sexual dimorphism is likely to exist in the A-2 stage as well. Clarification of the significance of these facts in the development of the ostracoda seems to be in order.

According to Kesling (1962), the gonad anlage becomes visible in the A-2 stage, or even in the A-3 stage in some species, and the gonads become mature in the A-1 stage. The genitalia anlage becomes evident in the A-1 stage, or occasionally in the A-2 stage, and is completed in the adult stage. Moreover, the other appendages also become complete by the A-2 stage. This means that the A-2 stage overlaps the period in which the development of the reproductive organs of each sex is initiated, and therefore it seems quite reasonable that sexual dimorphism in the carapace becomes observable in this stage. However, it is to be expected that the development of the genitalia of different species starts during different stages, proceeds at different rates, and thus reaches different levels of maturity. It is to be assumed, therefore, that the time when the sexual differences in carapace morphology become distinct may differ from one species to another. In taxa whose morphological features differ greatly between adult males and females, such as the genus *Cytheromorpha,* precocious sexual dimorphism will be easier to recognize.

In addition to *C. acupunctata,* we also observed distinct sexual dimorphism in juveniles of *Hemicytherura tricarinata* Hanai which inhabit similar environments. In this species, the female of the A-1 stage is about the same size as the adult male. If the sex is genetically determined in podocopid species, then precocious sexual dimorphism should be a common phenomenon. It is probably because sexual differences in the carapace morphology of juveniles are relatively small and thus hard to distinguish that only a few reports have been made concerning this phenomenon. The development of the genitalia in later juvenile stages will have to be examined closely and combined with the use of biometrical methods on the carapace. We expect that precocious sexual dimorphism will be found in a number of other Recent podocopid species as well.

Morphological Variations

As noted by Keen (1982) and Neale (1983), intraspecific variation in ostracod carapace morphology has been studied by a number of researchers in various species. The size, ornamentation, and shape of the pores (*e.g.* Rosenfeld and Vesper, 1977) are among the characters that have been analysed extensively and the possible causes of the variations in these characters have also been discussed.

The variations in size have been reported to be influenced by the following environmental factors:

1) Water temperature: At high temperature, the size tends to be small, and at low temperature, the size tends to be large (*e.g.* Elofson, 1941; Van Morkhoven, 1962; Szczechura, 1971; Urlichs, 1971).
2) Salinity: At high salinity, the size tends to be small, and at low salinity, it tends to be large (*e.g.* Van Harten, 1975a).
3) Dissolved chemicals: (*e.g.* Kaesler, 1975).
4) Geographical conditions: (Ishizaki, 1975).

5) Water depth: The size tends to be small in shallow places, while it is large in deep places (*e.g.* Van Morkhoven, 1972).
6) Environmental stability: (Kaesler and Lohmann, 1976).
7) Food supply: (*e.g.* Keen, 1971).
8) Races within a number of species: (Whatley, in discussion of Szczechura, 1971).

The influence of some environmental factors on the variation in ornamentation has also been reported as follows:

1) Salinity: The carapace tends to be thicker and the ornamentation stronger at higher salinity (*e.g.* Sandberg, 1964; Carbonnel, 1969; Vesper, 1975; Garbett and Maddocks, 1979, p. 878); Conversely, high salinity tends to cause reduction in ornamentation (*e.g.* Garbett and Maddocks, 1979, p. 863).
2) Water temperature: High water temperature favours development of ornamentation (*e.g.* Carbonnel, 1975; Hartmann, 1982).
3) Dissolved chemicals: (*e.g.* Urlichs, 1971; Carbonel and Peypouquet, 1983).
4) Genetic polymorphism: (Kilenyi, 1972).
5) Sex: Females tend to have coarser ornamentation than males (*e.g.* Sandberg, 1964; Garbett and Maddocks, 1979).

Intraspecific variations in size and ornamentation are either attributed to two separate causes (*e.g. Leguminocythereis? hodgii* in Ishizaki, 1975) or considered as variations associated with each other (*e.g. Limnocythere floridensis* in Garbett and Maddocks, 1979). Besides, the same variations in the same species are often attributed to different causes by different researchers (see a number of reports concerning *Cyprideis torosa*). In any case, it will not be easy to find out the direct cause of any morphological variation; a single variation may be caused by several environmental and genetical factors that are intricately associated with each other, and the environmental factors also have associations within themselves as reported by a number of authors (*e.g.* Van Morkhoven, 1962, p. 148). It has also been found that the same change in the environment may even cause variations in opposite ways in different taxa, which suggests that it will be difficult to establish universal relations between the environmental factors and the morphological variations that would be applicable to all the ostracod species. The variations in each taxon, therefore, are to be considered a consequence of its own adaptation.

It was observed in the monthly living specimens of *Cytheromorpha acupunctata* that the size becomes smaller in summer, while the reticulation develops from summer to autumn. We have tried to find out what kinds of change in the environment affect the morphological variations that fluctuate with the season. The hydrographical data at the sampling station are shown in Text-fig. 9. In summer, the water temperature rises while the salinity decreases; the change in temperature, however, appears to occur slightly earlier than that in salinity. The noticeable decrease in the salinity is probably caused by the increase in precipitation in summer. The dissolved oxygen concentration and pH-values are fairly stable throughout the year, particularly in the bottom water, and thus they are not likely to be factors affecting the morphological variations of this species around this station.

The decrease in size is apparently linked to the increase in water temperature and the decrease in salinity. Taking into account that the adult individuals survive for some period after the final moulting, it must be assumed that some of the adult specimens collected each month had undergone the final moulting well before they were collected: such individuals must have morphological features reflecting the environment at the time of moulting. Changes in carapace morphology must, therefore, take place somewhat later than those in the environmental factors. The changes in the water temperature certainly precede those in morphology, but no lag is observed between the changes in the salinity and those in morphology. The similarity between the size and the water temperature curves also suggests that the higher the temperature, the smaller the size tends to be. This observation agrees well with the reports that have previously been made in the case of a number of ostracod taxa.

Coarsening of ornamentation, on the other hand, also seems to be associated with the increase in water temperature and the decrease in salinity. This change takes place somewhat later than that in the size. However, for the same reason as in the case of the size, we consider this change to be affected more by the temperature than by the salinity. According to Sandberg (1964), development of ornamentation in *Cytheromorpha paracasteana* is positively correlated with increase in salinity. Our study which dealt with another species of the same genus, reached the opposite conclusion.

Although the changes in size and ornamentation are both likely to be correlated with water temperature, these two do not take place at exactly the same time, and therefore one cannot justify dealing with these two together. The possibility remains that the direct cause that induces either one or both of these two, lies not in the water temperature itself but rather in other environmental factors that are related to the temperature, such as the chemical composition or the food supply. The mechanism by which the morphological variations are induced may be explained in terms of the influence of the environmental factors discussed here on the calcification process of each individual. However, it may also be true that individuals with the gene that makes morphology adaptable to the environment are transiently selected in each period (see Kilenyi, 1972). It may not be appropriate, therefore, to call these morphological variations 'phenotypic'.

Our conclusion that these sort of morphological variations are strongly affected by genetic factors was drawn from the observations of the monthly samples containing individuals with different degrees of variations, as well as from the fact that the degree of ornamentation differs between the two sexes. It is also obvious that environmental factors exert a significant influence on morphology, since there are seasonal changes in morphology that occur parallel to the environmental factors. In other words, the variations in the two morphological characters in this species, namely the size and the ornamentation, are to be considered both genotypic and ecotypic. It is true that the variations in these two characters are associated in some way with the water temperature. However, geochemical and physiological approaches are necessary to elucidate the direct causes of these variations and the mechanism by which such variations are created.

ACKNOWLEDGEMENTS

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DISCUSSION

B. W. Scharf: How many generations has the species a year?

Ueda: Our work suggests that growth from egg to adult takes about three months. It also appears that breeding takes place throughout the year. Thus theoretically there could be as many as four generations per year although this would seem to be very unlikely. Without carrying out breeding experiments in the laboratory, we are unable to give a firm answer to your question.

D. A. Keyser: You showed fractures through the shell; were they larvae or adults?

Ueda: The shells were all adult males and you will find them referred to in the full text of the paper.

I. P. Wilkinson: One sample site had a 'flood abundance' of *C. acupunctata* (*i.e.* 75%). What was peculiar about that site to cause this occurrence?

Ikeya: The station in question lies about 200 m south-east of the station we deal with in our paper. The figure of 75% abundance refers to a collection made in November, 1974 which seems to represent an unusually high occurrence. Normally *Spinileberis quadriaculeata* is the most abundant form and we are unable to account for the high incidence of *C. acupunctata* at this particular time. We think that it may be due to the slightly different bottom conditions (sandy silts) combined with some chemical or other factor at present unknown.

The Ostracod Carapace as a Hydrochemical Source of Information at Water/Sediment Interface

P. CARBONEL AND M. TÖLDERER-FARMER
University of Bordeaux, Talence, France

ABSTRACT

This paper discusses the first results obtained from a quantitative microprobe analysis (SEM) of the chemical composition of ostracod valves living in limnic and lagoonal environments.

Enrichment of certain trace elements such as P, Fe, and Mn in the carapace generally occurs in eutrophic environments where autochtonous organic sedimentation thrives. High Al and Si values have been detected in an environment supplied mainly by allochtonous organic matter of terrigenous origin.

We have tried in this study to determine the extent of hazardeous distribution of certain chemical elements in carapaces or ornamentation. Mg contents, for instance, mostly located in the inner part of the carapace (Cadot *et al.*, 1972) have been found within the reticulated crests of *Cyprideis torosa* in all kinds of environments. Furthermore, the nodes of *Cytherissa lacustris, Limnocythere sancti patricii* and *Sclerocypris clavularis* proved to contain more amounts of silica than in the rest of the valve. It may, therefore, be assumed that:

—the overall chemical composition of valves is an indicator of the trophic quality of the environment (local or allochtonous organic matter);

—the "choice" of certain chemical elements to concentrate or locate in sites of particular structure (nodes) and ornamentation intensity (aggradation or degradation) reflect the concentration of these elements in the water, at water/sediment interface during moulting.

INTRODUCTION

It is commonly known that ostracods can build a variably ornamented carapace under the pressure of several factors controlling the physico-chemical environment at the water/sediment interface. This is particularly true for the carbonate equilibrium in environments inducing changes in the reticulation of shells through aggradation or degradation (Peypouquet *et al.*, 1980, 1986; Carbonel and Hoibian, 1985; Carbonel, 1980; Farmer and Carbonel, 1984, 1985). It is also an acknowledged fact that all elements forming the ostracod carapace are directly derived from water (Turpen and Angel, 1971).

In this paper we try to answer two main sets of questions:

1) Are phenotypic changes a chemical reality? Are they reflected in a change of the chemical composition of the test?
2) Does this change (if real) correspond to the intensity of variations in the ornamentation?

To be more exact, can the chemical composition of an ostracod carapace provide reliable information on the chemistry of waters where moulting occurred? Are morphological variations in ostracods marked by specific chemical elements within the sites studied? Can ornamentation be quantified?

In order to provide answers to these questions we chose to study two species, *Cyprideis gr. torosa* and *Cytherissa lacustris,* living in different environments, but showing practically the same polymorphic characteristics. In both cases, we first considered global data obtained from a chemical analysis of the carapace and later local variations in the chemical composition of the shell with respect to ornamentation.

HISTORICAL BACKGROUND

The chemical composition of the ostracod carapace has in the last thirty years interested a great many micropaleontologists. As early as 1958, Sohn analyzed and compared both carapace and body of the animal. Later scientists tried to establish a relationship between the chemical composition of valves and the environment [Cadot *et al.,* 1975, 1977—Mg content and temperature; Durazzi, 1975—Sr study, relationship with salinity; Bodergat, 1978, 1983—detection of pollution, the presence of elements in relation to ornamentation (Ba in nodes); Chivas *et al.*, 1983—influence of Mg/Ca, Sr/Ca ratios, insignificant Ba/Ca impact due to temperature and salinity; De Deckker, 1985 (in this symposium)—quasi continuous constance of the Sr partition coefficient for a given genus and correlation of variations in this element with salinity].

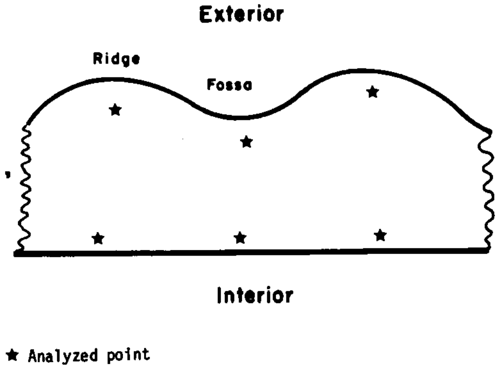
RESULTS AND DISCUSSION

Methods

In order to take into account both information on the composition of tests and the location of chemical elements in ostracod valves, we cross-sectioned as much as possible according to the anterior/posterior axes and perpendicular to the dorsal/ventral axes.

Valves analyzed belong to ostracods collected either alive or dead with appendages. They are either adults or juveniles from stage 8 (measures are globally similar).

Points analyzed cover both the outer and inner parts of the carapace, each external point corresponding in principle to an internal point (Text-fig. 1). Each section consists of at least a dozen



TEXT-FIG. 1—Location of S.E.M. analyses in carapace sections.

points and each sample of 2 to 3 sections, *i.e.* there are some 30 points per sample. Once polished and metallized with carbon, sections were analyzed with a CAMECA (Camebax micro) electronic microprobe having 3 spectrometers. Twelve chemical elements were measured according to their frequency both in water and in carbonates constituting the valves: Ca, Na, Mg, Sr, Si, Fe, Mn, Al, Ba, Cl, S, P (+ O by stoichiometry).

Analyses were run under the following conditions:
voltage: 15Kv,
current consumed: 0.42×10^{-9}A,
analysis field: $2.5 \times 2.5\ \mu$m.

The limits of the electron probe detection are of the order of $10^{-3}\%$ depending on the element and matrix considered. Results are given in 3 tables:

—atomic concentration %
—atomic weight %
—oxidized weight %

Oxidized weight percentages were used for *Cyprideis* while atomic concentration percentages were used for *Cytherissa*; our intention was to determine atoms in the crystalline network of Ca carbonate.

Cyprideis and Various Ralinity Environments

Cyprideis gr. torosa (Jones), a species living in fresh as well as brackish or oversaline waters, was chosen to determine the influence of environmental conditions. As ornamentation intensity is discussed later in the paper, we take into account here only punctuated forms, *i.e.* forms with fine granular valves (Carbonel and Pujos, 1982). These are individuals that have moulted in waters with analogous carbonate equilibrium states, thereby leading to similar ornamentation patterns (neither dissolving nor precipitating) (Peypouquet *et al.*, in press; Carbonel and Hoibian, in press; Tölderer-Farmer and Carbonel, 1985).

Global Composition

Among the multitude of milieus in which *Cyprideis* live, we chose three contrasting hydrochemical environments:

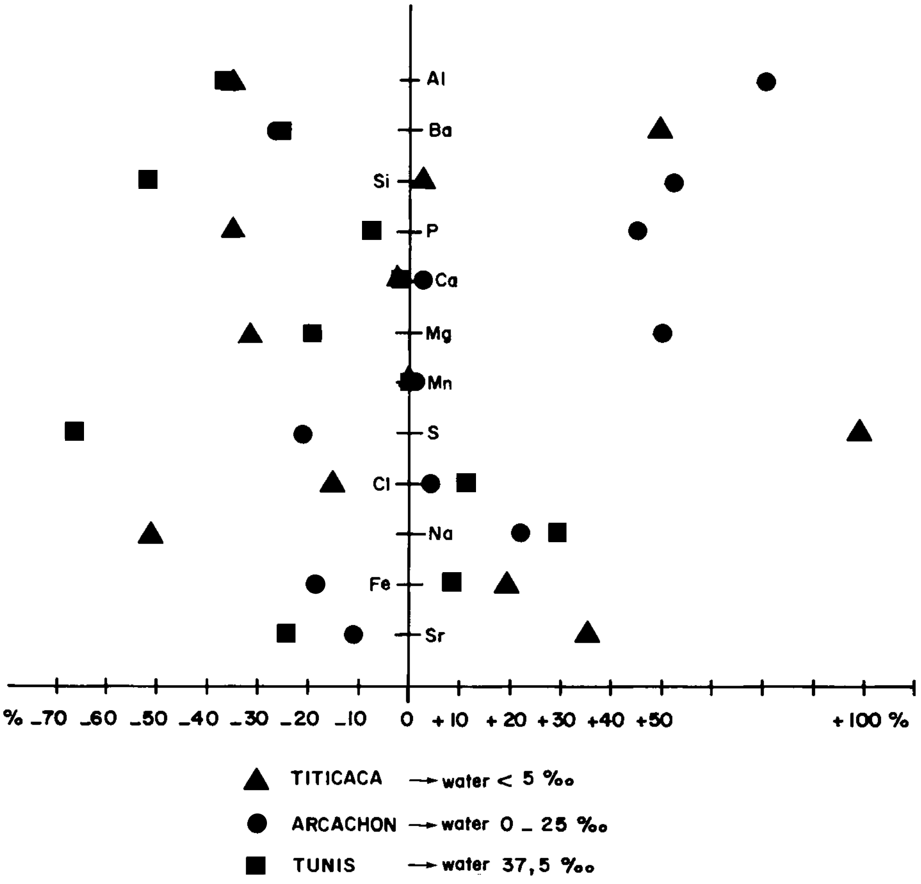
—Lake Titicaca (small Bolivian lake): less than 5 ‰ with a mineralization attaining 0.5 at 25 m M/l depending on the season (Carmouze *et al.*, 1978),
—Arcachon bay (inner part, France): salinity of 0 to 25 ‰ depending on the tide and season (Yassini, 1969; Oh, 1978; Carbonel, 1980; Cuignon, 1984),
—Tunis lake (Tunisia): average salinity 37.5 ‰. varying with the season (Jouirou, 1982; Carbonel and Pujos, 1982).

Elements measured display different behavior patterns: those associated with carbonates (Mg and Ca) increase with salinity (Text-fig. 2) while elements such as P-associated with the organic matter—increase in individuals having moulted in eutrophic (Arcachon, Tunisia) rather than oligotrophic environments (Titicaca). Conversely, Sr tends to increase more in valves from Lake Titicaca thereby suggesting enrichment of this element in the river basin.

In summary, there is a positive relationship between alkaline-earth elements and salinity, as well as between environmental trophism and S, P, Fe and Mn.

Chemical elements and ornamentation

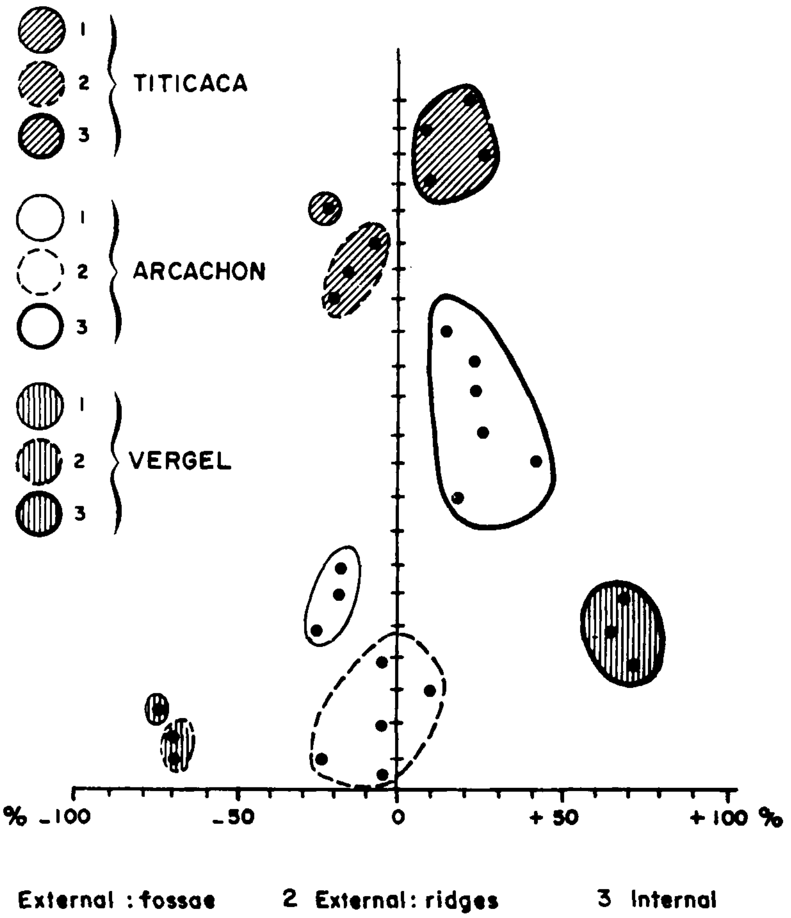
Chemical elements were measured at the periphery and outer parts (Text-fig. 1). At the outer



Text-fig. 2—General distribution of chemical elements in relation to three environments: percentages of variation with mean.

part, positive ornamentation (ridges) and negative ornamentation (cavity) zones were examined. We noted a concentration of elements both at the inner (Mg, S) and outer parts (Si, Na) (Text-figs. 3, 4). The Mg example is particularly interesting because its absolute maximum values are found in the inner part of the carapace when in contact with epidermic cells. This is in perfect agreement with observations made by Cadot *et al.* (1975). It is, in fact, a phenomenon observed in all environments whether fresh water or oversaline, eurythermal or euryhaline. Furthermore, this phenomenon is consistent with the fact that consolidation during moulting takes place from the inner to the outer parts of the carapace (Danielopol, 1980).

Another important point as far as the distribution of elements in the *Cyprideis* valve is concerned, is their positioning with respect to ornamentation. Ca is, for instance, more concentrated in reticulation cavities than in ridges, whereas Mg, Sr, Na, Fe, P and Si concentrate mostly in ridges (Text-fig. 3). Here, the Mg example is again interesting for its maximum deposition occurs in the inner part of the carapace whereas in the outer part it concentrates more in ridges than in cavities found between ridges (Text-fig. 3). Even if this difference in concentrations is insignificant—very low



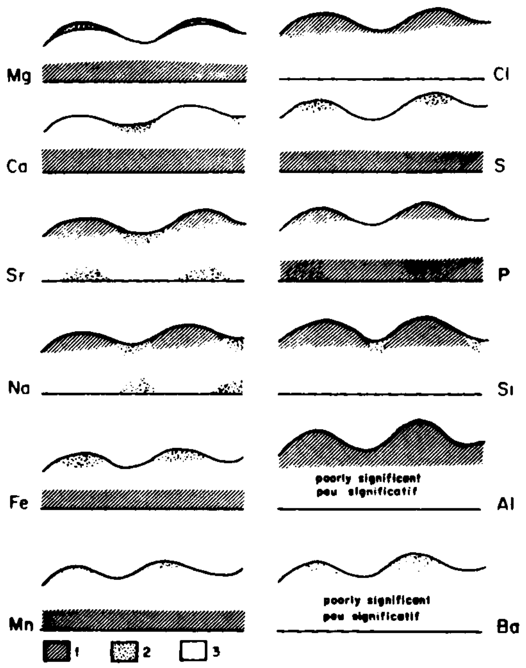
TEXT-FIG. 3—Relative values of Mg in ornamentation of *Cyprideis* in three environments, percentages in relation to mean.

in the case of individuals having lived in slightly mineralized waters—it exists in 90% of the cases considered (Text-fig. 4). This disposition is similar with that observed by Okada (1981) in epidermic cells in as much as the center of cells corresponds to a reticulation socket and the periphery of ridges. Maximum secretion at the periphery of these cells therefore appears to be underlined by a preferential site for Mg deposition. This increase in mineralization near ridges (positive point of ornamentation) could induce the concentration of Mg and other elements. This implies pumping of Mg from waters of all kinds of environments, even those poorest in this ion. Secretive cells extract and distribute Mg without stocking it in the organism. This observation totally agrees with the results obtained by Martin (1979) and Chivas *et al.* (1983).

Thus the distribution of chemical elements in ostracod valves is not hazardous. As we have chosen to study similar ornamentation types, absolute values of elements (especially Mg) reflect only those in the water in which *Cyprideis* moulted.

Cytherissa and Environments with Varying Trophic Levels

The *Cytherissa* species studied live in the cold waters of Alpine lakes. Measurements were taken



1: Maximum concentration
2: Mean concentration
3: Minimum concentration

	External		Internal	Mean
	Ridges	Fossae		
Mg	62	50	70	63.5
Ca	5641	5698	5721	5691.0
Sr	44	37	35	38.0
Na	37	25	10	21.0
Fe	2	1	2	1.7
Mn	—	1	2	1.1
Cl	3	4	2	2.8
S	2	0.5	2	1.8
P	12	2.5	14	10.8
Si	32	9	1	11.5
Sl	10	1	1	3.5
Ba	2	1	1	1.25

Text-fig. 4—Distribution of 12 chemical elements in ornamentation of *Cyprideis*; mean in relation to location.

at the 3 most characteristic stations of Lake Mondsee (Salzkammergut):

—an oligotrophic littoral station where organic matter is generally allochthonous: MO SEE (8–12 m),

—a "mesotrophic" littoral station where organic matter is both allochthonous and autochthonous: MO 7 (12–18 m),

—a eutrophic infralittoral environment where O.M. is mainly autochthonous and the environment, is, with respect to carbonates, dissolving: MO 3 (30 m).

Global Composition

The global composition of the carapace is very much like the ionic composition of water at the water/sediment interface for an average percentage of Ca^{++}, Mg^{++}, Na^{+}, K^{+} (cations) and of HCO_3^-, $CO_3^=$, $SO_4^=$, and Cl^-(anions) (Philipps, 1972).

Other elements such as N, P, Fe, and Si that are relatively less affected by salinity tend, from a biological point of view, to be very influential.

Cytherissa carapaces in the oligotrophic littoral station MO SEE, contain small amounts of P and Fe, a great deal of Na, Mg, Ca and S (Text-fig. 5), Ca is dominant, Na, Mg, S and Cl range between 0.3 and 0.1 %, Fe, Si and P vary between 0.1 and 0.4 %, Mn, Al and Ba do not exceed 0.4 %.

Cytherissa in the mesotrophic station MO shows increasing absolute values, especially for P and Cl.

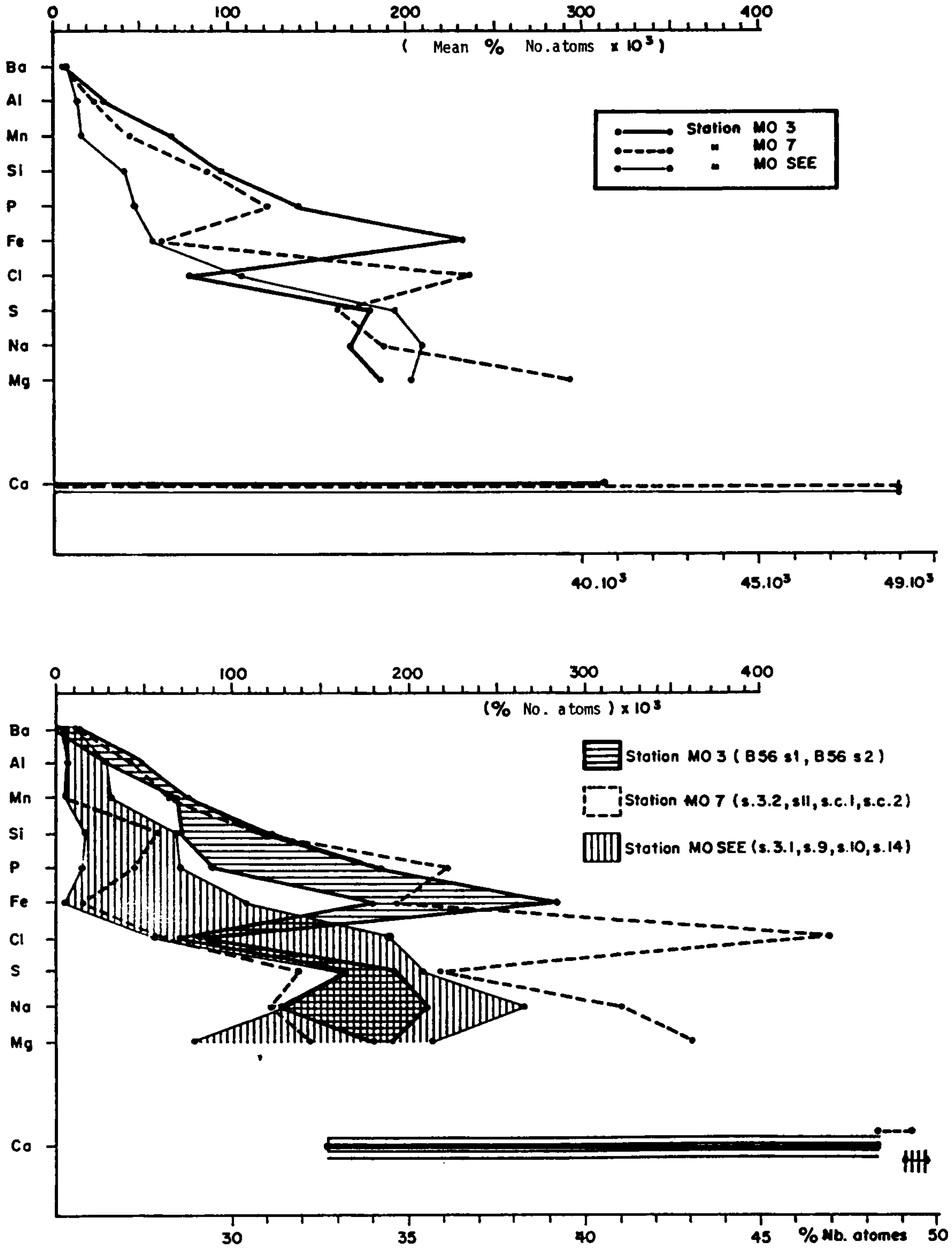
Finally, valves originating from the "deep" and eutrophic station MO 3, show a radical change. Ca decreases (Text-fig. 5), P and Fe increase in absolute values, and Mg and Cl decrease. The percentages obtained for each element are as follows: Ca 95 %, Fe, Mg, S, Na, P 0.3–0.1 %, Si, Cl, Mn 0.1–0.05 %, Al and Ba less than 0.01 %.

The average values obtained for each environment studied provide information both on the trophic level of the environment (increase in P, Mn, Fe, elements associated with autochthonous O.M.) and on the equilibrium of carbonates (decrease in Ca and Mg from the oligotrophic to eutrophic environments, Text-fig. 6). Valves from station 3 are, in fact, less calcified than those from the littoral environment.

Chemical composition and ornamentation

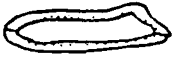
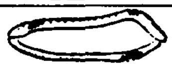
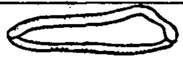
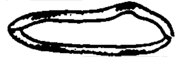
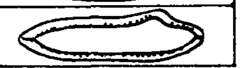
The dominant characteristic of *Cytherissa* is its capacity to form nodes on the carapace. In station MO SEE (littoral oligotrophic), nodes attain maximum capacity at station MO 7 (littoral mesotrophic) they are abundant to average and at station MO 3 (deep eutrophic) they are infrequent to average. The occurrence of nodes, often more intense in juveniles (St. 8) than in adults, is due to a salinity that is less than 10 ‰, and to the input of organosiliceous complexes from the river basin (Tölderer-Farmer and Carbonel, 1985; Tölderer-Farmer, 1985). In order to determine the chemical characteristics of these structures, we measured both elements in nodes (inner and outer) and between nodes (inner and outer). At the eye spot, the inner part is richer in Mg, S and Ba whereas in the outer part, most elements concentrate, especially Si and Al. The disposition of elements between nodes appears to be the same (Text-fig. 6) but with low values. At the place where *Cytherissa* should normally have one or two nodes, the same phenomena occur as if nodes really did exist. Nevertheless, regardless of the intensity of nodes, values are highly comparable. At the edge of the carapace, S and Ba values increase (Text-fig. 6).

Mg values are highest in oligo-and mesotrophic stations because of a rise in temperatures that accelarates the formation of nodes. Abundant S amounts observed at the edge of the carapace correspond to an increase in chitin (Benson, 1981). This element increases, together with Mg, in the inner part of the carapace. This phenomenon, already observed with *Cyprideis,* is probably due to the heterogenous structure of the carapace (cellular or compact), a supposition which will cer-



TEXT-FIG. 5—Variations of global value of the measured elements in *Cytherissa* valves at three stations.

ADULTS

	NODES		INTER-NODES		NODE PLACES		
	Int.	Ext.	Int.	Ext.	Int.	Ext.	
Ba	3	5	8	5	9	7	
Al	3	6	0	8	5	23	
Mn	25	27	22	28	19	21	
Si	33	131	7	15	12	139	
P	47	54	32	39	31	79	
Fe	121	140	88	106	81	94	
Cl	128	160	103	126	96	115	
S	212	123	173	112	186	121	
Mg	181	158	203	190	151	168	
Na	216	308	254	230	233	227	
Ca	% 49,238	49,153	49,309	49,311	49,382	49,036	

JUVENILES

	NODES		INTER-NODES		NODE PLACES		
	Int.	Ext.	Int.	Ext.	Int.	Ext.	
Ba	14	6	6	3	20	5	
Al	17	40	27	29	5	0	
Mn	39	46	39	51	38	19	
Si	74	131	45	61	52	80	
P	202	179	163	133	170	121	
Fe	33	49	41	55	43	79	
Cl	439	241	265	213	345	153	
S	229	150	208	156	221	137	
Mg	354	348	344	340	335	284	
Na	141	197	99	135	151	167	
Ca	% 48,634	48,630	48,874	48,898	48,743	49,017	

TEXT-FIG. 6—Distribution of 12 chemical elements in ornamentation of *Cytherissa*; mean values in function of location.

tainly be validated by ongoing studies. Other elements considered to show similar distributions as those observed for *Cyprideis* are shown in Text-fig. 6. It must be noted that they are at equilibrium with water concentrations.

In summary, the distribution of elements varies with ornamentation. This variation is nevertheless due to the type of ornamentation and not to its intensity. Regardless of the size of the node, the change in values is consistent with that of the background noise associated with each individual. It is also very important to note that carapaces without nodes show at the place a node should exist, the same values as carapaces with nodes. One may therefore assume that these sites favor accumulation of elements such as Si at the outer part and of elements such as S and Ba at the inner part. Hence, a physiological control of the calcite intrusion, especially at the procuticule where organic matter contents are high, accounts for the increase in Ba and especially S.

CONCLUSIONS

This study has both confirmed results already obtained and provided new information on the following points:

Mg is preferentially distributed in the inner part of the valves and appears to be influenced by temperature (*cf.* Cadot *et al.*, 1975, 1977).

Ba appears to be linked to *Cytherissa* nodes (*cf.* Bodergat, 1983, for *Cyprideis*).

The distribution of certain elements within specific ornamentation sites does not seem to be hazardous.

Mg on reticulation ridges is more abundant than in cavities.

Si, Na, and Al concentrate on the outer part of nodes while Ba, S and Cl concentrate in the inner part at the contact of epidermal cells.

The occurrence of certain elements, *e.g.* alkaline-earth elements (except for Sr) depends on the concentration of salt in the water.

The occurrence of other elements such as P, Fe and Mn appears to be systematically associated with the trophic level of the environment.

The distribution of elements may also be influenced by the carapace structure (compact or lamellar layer). Studies in progress dealing with valve crossings show, in fact, a difference in the behavior of elements depending on which layer they are found in. These elements may be grouped as follows: Fe, S, Mg and M; and Na, Cl, Si and Al (Carbonel and Tölderer-Farmer, to be published).

Although data gathered hitherto need to be tested by using other species, environments and ornamentation, they show that this kind of investigation is an efficient means of clearly revealing the relationship between the chemistry of the environment and the carapace of the ostracod. They therefore help us to understand better present environmental conditions at the water/sediment interface and to extend relevant information to paleoenvironments.

ACKNOWLEDGEMENTS

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The Impact of Organic Matter on Ostracods from an Equatorial Deltaic Area, the Mahakam Delta-Southeastern Kalimantan

P. CARBONEL AND T. HOIBIAN
University of Bordeaux, Talence, France

ABSTRACT

In many systems where fresh/saltwater interface, benthonic faunas, particularly ostracods, show a longitudinal succession from upstream to downstream. This succession is due to mixing between fresh and saltwaters. The lateral variations are often linked to vegetal communities and to the intertidal characteristic of the environment.

The main characteristics of the ostracofauna in the Mahakam delta area are:

— Longitudinal succession is not found. There exist only supratidal fauna and mostly marine fauna of the delta front.

— Faunal assemblages show lateral variations at the same longitudinal place and at the same place in relation to the intertidal zone.

These lateral variations concern:

— Faunal diversity: The number of species decreases in the biotopes in front of the delta mouth. Some species become dominant (*Hemicytheridea reticulata*).

— In the same biotopes, ornamentation of polymorphic species decreases ("degradation" of ornamentation). In biotopes located between delta mouths, ornamentation within the same species increases ("agradation" of ornamentation).

The parameter which starts this variation is "organic matter effect." Its influence explains both cases of ornamentation variation:

— A consumption of organic matter at the water/sediment interface by bacterial action starts the O_2, pH decrease. Carbonate shelled organisms cannot build their carapaces by bioprecipitation. When the organic matter action is very diluted in marine waters in front of the delta mouths, ostracods have difficulty building their shells and they use a minimum of $CaCO_3$, which result in a weak ornamentation. Between delta mouths, the influence of organic matter degradation is completely absent. The ostracods can build their shells by bioprecipitation in a carbonate saturated environment and ornamentation is most important with reticulation. spines, etc.

The variation of this parameter is linked to the size of the deltaic plain. The recording of this effect on the ostracofauna yields information regarding palaeohydrological evolution of delta areas under equatorial climates.

INTRODUCTION

In numerous transition fresh/saltwater systems, benthonic faunas, namely ostracods, undergo a population transformation marked by the successive replacement of species or specific groups, controlled by progressive mixing of waters. This water mixing/species replacement relationship suggests the existence of factors such as tide and season (high and low water level) as determining the positioning of the zone in which waters mix. Similarly, these factors condition the dynamic intensity and mode of action and subsequently, the formation or extinction of biotopes. They also affect the biological rhythm responsible for the productivity, *i.e.* supply on the bottom. This 'longitudial' evolution is overlain by a 'vertical' evolution dependent upon the environment's intertidal quality (Carbonel, 1978, 1980, 1982). Such an evolution is typical of fresh/saltwater systems under temperate climatic conditions. By contrast, in an equatorial climate, the smoothness of seasonal effects and the reduced euryhaline impact produce a completely different situation, which we attempt at explaining here through the use of the Mahakam delta example in Indonesia.

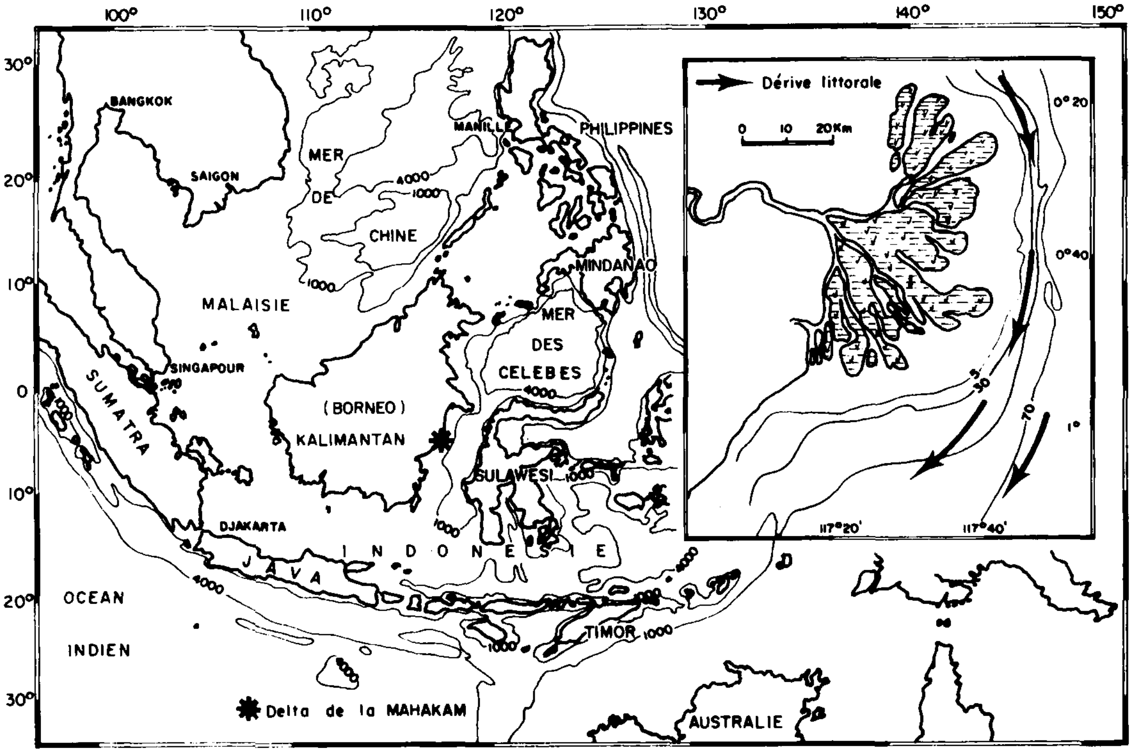
The Mahakam Delta

Generalities

The Climatic and Hydrosedimentary Context

The Mahakam delta covers an area of 5000 km^2 ranging between 0° 4′S and 1° 10′S and 117° 15′E and 117° 40′E. It presently represents a crisscross of marsh land and channels where sea and delta are closely interrelated (Text-fig. 1). It is a transitional system of fresh/saltwater functionning under equatorial climatic conditions. This system implies:

— constant humidity leading to diminished salt in intertidal environments. The salt deficiency phenomena are linked to rainfall frequency and supply of fresh water by aquifers;



Text-fig. 1—Mahakam delta: a) Geographic area; b) General surface water circulation in the Makassar strait.

— high water temperature provoking an oxygen deficit at the water/sediment interface;

— relatively low salinity (32 ‰.) at least in the upper water section.

The drainage of the river basin brings water masses which have passed through areas of exceedingly dense vegetation into the delta. The crossing of these areas induces:

— water bearing organic matter (O.M.) with low pH, depleted even more by the rate of precipitation;

— heavy solid charge.

Parameters, results of the marine influence, are active at several levels:

— the mean tidal range is 1.20 at 1.50 m with quite strong tidal currents of the order of 1 m/s;

— the low tidal range is due to a very high complex topography.

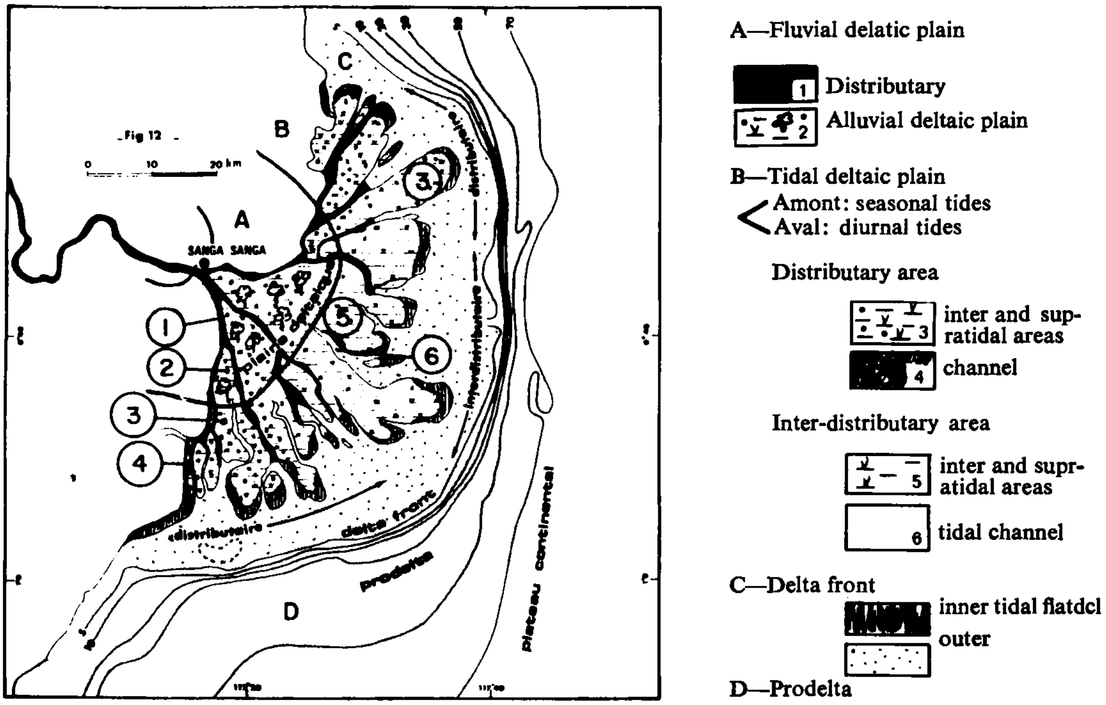
The delta itself is the result of sedimentary accumulation taking place when the river attains its basal level. In the midst of this complex channel tangle, 2 large units may be observed (Text-fig. 2), characterised by specific hydrological regimes (Allen *et al.*, 1979; Hoibian, 1984; Carbonel *et al.*, 1985; Gayet et Legigan, 1985).

The deltaic plain is subdivided into 2 groups: (a) the fluviatile deltaic plain grouping milieus in the upstream limit of the salt intrusion and (b) the tidal deltaic plain delineating the milieus affected by the saline increase.

Within this tidal complex (s.l.) a distinction may be made between channels of fluvial run-off or distributaries, and tidal channels or interdistributaries (Text-fig. 2).

The delta front is characterised by environments of a quasi-permanent marine character. It occupies the area between the downstream limit of inlets and the prodelta edge. Its inner most part may undergo slight desalination (Hoibian, 1984).

The prodelta area corresponds to the talus, limited at the top by the -5m isobath. It is a strictly marine environment.



Text-fig. 2—Mahakam delta: General morphology (after Gayet 1985).

TABLE 1

Environment	Diversity	Density	Dominant Ornamentation	Characteristic Forms
Supratidal marsh	monospecific	poor	–	*Cyprideis* sp.
Intertidal	poorly diversified	fairly rich	–	*Propontocypris* sp.
Inter to Infratidal	diversified	common	–	*Neomonoceratina mediterranea* *Clithrocytheridea atjehensis*
Coastal Infratidal				*Cytherelloidea* gr. *atmai* *Hemicytheridea reticulata* *Neomonoceratina microreticulata*
Inlets	poorly diversified	common	–	*H. retic.:20% Alcopocythere* *N. micro degrd. kendengensis*
Intermediary zones	poorly diversified	v. rich	+	*H. retic.:10% Trachyleberis dacyi* *N. micro agrad. Cythereis resmani*
Exposed areas	poorly diversified	common	±	*Bicornucythere papuensis* *Trachyleberis scutigera*
Inner Infra. (prodelta) Inlets	diversified	rich	±	*Keijia* sp., *Cythereis zenkeri* *Echinocythereis cribriformis*
Intermediary zones	v. diversified	v. abundant	+	*Argilloecia* sp. *div.* *Trachyleberis* sp.

– = degraded, v = very, + = aggraded.

The Present-day Characteristics of Ostracod Fauna

The Mahakam ostracod fauna may be qualified as:

Indopacific, for it is more similar to the Persian Gulf fauna than to the Birman coast fauna (Paik, 1976; Keij, 1964; Malz, 1980).

Small-sized, compared with the corresponding species of the continental shelf.

Mixed, a mixture created by their habitat (local currents, topography).

Because of the low pH in the river waters ($pH<5$) carbonates are absent. Calcareous fauna appear to be limited in slightly desalinated waters. The hydrochemical factor plays a most significant part especially with regard to carbonate equilibrium. Five population communities have been identified (Hoibian, 1984; Carbonel *et al.*, 1985).

MECHANISMS RESPONSIBLE FOR THE DISTRIBUTION OF OSTRACODS

Distribution of ostracod assemblages is very heterogeneous (Text-fig. 3) and influenced by three factors:

— stable marine salinity;

— topography (channels, intertidal zones);

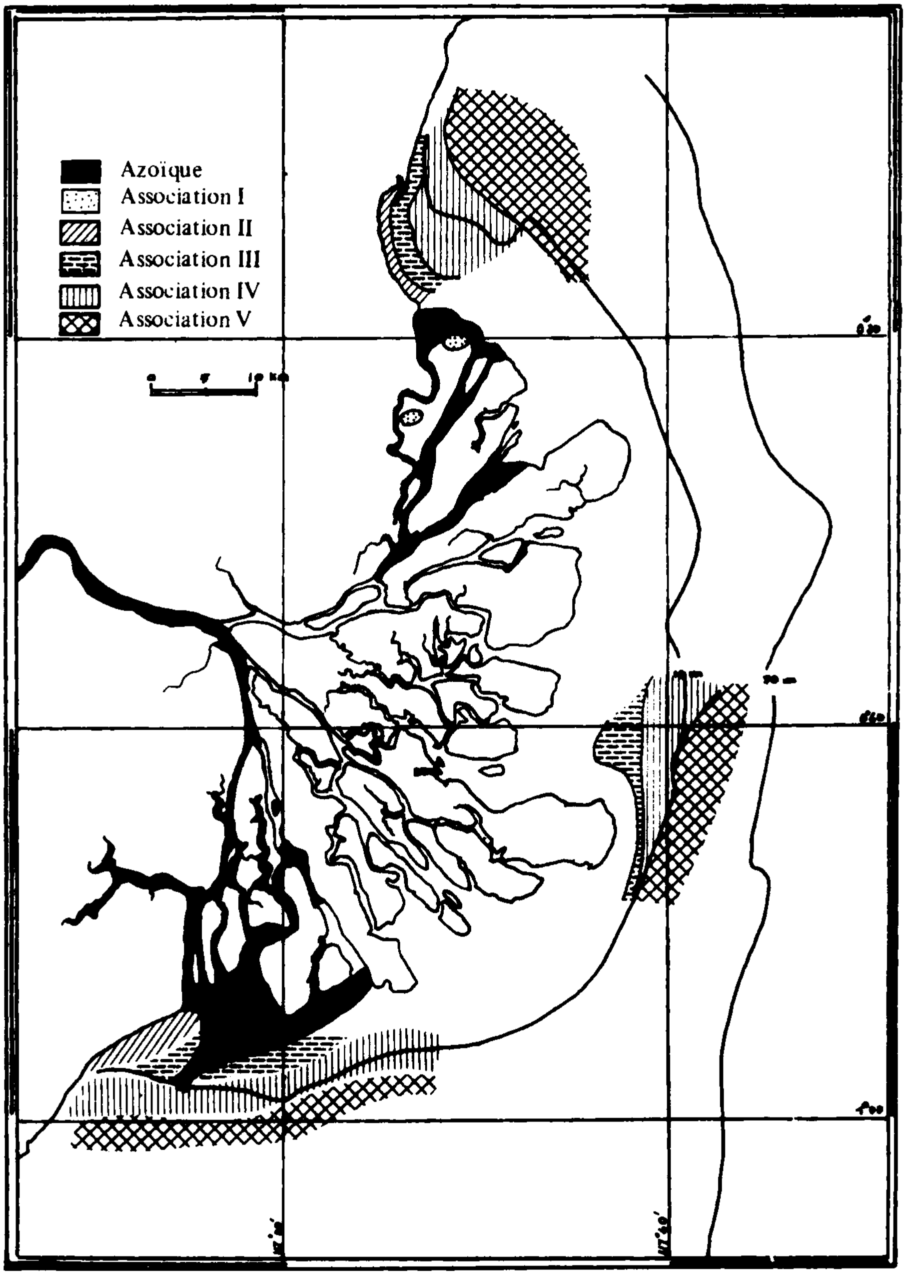
— location (inlets, intermediary zones *i.e.*, areas free of deltaic water influence).

Salinity

The occurrence of ostracods only in euhaline waters suggests intolerance of the dissolving river-borne effect of waters at pH 5. It is only when pH is sufficiently high (*i.e.* in marine waters) that organisms can bioprecipitate their carbonate test; the development of these organisms is discontinuous.

Topography

Topography exerts its classical effect and also reveals the dynamics and emersion impact (Car-

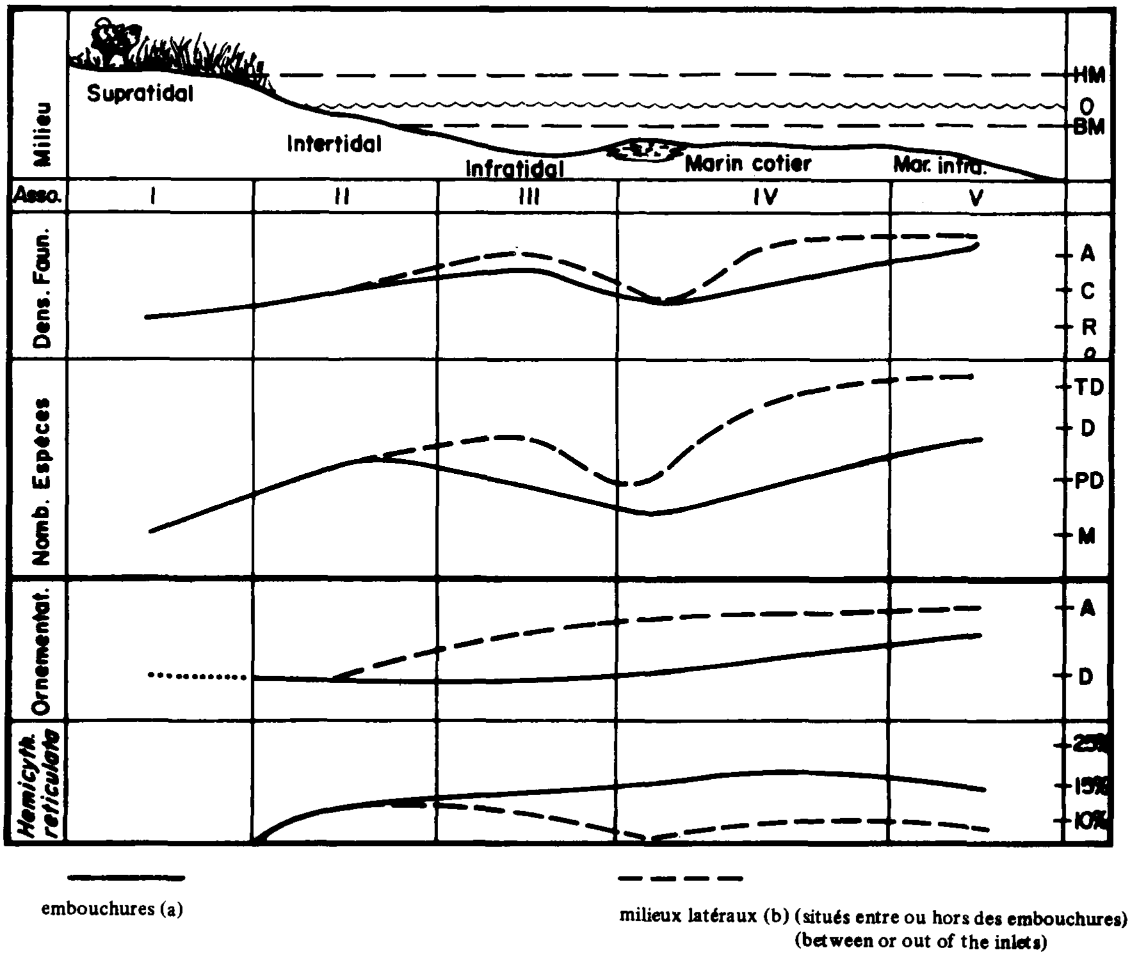


Text-fig. 3—Ostracod distribution in the Mahakam delta area (after Carbonel *et al.*, 1985).

bonel, 1980). Ostracods proliferate in intertidal biotopes thanks to the enrichment in nutritive (N, P) and constructive elements (S) which is more intense in these oxygen-rich areas than in emerged low-oxygenated environments. The intense water circulation in channels also prevents the proliferation of ostracods.

Location

The difference in composition and diversity of ostracods within the same assemblage depend-



Densité :
A : Abondant / Abundant
B : Commun / common
C : Rare / Rare

Nd espèces
TD : Très diversifié / very diversified
D : diversifié / Diversified
PD : peu diversifié / slightly diversified
M : monospécifique / monospecific

Ornementation
A : Agradé
B : Dégradé

TEXT-FIG. 4—Ostracod fauna characteristics in the Mahakam delta area (after Carbonel *et al.*, 1985).

ing on location as well as ornamentation differences in certain species, is more difficult to account for. Indeed, it must be noted that quality of fauna, its quantitative characteristics (density and diversity) and the polymorphism of certain species change according to the habitat zone and the place where biotopes are found, whether in the inlet or intermediary zones of the delta front. These faunas follow a faunal gap which prevailed in almost all the deltaic plains. With respect to those in the intermediary zones, the inlet zone faunas are richer, less diversified and less ornamented (Text-fig. 4). There is in all likelihood a 'continent' phenomenon. This statement being vague, other facors are necessary to reveal the effects of chemical equilibrium at the water/sediment interface, namely the carbonate equilibrium. These factors must be able not only to stop bioprecipitation of calcite during the moulting stage, but also to upset the osmotic processes, *i.e.* modify the pH input and eventually, salinity. This context becomes the action field of organic matter.

THE ORGANIC MATTER ROLE

The dominant characteristic in the Mahakam deltaic zone is the abundance in organic matter issuing from both the mangrove swamps and vegetation throughout the river basin and from true bacterial mixtures developing in the interdistributary zones.

The nature of the organic matter differs in accordance with the drainage of the deltaic plain (distributary or tidal channels). Referring to the model proposed by Etcheber (1983) it may be noted that this envisages:

— a distributary zone in which the dominant part of the organic matter is allochthonous and highly degraded because of a long 'journey' before its arrival into the estuary. The organic matter becomes polymeric with its most labile molecules entirely mineralized under the action of exoenzymes, light, etc. Furthermore, the remaining organic matter is likely to be closely associated with a particularly abundant inorganic phase of clays and colloids. It is also probable that the autochthonous organic matter, *i.e.* the matter in the estuarine waters, represents only a minor fraction because of:

— abundance of suspended matter (S.M.) darkening the water layer and greatly restricting phytoplankton and aquatic plant development (Head, 1974);

— the current intensity toward the lower part of the estuary preventing colonisation by zooplankton Castel, 1980);

— the occurrence of maximum turbidity prohibiting the development of benthos (Pujos, 1976).

— an interdistributary zone in which the organic matter is more abundant and diversified. It is often allochthonous and at certain evolutionary stages it may be represented by a material very little developed, made up of biopolymers and a complex original organic matter (cellulose, lignite, resin . . .) arriving in the estuary after a short transport period. These poorly transformed molecules become a very attractive pole for bacteria responsible for the proliferation observed, and the autochthonous organic matter made up of an exceeding abundance of phyto and zooplankton, the debris of which will increase the bacterial population.

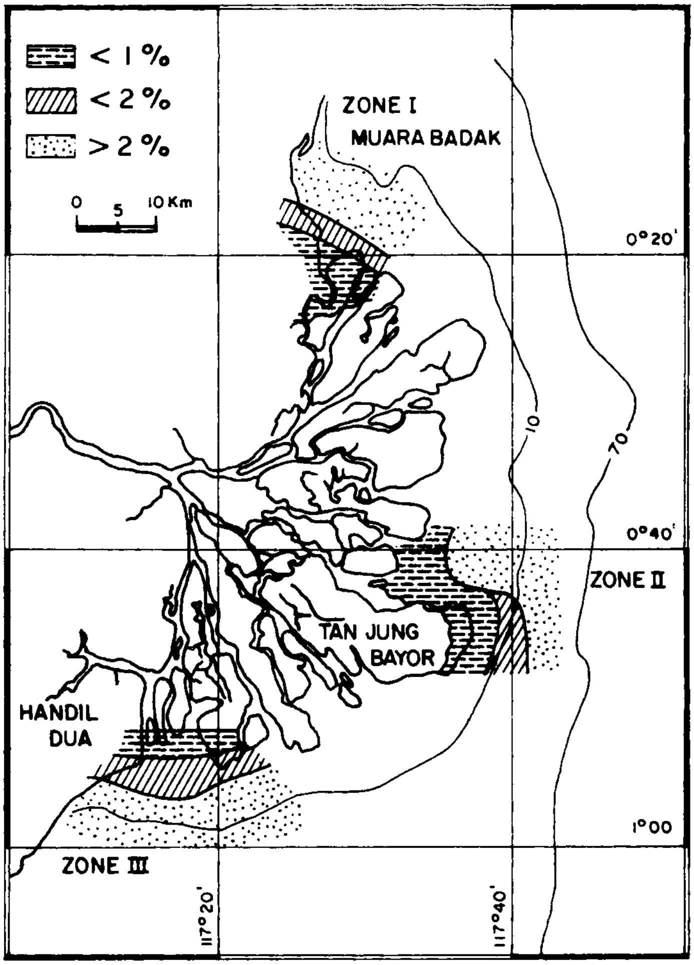
On the bottom, the extremely variable organic matter sources are associated with the residence time rate of organic elements determining oxygenation and pH conditions. The latter are particularly negative until levels outside the 'inlet' areas are reached (Allen *et al.,* 1979).

The abundance of organic matter transported by water may be reflected in different ways:

— precipitation of iron in the inlets of the interdistributaries, a phenomenon not observed in the distributary zones (Goldsmith, 1954; Dussart, 1960).

— low development of carbonates in the inlet areas (Allen *et al,* 1979, Text-fig. 5).

— equilibrium of carbonates dissolved at the water/sediment interface with repect to bioprecipi-



Text-fig. 5—Percentage of carbonates in the sands (after Allen *et al.*, 1979).

tation of the shelled benthonic organisms, this point being essential in the development of ostracods (Text-fig. 5).

The precocious degradation of organic matter on the bottom by bacteria increasing the pCO_2 and provoking a drop in pH (Lalou, 1957) results in a dissolving environment for carbonates. This result is herewith called 'the organic matter effect' having in our study a twofold impact: organic matter intensity and dilution by marine waters.

Intensity

Ostracods in channels, whether distributary or tidal, are practically non-existent. In distributary channels, this absence is probably due to the transitory water mass which is highly turbide, preventing the development of a benthonic fauna. By contrast, the development of faunas may be encountered in intertidal zones.

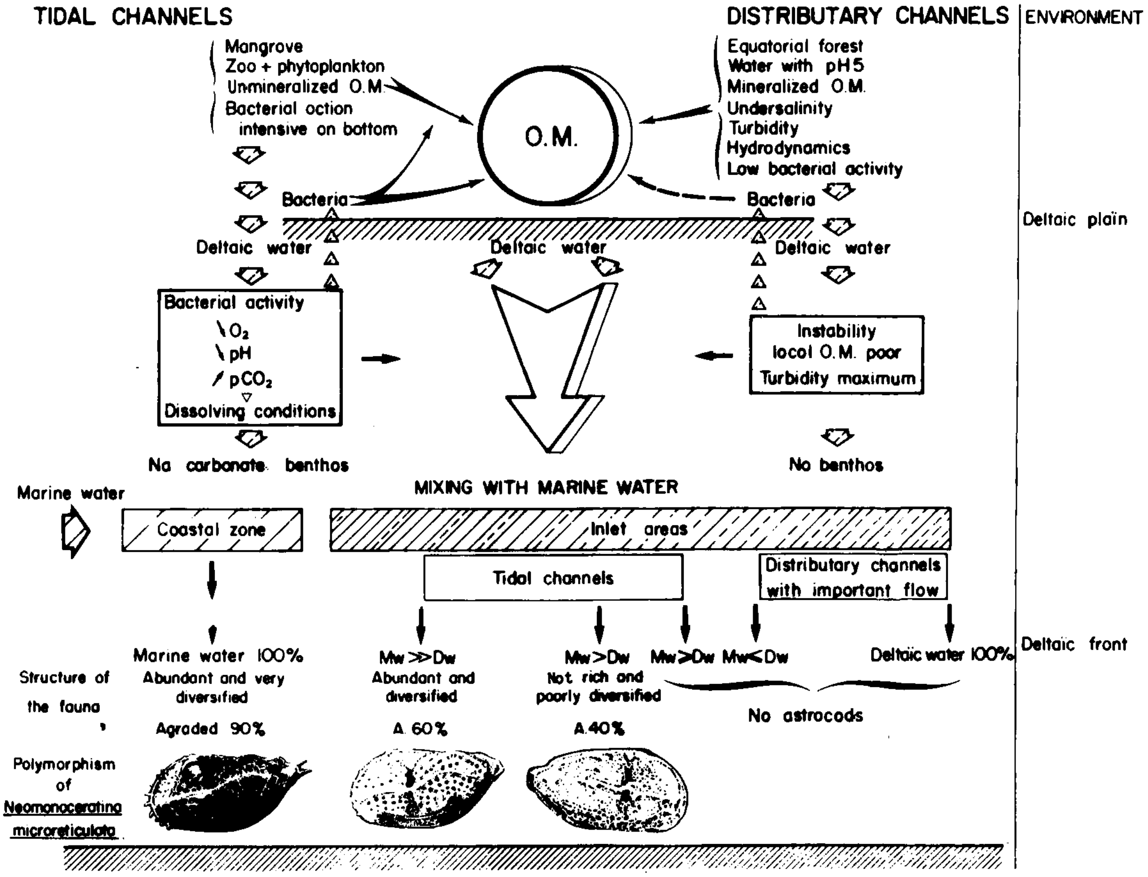
In the tidal channel, maceration of the organic matter leads to true bacterial culture mediums, the high activity of which provokes quasi-anoxic conditions on the bottom (Allen *et al.*, 1979; Etcheber, 1983). Anoxia is also an obstacle in the development of a benthonic fauna, hence, the lack of fauna in the deltaic zone and in the intertidal zones of tidal channels.

Dilution

In the inlet areas of the delta front, *i.e.* in places where the organic matter impact remains highest despite its diluted state, as regards the assemblage diversification there was (1) a considerable decrease and (2) a change in the quality when certain species such as *Hemicytheridea reticulata* Kingma became dominant after the elimination of many other species.

Polymorphism observations were also noted in the ornamentation of certain species due to the 'agradation/degradation' phenomenon (Peypouquet *et al.*, 1980; Farmer and Carbonel, 1984). This phenomenon is reflected in the reduction or increase of the valve sculpture; a variation associated with carbonate equilibrium at the water/sediment interface where ostracods live and moult. Within a dissolving environment, *i.e.* where ostracods must use maximum energy to bioprecipitate the calcite of their test, organisms work 'economically'; their valves have very little ornamentation. By contrast, within a precipitating environment, where ostracods can bioprecipitate their carapaces without great effort, ornamentation is much more elaborate.

To conclude, 'the organic matter effect' differs according to the biotope location induced by a more or less intense dilution. This effect may be reflected in the following model (Text-fig. 6).



Text-fig. 6—Modes of action of organic matter in the Mahakam delta area. Effect on the ornamentation of *Neomonoceratina*.

In the delta front inlet areas (mostly tidal channels) the organic matter impact is somewhat slowed down whilst the specific diversity is reduced and the majority of polymorph individuals are inclined to lose their ornamentation (degradation of the organic matter induces bottom dissolving conditions). Correspondingly, oxygenation is low, accounting for the presence of ostracods such as *Parakrithe* or *Pseudopsammocythere* with a large vestibule characteristic of low oxygen content (Peypouquet, 1977) and *Alocopocythere* with a highly sinuous inner margin (Hoibian, 1984) (Text-fig. 7).

In the delta front intermediary zones the organic matter effect is practically nil and the specific diversity at its maximum. Although at a deficit, oxygenation is normal for these types of equatorial environments where the milieu is precipitating and the polymorph individuals are generally agraded.

The distribution of *Neomonoceratina microreticulata* morphotypes is highly explicit (Text-fig. 8); poorly ornamented individuals prevail in the zones subjected to the deltaic influence. Further off or towards the north, ornamentation increases and becomes the dominant characteristic in the intermediary zones.

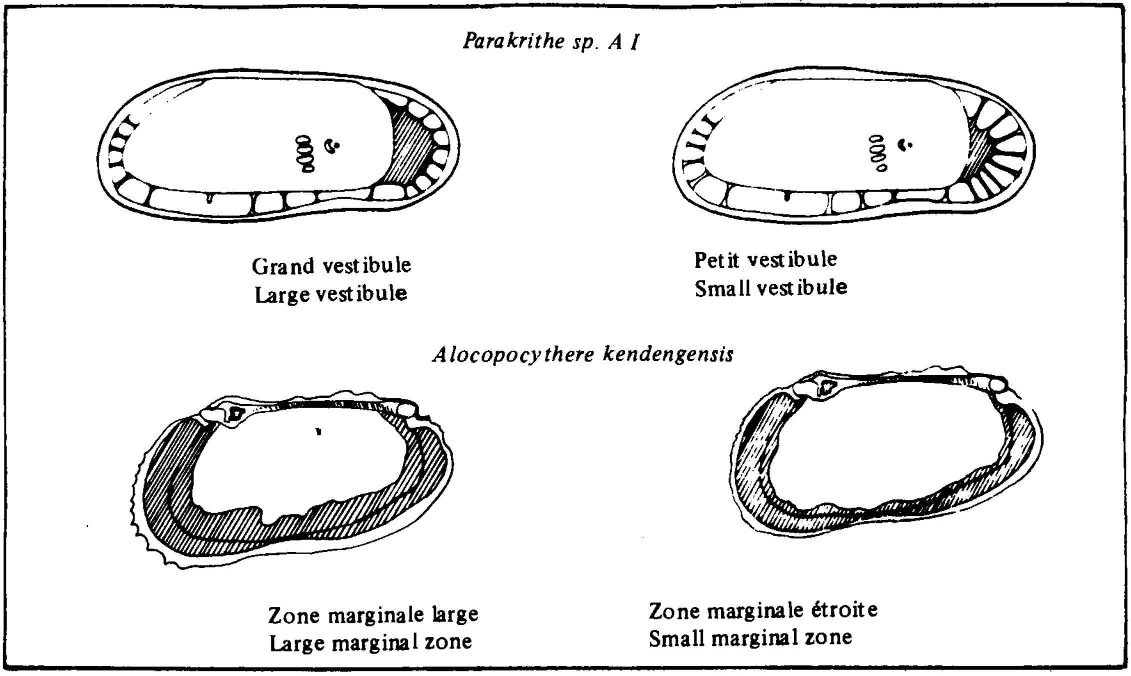
The above phenomenon elicits the irregular distribution of ostracods within the different areas of the delta front (Fig. 9):

— the Muara Badak northern zone corresponds to a small distributary channel in which the organic matter input is low, highly marine and reinforced by littoral outflow to the south (Allen *et al.*, 1979). It is in this area that ostracods reach the inner most part of the delta front (Hoibian, 1984).

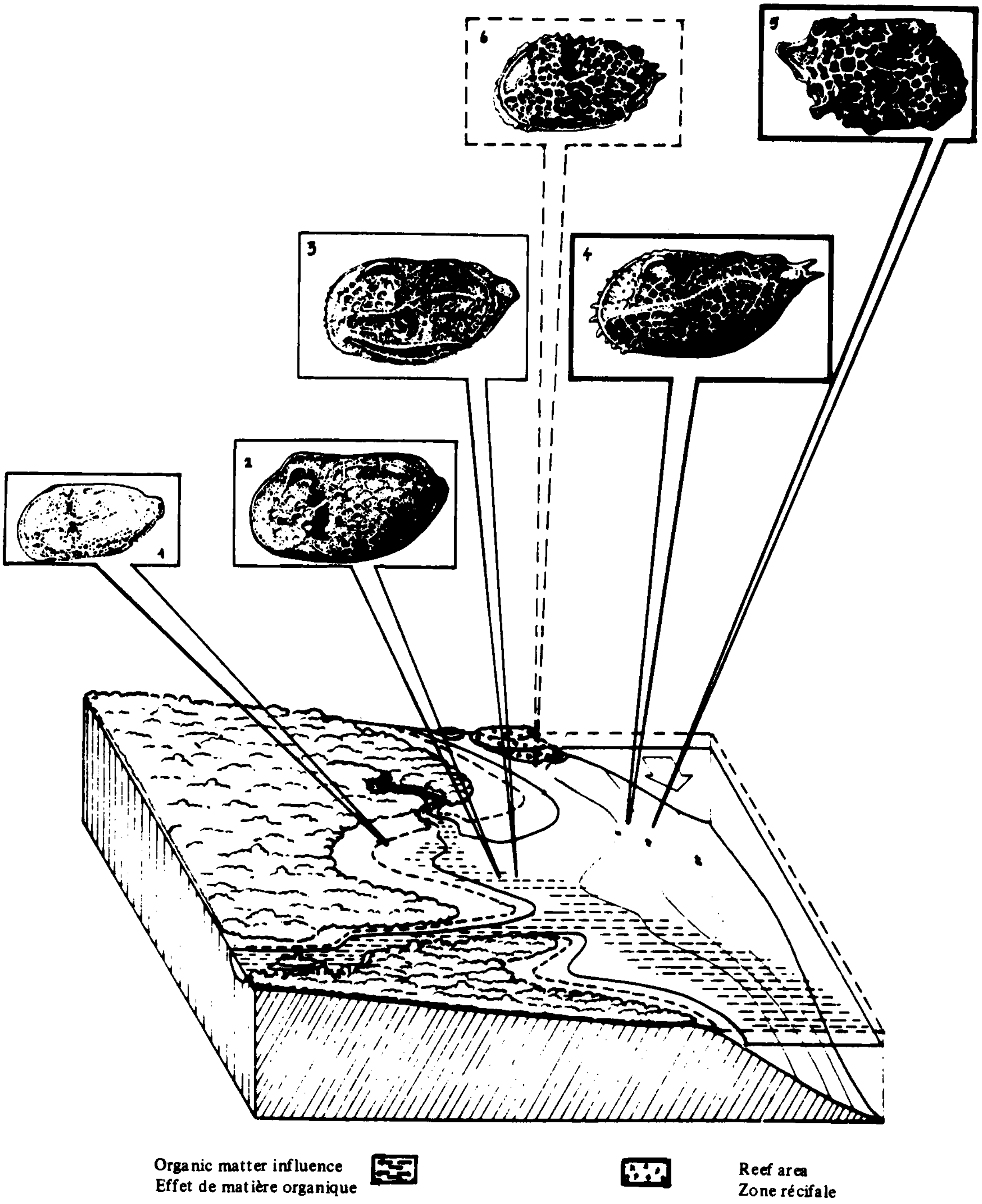
— the Tanjung Bayor central zone showing a vast fauna-free area around and off the interdistributary channels (maximum organic matter effect).

— the Handil Dua southern zone, a major distributary, expelling the faunas to the outer part of the delta front, but maintaining, however, a normal development of the intertidal faunas.

Finally, broadly speaking, the fauna is better ornamented in the north (low input, nearby reefs supplying $CaCO_3$) than elsewhere. This phenomenon was observed in the ostracod fauna of the

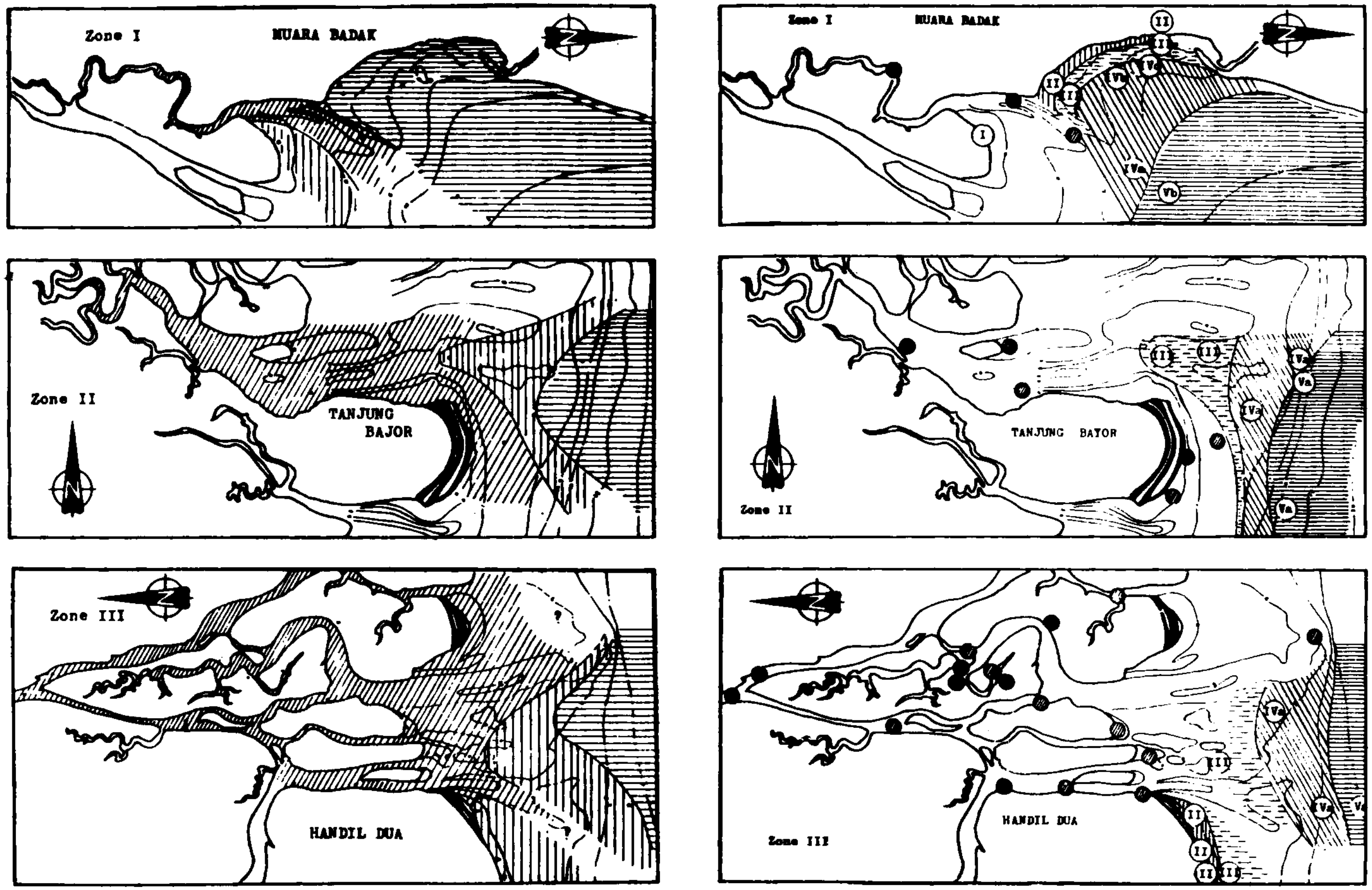


TEXT-FIG. 7—Anterior vestibule of *Parakrithe* sp. and ventral margin of *Alocopocythere kendengensis*.



1 Neomonoceratina cf N. mediterranea
2 Neomonoceratina microreticulata deg.
3 Neomonoceratina microreticulata
4 Neomonoceratina microreticulata agr.
5 Neomonoceratina entomon
6 Neomonoceratina sp. A

TEXT-FIG. 8—Distribution of some species and morphotypes of *Neomonoceratina microreticulata*; effect of organic matter.



Densité de la faune d'ostracode dans le delta de la Mahakam

▨ Pas d'ostracode / no ostracods

▥ Faune pauvre / poor

▤ Faune abondante/ abundant

Distribution des associations d'ostracodes dans les zones étudiées.

I Faune des marais supratidaux / supratidal marsh

II Faune des slikkes / intertidal

III Faune inter à infratidale / inter to infratidal

IV Faune infratidale côtière
- a : embouchures /inlets
- b : zones intermédiaires / intermediary areas

V
- a : embouchures/ inlets
- b : zones intermédiaires / intermediary areas

TEXT-FIG. 9—Ostracod distribution in areas of the Mahakam delta.

delta front. Similar, but less intense, trends were noted for the infralittoral fauna of the prodelta zone (Hoibian, 1984; Carbonel *et al.*, 1985).

CONCLUSION

The dilution impact of the organic matter appears to be a determining factor in the distribution of ostracods within the delta front and prodelta zones. This impact is enhanced by the equatorial environmental conditions which provoke an overproduction of the organic matter associated with vegetation, temperature and rainfall. This statement is supported by a similar distribution pattern observed in the delta of Dique in Columbia.

In general, the organic matter input and its subsequent field of action are mainly dependent upon the location of its production *i.e.* on the size of the deltaic plain. It is for this reason that present-day faunas correspond almost wholly to faunas from inlets of the delta front. Only those faunas from the Muara Badak region are intermediary environment faunas because of the sluggish flow of the river basin. This contrast becomes spectacular at the beginning of transgression during which the marine inflow invades the major part of the deltaic plain (Carbonel *et al.*, 1985).

The ostracod response under these circumstances is particularly instructive for such milieus have already existed in the past implying that a precise reconstruction may not only be fruitful for knowledge but also essential for evident economic reasons.

ACKNOWLEDGEMENTS

Thanks are due to the MISEDOR group who made it possible to carry out this study. We are also grateful to J. P. Peypouquet for his criticisms and suggestions for improvement of the manuscript and to D. Morel for her valuable assistance in the translation of the text.

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DISCUSSION

Keyser: I am surprised that in such a highly productive area there should be no ostracods at all. Could this be due to the sampling methods?

Carbonel: There are two reasons for the absence of fauna in the highly productive environments in the Mahakam area: (1) The pH of the Mahakam river is 5; only *Cytherissa lacustris* can live and moult in such conditions (experimental conditions). In some supratidal samples, we find "association 1" *Cyprideis* sp., see paper), but waters of this environment are rain waters or phreatic waters with a pH of not less than 6. However, this fauna is poor. (2) In infratidal samples with brackish (meso-polyhaline) waters, the pH is about 5–6, but O_2 is very poor (due to degradation of organic matter and stagnation) in tidal channels (interdistributary areas). Currents are too strong in distributary areas. In euhaline waters, pH increases and oxygenation is sufficient (but weak) for the development of an ostracod fauna (external delta front area). The organic matter is already in part consumed and bacterial activity decreased.

Variation of *Pistocythereis* and *Keijella* Species in Gamagyang Bay, South Coast of Korea

KATSUMI ABE AND KAE-LIM CHOE
University of Tokyo, Japan and Korea Institute of Energy and Resources, Korea

ABSTRACT

Gamagyang Bay is located on the southern border of the Korean Peninsula. It is a geographically half-closed shallow embayment with a ria-type coastal topography, which provides a variety of environments for ostracod habitation. Among the ostracod species, *Pistocythereis bradyi, P. bradyformis* and two members of the *Keijella bisanensis* species group are dominant. Although all these species crawl on the muddy bottom surface in a similar way, their main distribution ranges are limited to either the inner or the outer half of the bay. Each of the four species was recognised as having two distinct morphs within the species. Each morph has its own pattern of geographical distribution which is probably controlled by environmental factors or by the origin and history of migration of the species into Gamagyang Bay. Variation in *P. bradyi, P. bradyformis* and *K. bisanensis* occurs in the features of the mural elements, the continuity of the ventral ridge and the H/L ratio of the carapace, respectively.

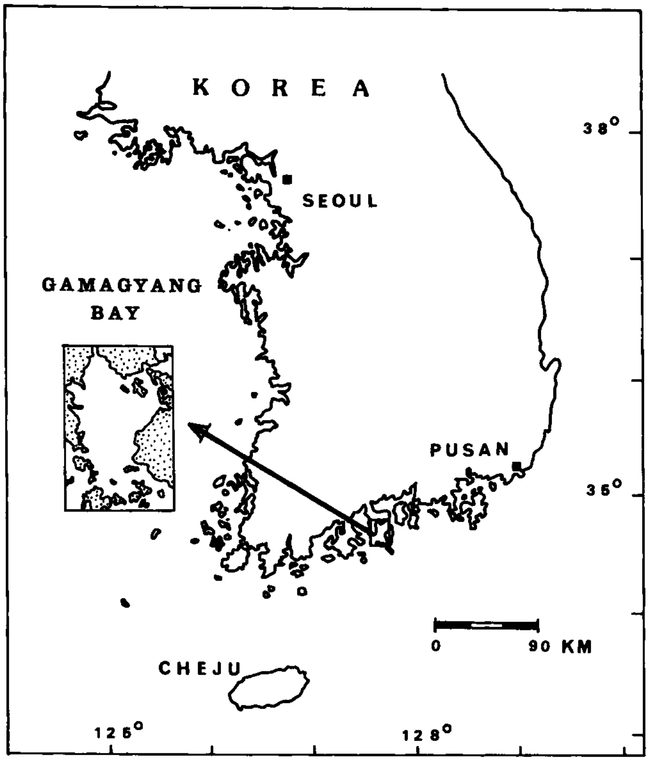
INTRODUCTION

Most ostracods are known to have a considerable spectrum of intraspecific variation of carapace morphology. The origin, and thus the biological meaning of such variation, however, may be completely different in each case, and some of them may represent true polymorphism. In Gamagyang Bay, four species of two genera show similar kinds of morphological variation though the variation must have developed independently in each species. This study deals with species of *Pistocythereis* and *Keijella.* [For the taxonomy of *Keijella,* see Abe (1985) in this volume.]

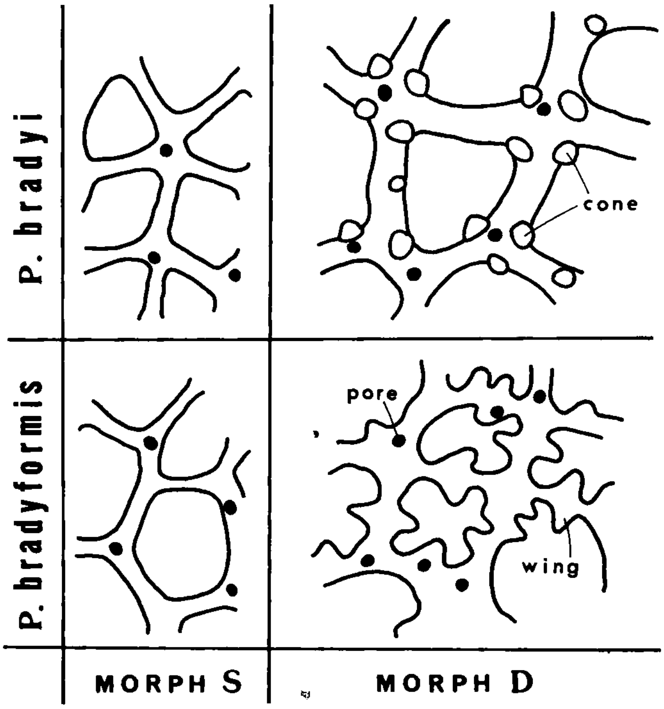
Gamagyang Bay is situated at the southern end of the Korean Peninsula (Text-fig. 1). The physiography and other information on bottom sediments, depth, pH, current etc. was given in detail by Chough (1983). The ostracod fauna of the area was studied by Choe (1985).

VARIATION IN SPECIES OF *Pistocythereis*

The genus *Pistocythereis* from Gamagyang Bay contains two species, *P. bradyi* and *P. bradyformis.* The species differ in their distributional range within Gamagyang Bay. *P. bradyi* occurs over the whole area, but *P. bradyformis* is limited to the outer half of the bay. The two species differ in the presence of anterior and ventral ridges. Apart from this species diagnosis, two forms are



TEXT-FIG. 1—Location of Gamagyang Bay.



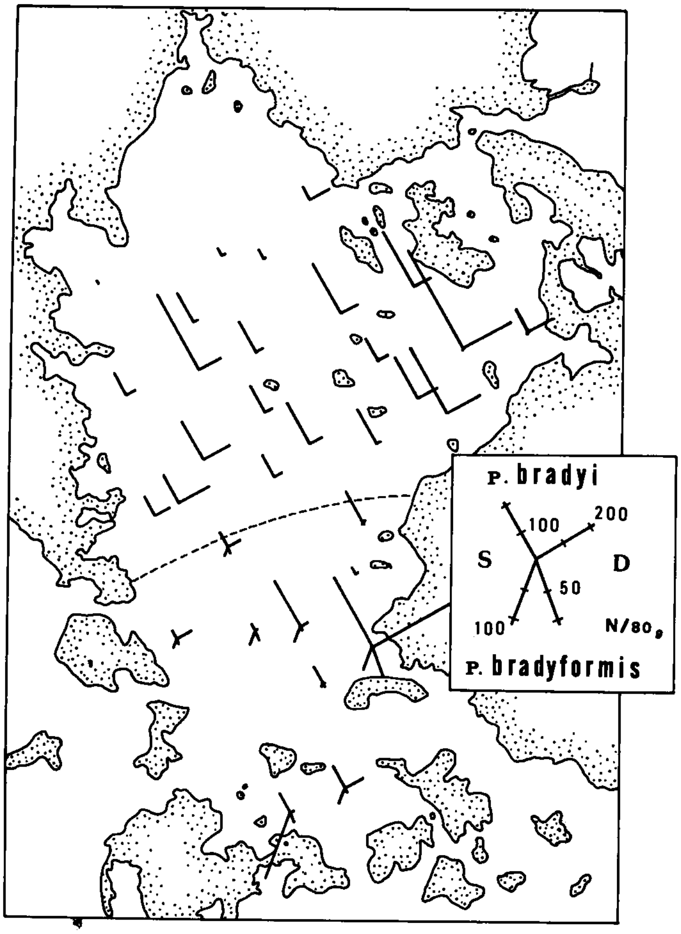
TEXT-FIG. 2—Features of the mural elements of *P. bradyi* and *P. bradyformis*. In both species two morphs are defined by the presence/absence of the additional ornamentation on the top surface of the muri.

recognized within each species based on surface ornamentation of the carapace. These forms are recognizable in both males and females of the adult population and can be traced back to adult-2 juveniles in *P. bradyi,* and back to the adult-3 stage in *P. bradyformis* (juveniles younger than adult-3 were not collected in this area).

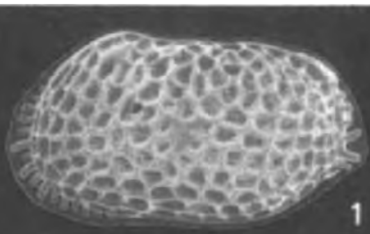
The difference between the two forms in both species lies in the shape of the top part of the muri. One form has a simple murus, the other a decorative murus with additional ornamentation. In *P. bradyi* the additional ornamentation consists of a large number of small cones projecting normally from the summit of the muri. In *P. bradyformis,* on the contrary, the additional ornamentation consists of wings stretching over the fossae. We call the form with the simple muri "morph S (simple)" and the form with additional ornamentation on the muri "morph D (decorated) (Text-fig. 2).

Text-figure 3 shows the distribution pattern of these two morphs in Gamagyang Bay. There seems to be no definite difference in the distribution patterns of the two morphs of *P. bradyi.* There is also no correspondence between their distribution pattern and important environmental factors such as temperature and salinity.

As for *P. bradyformis* all we can do is to present the distributional data at hand because of the small sample size. Moreover, it is possible that the two morphs are in fact two different species.



TEXT-FIG. 3—Distribution pattern of the four morphs of *P. bradyi* and *P. bradyformis* in Gamagyang Bay. *P. bradyformis* is restricted to the outer half of the bay.



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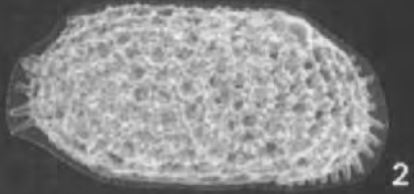

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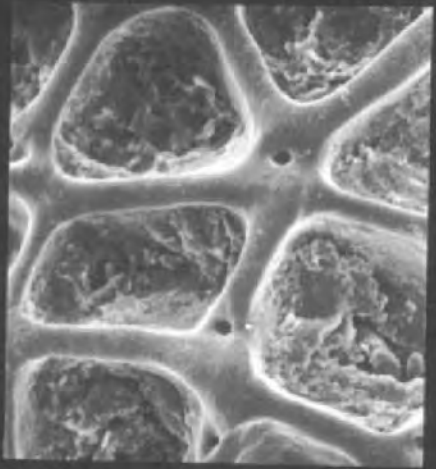

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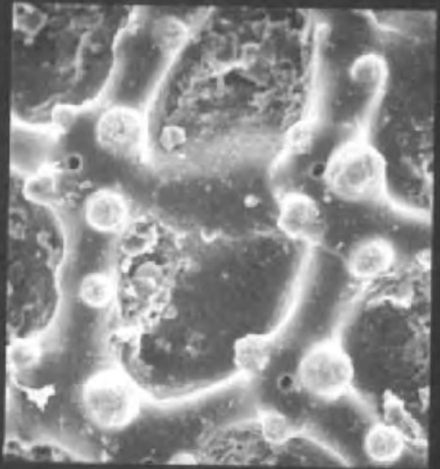

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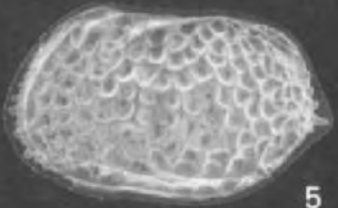

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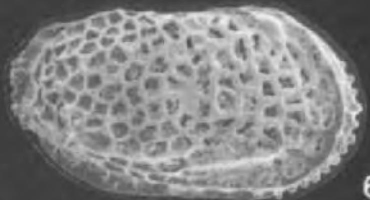

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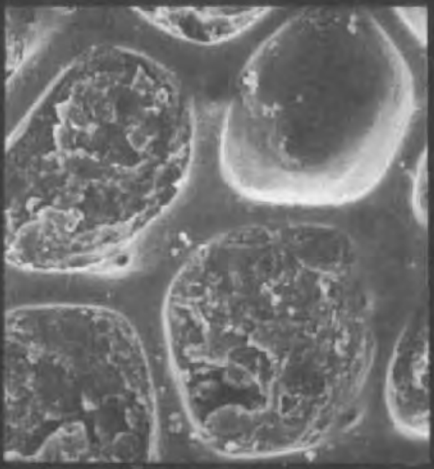

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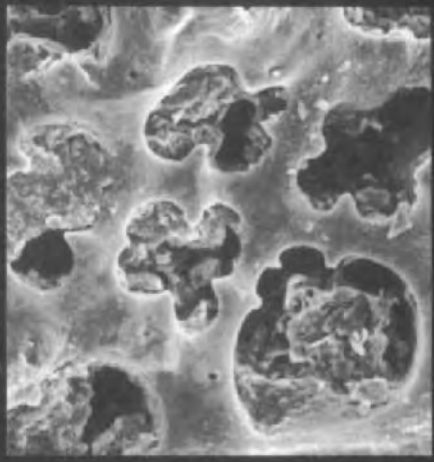

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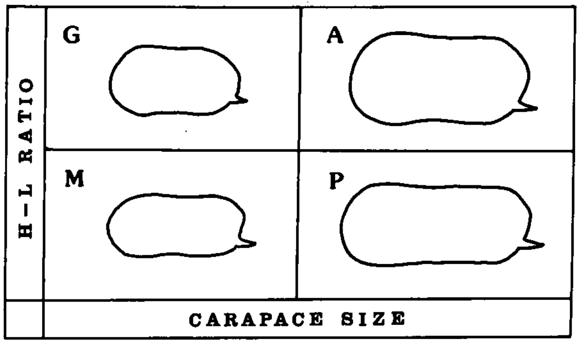
VARIATION IN SPECIES OF *Keijella*

As Abe discusses in this volume, the *K. bisanensis* species group from the East Asian region consists of four different forms. They can be separated on the basis of size and the H/L ratio of the carapace (Text-fig. 4). Abe concludes that the two groups defined by carapace size should be considered different species. In these two species, two forms can be distinguished by their H/L ratio.

Three of these four forms are present in Gamagyang Bay. Text-figures shows their distribution pattern. Distribution patterns of the two forms (form A and form P) belonging to the same species are slightly, but significantly different.



TEXT-FIG. 4—Classification of *K. bisanensis* species group into four forms.

BIOLOGICAL SIGNIFICANCE AND PERSPECTIVES OF THE VARIATIONS

The main habitat of *P. bradyformis* is restricted to the outer half of the bay. Habitat segregation is stricter between the two species of *Keijella*. In each species of these two genera, two different forms have been recognized in addition to sexual dimorphism. The speciating process or the origin of two *full species* can be discussed only in a broader context based on data from a much larger region (*e.g.* Asia). However, it may be possible to attribute the phenotypic *variation within a species* either to genetic polymorphism or ecophenotype because the two forms in each species are almost sympatric.

Morphological variation of *P. bradyi* and *P. bradyformis* is similar in that it is based on whether the tops of the muri are simple or decorated. However their biological significance may be quite different. Small sub-conical projections on the muri of *P. bradyi* are well developed around the pores of sensory hairs which are situated only at the junction of the muri and they are naturally assumed to affect the function of the sensory organ, perhaps by protecting the hair or preventing intrusion by foreign matter from outside. On the other hand, it is difficult to see how the additional ornamentation can affect the sensory hair in the case of *P. bradyformis,* because the decoration

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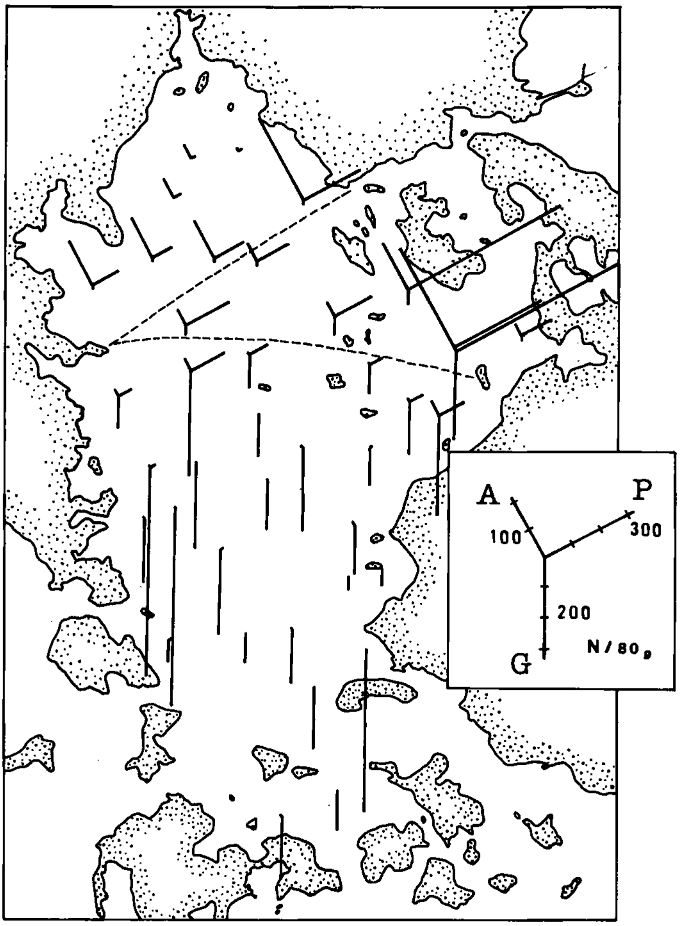
PLATE 1—Figs. 1, 3. Morph S of *Pistocythereis bradyi.* 1. Left valve of adult female, ×50; 3. Simple muri, ×540.

Figs. 2, 4. Morph D of *Pistocythereis bradyi.* 2. Right valve of adult male, ×50; 4. Decorative muri, ×540.

Figs. 5, 7, Morph S of *Pistocythereis bradyformis.* 5. Left valve of adult female, ×50; 7. Simple muri, ×540.

Figs. 6, 8, Morph D of *Pistocythereis bradyformis.* 6. Right valve of adult male, ×50; 8. Decorative muri, ×540.



TEXT-FIG. 5—Distribution pattern of form A, form P and form G in Gamagyang Bay. Form A is dominant in the northwestern part, form P in the northeastern part and form G is almost restricted to the southern half of the bay.

consists of just a wing stretching out to cover the fossae. Secondary ornamentation of the muri hanging over the fossae is often observed in subtropical and tropical species. Thus, this kind of additional ornament may be temperature-dependent. If the developmental degree of such mural decoration depends only on a physical factor such as temperature, and the decoration itself has no biological meaning and is thus neutral for natural selection, then the murus might easily change its morphology innately.

Variation of *Keijella* species concerning the H/L ratio of the carapace produces no effect upon the number and the distributional pattern of the reticules and thus the epidermal cells (*cf.* Abe, 1983; Okada, 1981). In the group with the smaller value of H/L the elongation is remarkable, particularly in the posterior half of the carapace. Since even in this group the variation is not so striking in juveniles, but is extremely remarkable in adult males, this kind of variation might be related to the reproductive behaviour and sexual selection. What factor controls the distributional range of the two forms as shown in Text-fig. 5? Form P occurs more abundantly in the northeastern part of the bay where the tidal currents flow from the outer sea and form A occurs more abundantly in the very calm environment of the northwestern part. Why then is form P not found in the outer half of the bay? We should investigate the history of migration of these species and forms into Gamagyang Bay.

In conclusion, several kinds of phenotypic variation have been recognized in the ostracods from Gamagyang Bay. The southern coast of the Korean Peninsula faces the Kuroshio Current and is characterised by numerous post-glacial embayments and nearshore islands forming a typical ria-type coast. Thus the sea of this area provides a variety of environments for ostracod habitation. It is likely, therefore, that many ostracod species have developed morphological variations and that such variations have been easily maintained within a species. Study of the morphological variation in this region dealing not only with the carapaces, but also with the inner body will greatly contribute to the understanding of the biological meaning of ostracod variation.

ACKNOWLEDGEMENTS

We thank Emeritus Professor Tetsuro Hanai, Professor Itaru Hayami and our other colleagues at the University of Tokyo for their discussion. Professor Sung Kwun Chough of Seoul National University kindly provided the bottom samples for this work. We are indebted to Dr. Paul M. Frydl for reading the manuscript.

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DISCUSSION

Schweitzer: I think that you should show the statistical analyses of shape (H/L) and size (H/L). We need to see the distribution of these values in order to assess the dichotomy that you described. Size ought not to be characterized by one of H or L if shape is characterized by H/L; doing so introduces spurious correlation to your study. Lohmann's eigenshape analysis of microfossils, a general morphometric procedure for describing changes in form (*Mathematical Geology,* 1983) might help such an analysis.

Reyment: With respect to your observations on the assumedly discrete variational states of the muri (decorated and simple), I should like to mention that a similar condition occurs in *intrapopulational* samples of *Buntonia olokundudui* (Recent) from the Niger Delta. With respect to posterior elongation of the carapace, a study by Gilchrist (1960) on *Artemia salina* may be of comparative significance with respect to the quantitative aspects. I think you might be advised to advance beyond the use of length/height ratios (which obscure the effects of differential growth) and contemplate utilizing some established multivariate statistical technique. In the present examples, the posterior distortion in males, on passing to the adult stage of growth, is doubtless liable to render the L/H ratio unfit as a reference. Moreover, any variational measure based on such a ratio will underestimate the true variance if a covariance term is not included.

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To See and Not to Be Seen:
The Evolutionary Problems
of the Ostracoda Xestoleberididae

GIOACCHINO BONADUCE AND DAN. L. DANIELOPOL
Stazione Zoologica, Naples, Italy and Limnologisches Institut, Mondsee, Austria

ABSTRACT

The ocular structures of Xestoleberididae play an important role in the perception and delineation of a "useful" microenvironment in the case of ostracod dwellers that inhabit the aquatic photic zone. In many cases, the colour pattern of the carapace helps the ostracosd to pass unnoticed by predators.

We describe the various types of ocular structures recognized in the carapaces of Xestoleberididae. Several of the interstitial and bathyal Xestoleberididae we have studied display reduced dioptric structures and/or "*Xestoleberis* spots" on the carapace. We have tried to reconstruct some of their evolutionary pathways.

The limits of the usage of ocular structures as palaeoecological indicators for bathymetric and habitat reconstructions are emphasized. Comparisons with another ostracod group, the freshwater Notodromadinae (Cyprididae), are presented in order to stress the convergence of the evolution of the ocular structures within the podocopid Ostracoda.

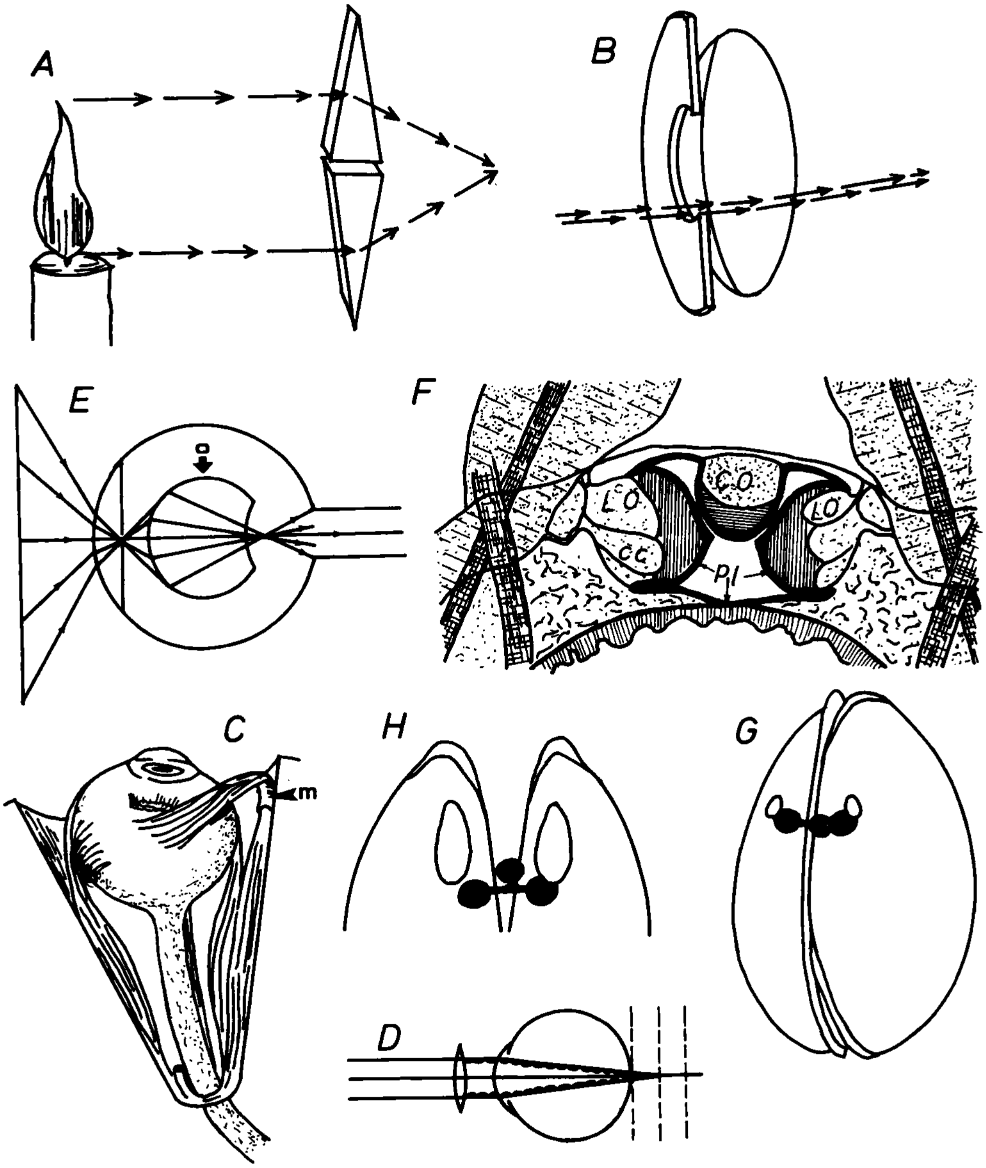
We also describe the Xestoleberididae new genus *Platyleberis* and *Xestoleberis prognata* n. sp.

INTRODUCTION

The Ecology of Vision, an "Eternal" Problem

The eye is one of the most fascinating organs that animals have been able to produce. Above all, it is functionally very important as an integrative system which allows an organism to delineate the microcosm within which it lives. Any improvement in visual capabilities allows an animal to enlarge the boundaries of its microcosm (the cognitive type of adaptation discussed by Piaget, 1976). The behavioural adaptation of animals, according to this author, consists in a continuous structuring of the environment within which the animal lives. The importance of vision for an animal,'has also been discussed in the review of Salvini-Plaven and Mayr (1977). These authors showed that photoreceptors evolved independently in more than 40 phyletic lines.

The anatomy of the human eye and its visual capabilities has fascinated mankind since ancient times (for a review see Pierantoni, 1981). Some of the most famous philosophers, scientists and artists have intensively investigated questions pertaining to vision, *e.g.* Pythagoras, Euclid, Galen, Leonardo da Vinci, Kepler, Descartes etc. The structure and physiology of small invertebrates became an object of study only in the last decades. Based on some of these latter developments,



TEXT-FIG. 1—A. Schematic principle of light diffraction through a double prism (lens). Redrawn after Gregory, 1966. B. Focusing of the iris, Redrawn after Gregory, 1966. C. The human eye with the schematic system of the ocular muscles and ligament. Redrawn after Gregory, 1966. D. The principle of focusing of a correcting additional lens. Redrawn after Weymouth, 1963. E. Scheme of the eye function, following Leonardo da Vinci. Redrawn after Kemp, 1981. F. Structure of the median eye of *Cypris pubera* (horizontal section). Schematic drawing from Novikoff, 1908, redrawn after Hartmann, 1967. (Lo–lateral ocellus; Co–central ocellus; cc–corneal (lens) cell; pl–pigment layer). G, H. Carapace lenses and median eye in *Notodromas monacha.* G:♀; H:♂. Redrawn after Fox, 1966.

Salvini-Plaven and Mayr (1977) tried to reconstruct the major pathways of the evolution of photoreceptors and eyes.

Three problems concerning vision have fascinated mankind: how we perceive objects, how images form and how visual experience is further transmitted. These problems mainly represent the domain of human anatomy, physiology and psychology (for this last domain see Gregory, 1966). Zoologists and ecologists in modern times are faced more and more with similar problems (*e.g.* see the discussion on copepod perception, cognition and adaptation in Marcotte, 1983).

Animals are not faced only with the problems of what they see but also with the problem that other animals see them and can prey on them. Many organisms have developed special shapes and colour patterns which help them to become better integrated in a three-dimensional environment that is biologically and physiologically structured. In fact, colour patterns help them pass unobserved by predators. Man has been faced with similar problems and during his cultural evolution we can see the development of a tremendous diversity of colours and shape patterns, most of which display a sense of order. We present here a description and interpretation of the ocular structures of ostracodes and in a later paper the colour patterns of the Xestoleberididae which represent an aspect of the general problem which has interested mankind for more than two thousand years.

THE OSTRACODA XESTOLEBERIDIDAE SARS, 1928

General Information

The Xestoleberididae are ostracods which live in marine and brackish waters. Hartmann (1975) noted that this family is a very diversified cytherid group, represented by seven genera and about 200 species, more than half of which are known only as fossils. Xestoleberidids diversified during the last hundred m.y. (*e.g.* during the Cenomanian and Senonian in the Cretaceous and later on during the Tertiary and Quaternary; for the Mesozoic Xestoleberididae, see Whatley and Stephens, 1976).

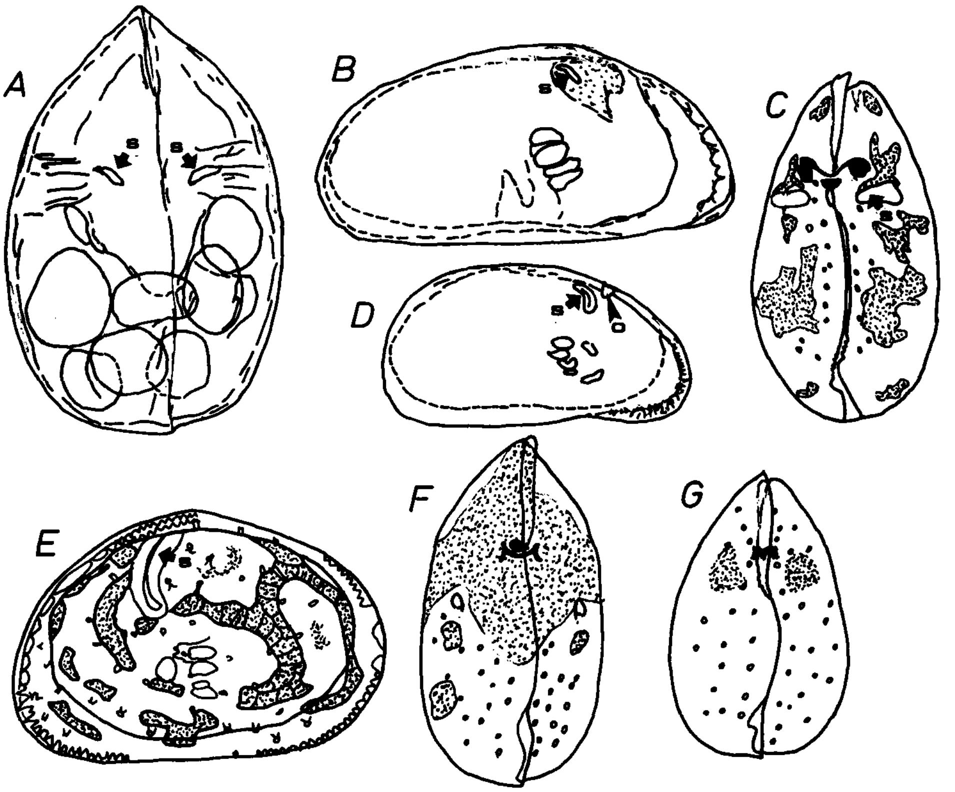
The Xestoleberididae are creeping crustaceans which move slowly on or into the substrate. Most of the species live in shallow marine environments in the photic habitats of the littoral and sublittoral zones, on sandy substrates or on various algae. Some Xestoleberidids colonise interstitial habitats in coarse-sandy substrates and a few species have adapted to living at great depths (*e.g.* the bathyal zone ranging from 600 m to more than 1300 m in the Mediterranean basin). Other species are commensals on Crustacean Malacostraca as *Aspidoconcha limnoriae* which lives fixed on the wood boring isopod *Limnoria lignorum* (McKenzie, 1972).

As a group the Xestoleberididae is easy to identify using several morphological characters: the ocular structures are well developed, the median eye has 3 separate ocelli (Text-figs. 2C, F, G). A semilunar "imprint" called the "*Xestoleberis*-spot" (*e.g.* Text-figs. 2C, D) occurs behind the lateral ocellus on the valve.

Many Xestoleberididae which live in photic habitats have developed dioptric structures and "*Xestoleberis*-spots" on the carapace. They also display various epidermal pigmented patterns which alow the animal to pass unnoticed by predators (Text-figs. 2C, E, F, G).

Systematics and Material

This chapter deals with the description of *Platyleberis* n. genus and of *Xestoleberis prognata* n. sp.; for those species sufficiently described, 3 groups of the *Xestoleberis* are proposed in relation to their morphological affinities. The chapter also furnishes information on the origin of the Xestoleberididae material utilized. The data on the material used are reported in Table 1.



TEXT-FIG. 2—A, B. *Xestoleberis delamarei* ♀. A. Carapace in dorsal view with *Xestoleberis*-spots (s). B. Right value in external view with *Xestoleberis*-spot and surrounding milky area. C. *Xestoleberis decipiens* ♀. Carapace in dorsal view with median eye, *X*-spot (s) and colour-patterns. D. *Xestoleberis dispar* ♀. Right valve with transparent lens (o) and *X*.-spot (s). E. *Xestoleberis communis* ♀. Left valve with *X*.-spot (s) and colour patterns. F. *Xestoleberis plana* ♀: Carapace in dorsal view with median eye and colour patterns. G. *Xestoleberis parva* ♀. Carapace in dorsal view with reduced pigmented areas. (C, E, F, G: Redrawn after Müller, 1894.)

Genus PLATYLEBERIS n. gen.

Etymology.—From greek platys = flat

Type species.—*Microxestoleberis profunda* Breman 1975 (Pl. 1, A–F; Pl. 2. A–D)

Diagnosis.—A genus of the family Xestoleberididae characterised by a small, well-calcified, subrounded or triangular carapace in lateral view, and a completely smooth exterior surface. The size is generally smaller than $500\,\mu m$ in length. The hinge is of a merodont-type (*sensu* Hartmann, 1966) with a well-developed and uncrenulated central bar in the left valve and a smooth and elongated posterior cardinal tooth in the right valve; the anterior tooth is not defined and substituted by a strong long bar within which the posterior extremity steeply protrudes. It shows the presence of a

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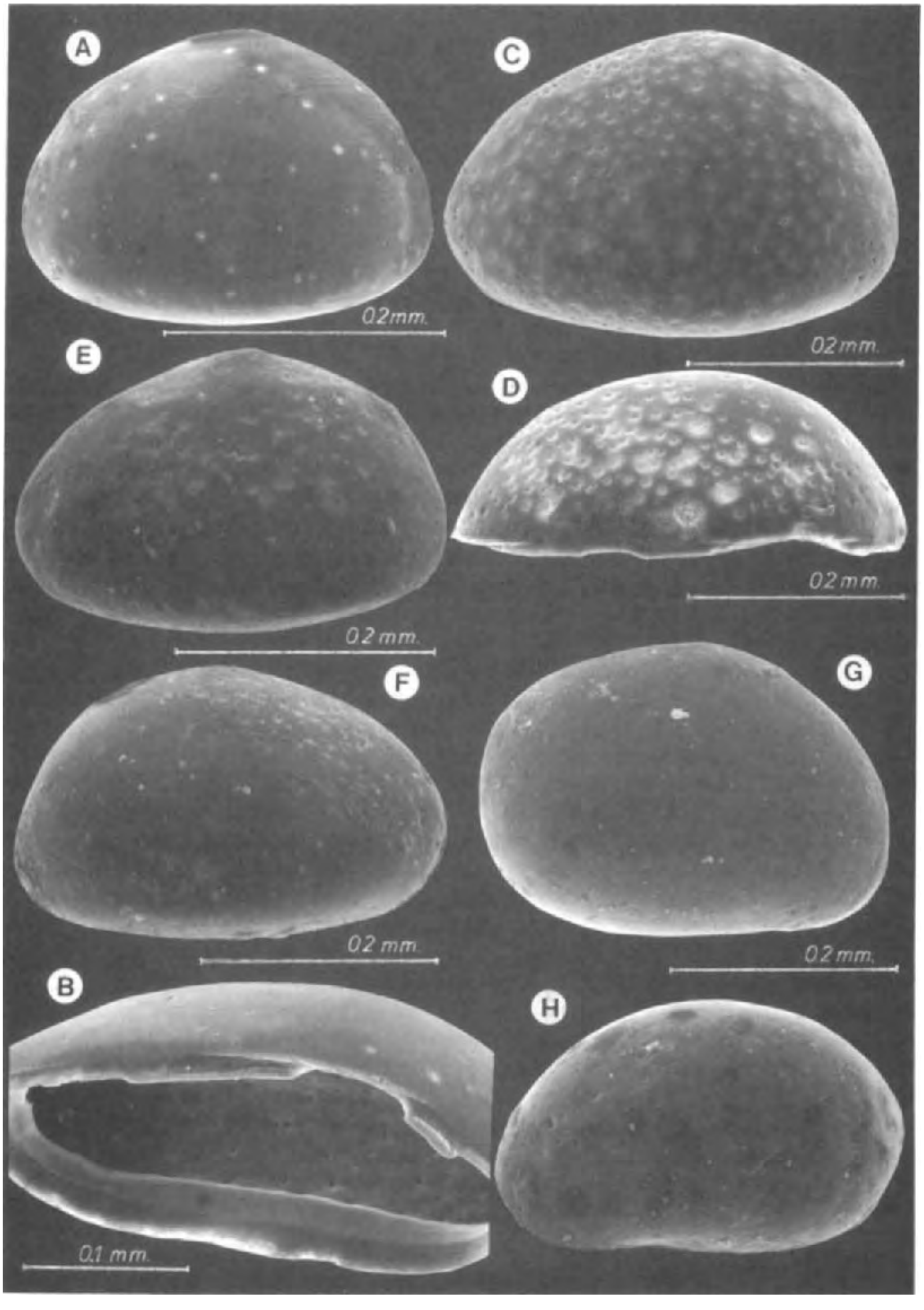
PLATE 1—Figs. A–F. *Platyleberis profunda*. A. LV from outside. Holocene: Alboran Sea Stn. SV–8107. B. Detail of the hinge of the RV. C. LV from outside. Saba Bank Stn. 108. D. RV in dorsal view. Saba Bank: Stn. 108. E. LV from outside–Upper Pliocene: Mount S. Nicola, Stn. 53. F. RV from outside. Upper Pliocene: Mount S. Nicola, Stn. 53. Figs. G. H. *Xestoleberis prognata* n. sp. G. RV from outside. Upper Pliocene: Mount S. Nicola Stn. 53. H. LV from outside (slightly tilted). Upper Pliocene: Mount S. Nicola Stn. 53.


A
C
0.2mm.
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E
D
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G
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H
0.1mm.

TABLE 1—XESTOLEBERIDIDAE AND NOTODROMADINAE MATERIAL.

TAXON	LOCALITY	HABITAT	AGE	REMARKS
Platyleberis n. g.				
P. profunda (Breman)	Mnt. S. Nicola-St 53 (Sicily, Italy)	bathyal (±600–800 m)	Up. Pliocene	deep-sea assemb. (G.B. leg.)
	Alboran Sea-SU8107 (W. Mediterranean)	bathyal (1375 m)	Holocene	deep-sea assemb. (NACHITE leg.)
	Saba Bank–St 108 (Caribbean Sea)	bathyal (720 m)	Recent	deep-sea assemb. (VAN HARTEN leg.)
Microxestoleberis Müller				
M. nana G.W. Müller	Argeles-Banyuls/M (W. Mediterranean)	sublittoral (6–10m) Amphioxus sand	Recent (living)	psammophilous, interstitial assemb. (D.L.D. leg.)
Xestoleberis Sars				
gr. *communis*				
X. communis G.W. Müller	Banyuls/M (W. Mediterranean)	supralittoral, interstitial	Recent (subfossil)	psammophilous, interstitial assemb. (D.L.D. leg.)
	Scario (Policastro bay) (Tyrrhenian Sea, Italy)	littoral (4 m)	Recent (living)	phytal assemb. (D.L.D. leg.)
X. sp. (aff. *X. communis*)	Scario (Policastro bay)	littoral, interstitial (1 m)	Recent (living, subfossil)	phytal, interstitial assemb. (D.L.D. leg.)
X. glabrescens (Reuss)	Steinerbrunn (Lower Austria)	littoral	Mid. Miocene (Badenian)	littoral assemb. (MAHDI leg.)
X. prognata n. sp.	Mnt. S. Nicola-St 53 (Sicily, Italy)	bathyal (±600–800m)	Up. Pliocene	deep-sea assemb. (G.B. leg.)
	El Cuervo (Andalusia Spain)	bathyal (not less than 600 m)	Up. Miocene	deep-sea assemb. (BENSON, in BERGGREN *et al.*, 1976)†
gr. *plana*				
X. plana G.W. Müller	Argeles-Banyuls/M (W. Mediterranean)	sublittoral (6–10m) Amphioxus sand	Recent (living, subfossil)	psammophilous, interstitial assemb. (D.L.D. leg.)
X. dispar G.W. Müller	Banyuls/M	supralittoral, interstitial	Recent (living, subfossil	psammophilous, interstitial assemb. (D.L.D. leg.)
X. parva G.W. Müller	Scario (Policastro bay)	littoral (4m)	Recent (living)	phytal assemb. (D.L.D. leg.)
X. sp. 1 Nascimiento	Cacela (Algarve, Portugal)	littoral	Up. Miocene	littoral assemb. (NASCIMIENTO)
gr. *arcturi*				
X. arcturi arcturi Triebel	Arcturus lake (Power Isl., Galapagos)	littoral (1m) brackish water	Recent (living)	EIBL-EIBESFELDT leg.)
X. arcturi darwini Gottwl.	Academy beach (Santa Cruz Isl., Galapagos)	supralittoral, interstitial	Recent (living)	interstitial assemb. (SCHMIDT leg.)
X. galapagoensis Gottwl.	Tower Isl., Galapagos	supralittoral, interstitial	Recent (living, subfossil ?)	interestitial assemb. (SCHMIDT leg.)
X. delamarei Hartman	Banyuls/M	supralittoral, interstitial	Recent (living)	psammophilous, interstitial assemb. (D.L.D. leg.)
	Scario (Policastro bay)	supralittoral, littoral, interstit.	Recent (living)	*ibid.*
X. xenomys Barb.-G.	Gulf of Taranto -St 134E (Ionian Sea, It.)	littoral, sandy substrate	Recent (subfossil)	(G.B. leg.)

(*Continued*)

TABLE 1—(*Continued*)

TAXON	LOCALITY	HABITAT	AGE	REMARKS
Ornatoleberis Keij				
O. morkhoveni Keij	Balikpapan Bay (Kalimantan, Indonesia)	littoral (5 m)	Recent(?) (subfossil)	KEIJ, 1975†
Foveoleberis Malz				
F. foveolata (Brady)	Seria (N. Borneo)	littoral (26–53m)	Recent subfossil	MALZ, 1980†
F. ymchenzi Malz	S. Maanhan-Pr. 7826 (Taiwan)	littoral	Pliocene	MALZ, 1980†
Notodromas Lilljeborg				
N. monacha Liljbeborg	Neusiedlerssee (Bur genland, Austria)	littoral (1.5 m)	Recent (living)	littoral assemb. (MENDEZ leg.)
N. persica Guerney	*ibid.*	*ibid.*	*ibid.*	*ibid.*

† material not directly examined by G.B. & D.L.D.

well-defined "*X.*-spot" which does not protrude into the valve interiorly. *Platyleberis profunda* (Breman) is the only species so far described which belongs to this new genus.

Occurrence.—Holocene–Recent: bathyal Atlantic Ocean and Mediterranean (Breman, 1975; Nachite, 1984).

Upper Pliocene: Mount S. Nicola (Sicily): Stn. 53 (Bonaduce leg. and det.). Another undescribed species is known from the Early Oligocene of Southern Moravia (Pokorny, 1981 and pers. comm.).

XESTOLEBERIS PROGNATA n. sp.

(Pl. 3, figs. A, B, C; Pl. 1, figs. G, H)

Etymology.—From latin prognatus = descending

Holotype.—A right valve (Pl. 3, fig., A). Upper Pliocene: Mount S. Nicola (Sicily) Stn. 53–B.O.C. (Bonaduce Ostracode Collection): 795.

Paratypes.—2 valves from the same sample. B.O.C. 796.

Description.—The shape of the valves is very similar to that of *X. communis* Müller in lateral view, with an anteriorly obtusely rounded, postero-ventrally upturned and antero-ventrally gently concave left value (Pl. 1, fig. H). The right valve appears less elongated (Pl. 1, fig. G). In dorsal view, the carapace is subacutely rounded anteriorly and very inflated postero-ventrally.

Size.—L = 350–370 μm, H = 250–260 μm.

Affinities.—*Xestoleberis prognata* n. sp. differs from *X. communis* Müller and *X. glabrescens* Reuss due to its smaller size (*X. communis*, L = 600 μm; *X. glabrescens*, L = 600 μm), more upturned postero-ventral margin and peculiar posterior inflation that is best seen in dorsal view.

Environment.—This species has been found at the type-locality associated with numerous species of *Krithe, Henryhowella, Buntonia, Cytheropteron testudo* etc. and the assemblage appears absolutely uncontaminated by shallower fauna. The evaluated minimum palaeodepth corresponds to 600–800 m.

Remarks.—Benson (1976) and Berggren *et al.* (1976) cite *X. prognata* n. sp. as *X. glabrescens* Reuss in an Upper Miocene deep-sea ostracod assemblage from El Cuervo (Span).

THE *Xestoleberis* GROUPS

The *Xestoleberis* species taken into consideration have been classified into three groups on the basis of their morphological features.

1. XESTOLEBERIS COMMUNIS Müller group
(Text-fig. 2 E; Pl. 4, fig. A; Pl. 5, figs. A, B; Pl. 3, figs. D–H)

A *Xestoleberis* group of species, characterised by more or less rounded valves in lateral view (especially the LV). The hinge is hemi- and antimerodont with long, crenulate cardinal teeth. The calcareous lamella shows (*e.g. X. communis*) opaque patches in some species. The "*X*.-spot" is commonly divided into two cells. In the littoral species, the "*X*.-spot" is strongly calcified and protrudes on to the inner side of the calcareous lamella. The ocular dioptric structure is generally plano-convex and sometimes appears delineated by a shallow groove. The anterior part of the selvage in the left valve is widely rounded and does not reach the outer margin.

The second antenna does not show a dimorphic distal claw "Gm". The hemipenis includes a thin conical vas deferens and an ejaculatory tube of intermediate length that is commonly S-shaped. The sclerotized sleeve of the ejaculatory tube is large. (See Müller, 1894, Pl. 25, fig. 32; and Athersuch, 1976, Text-fig. 8).

Species.—X. communis Müller, 1894; *X. rara* Müller, 1894; *X. ventricosa* Müller, 1894; *X. glabrescens* Reuss, 1850, etc.

2. XESTOLEBERIS PLANA Müller group
(Text-fig. 2 D, F, G; Pl. 4, figs. E–G; Pl. 2, figs. E, F; Pl. 3, figs. I, J)

A *Xestoleberis* group of species which ranges between 400 and 700 μm in size and which is characterized by generally elongated valves with a gently concave ventral margin. The "*X*.-spot" is from weakly to well-deveoped but always without a protrusion and consists of only one cell. When present the lenses are plano-concave. The distal part of the central hinge-bar is denticulate. The second antenna does not show a dimorphic distal claw "Gm". The hemipenis (Text-fig. 3 E) includes a large membraneous vas deferens and a long ejaculatory tube that is largely coiled and conically shaped.

Species.—Xestoleberis plana Müller, 1894; *X. dispar* Müller, 1894; *X. plauta* Athersuch, 1976; *X. fuscomaculata* Müller, 1894; *X. parva* Müller, 1894; *X. perula* Athersuch, 1976; *X. pellucida* Müller, 1894; *X.* sp. Nascimiento.

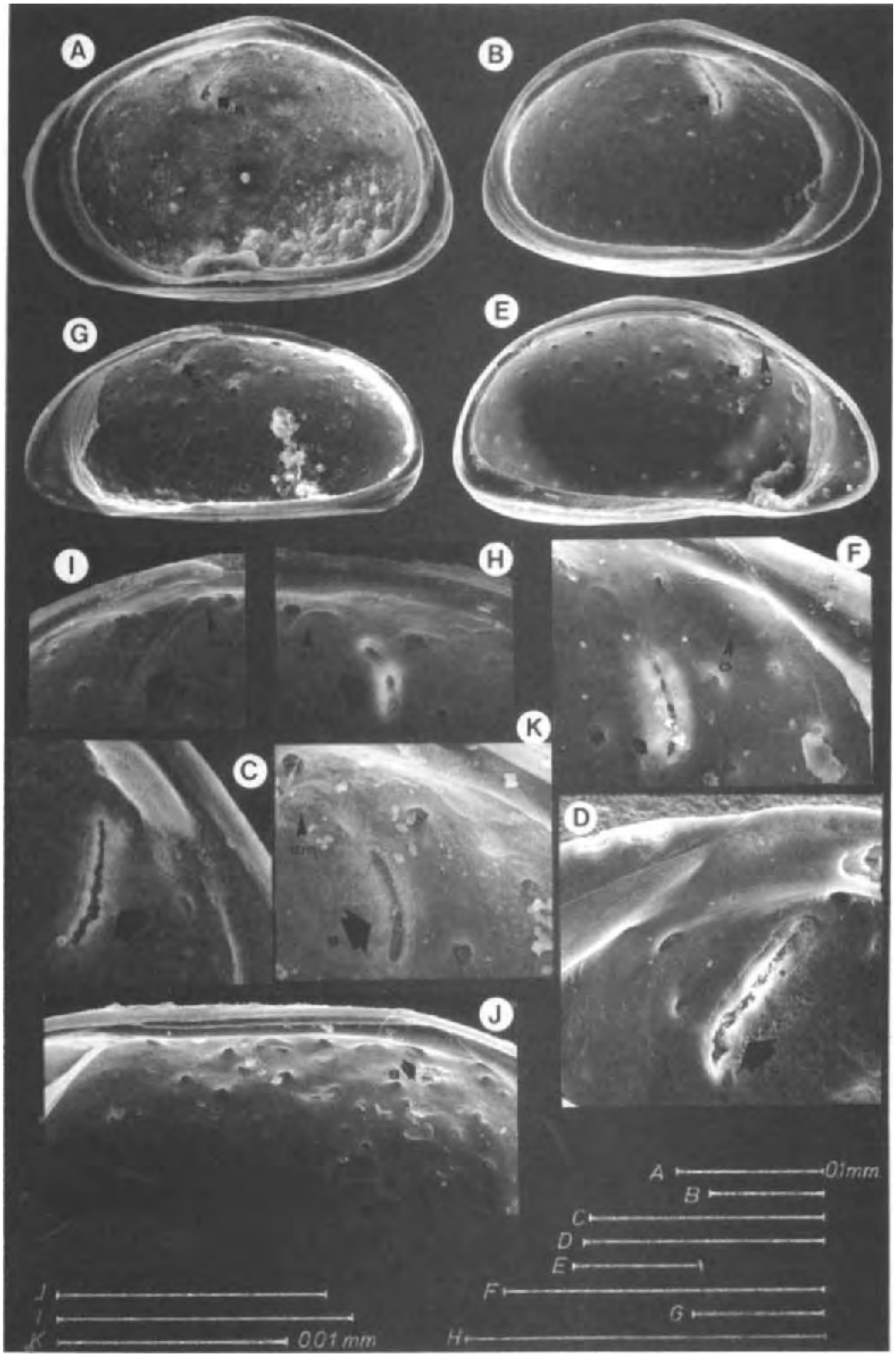
3. XESTOLEBERIS ARCTURI Triebel group
(Text-fig. 2 A, B; Text-fig. 3 A–D; Pl. 4, figs. H, I; Pl. 5, figs. E–J; Pl. 2, figs. G–K)

A *Xestoleberis* group of species characterised by elongated valves with a gently arched dorsal margin. The hinge is of hemimerodont-type with slightly crenulate cardinal teeth. The central hinge-bar appears thin, poorly-developed and smooth. The selvage extends anteriorly to the proximity of the outer margin. The "*X*.-spot" is weakly developed even in surface literal dwellers. The size of the carapace is generally less than 400 μm.

The second antenna (Text-fig. 3 A, B) shows a dimorphic distal claw "Gm": The male claw is strongly pectinate as compared to that of the female.

The hemipenis (Text-fig. 3 C, D) includes a large membranaceous vas deferens and a short ejaculatory tube, that is well sclerotized and commonly L-shaped. The distal lobe "a" of the hemipenis is elongated.

PLATE 2—Figs. A–D. *Platyleberis profunda*. A. RV from inside. Alboran Sea. Stn. SU-8107. B. LV from inside. Upper Pliocene: Mount S. Nicola Stn. 53. C. *X*.-spot of LV from inside of the same specimen of B. D. "*X*.-spot" of RV from inside. Saba Bank (Caribbean Sea) Stn. 108. Figs. E. F. *Xestoleberis dispar*. E. LV from inside. Banyuls/Mer. F. *X*.-spot and ocular lens. Same specimen of E. Figs. G–K. *Xestoleberis delamarei*. G. RV from inside. Banyuls/Mer. H, I. *X*.-spots of RV (I) and LV (H) from inside. Banyuls/Mer. K. *X*.-spot and ocular area of LV from inside. Scario; J. *Microxestoleberis nana*. LV from inside with eye-spot. Argeles. (s = *X*.-spot, o = lens, dm = dorsal muscle scars).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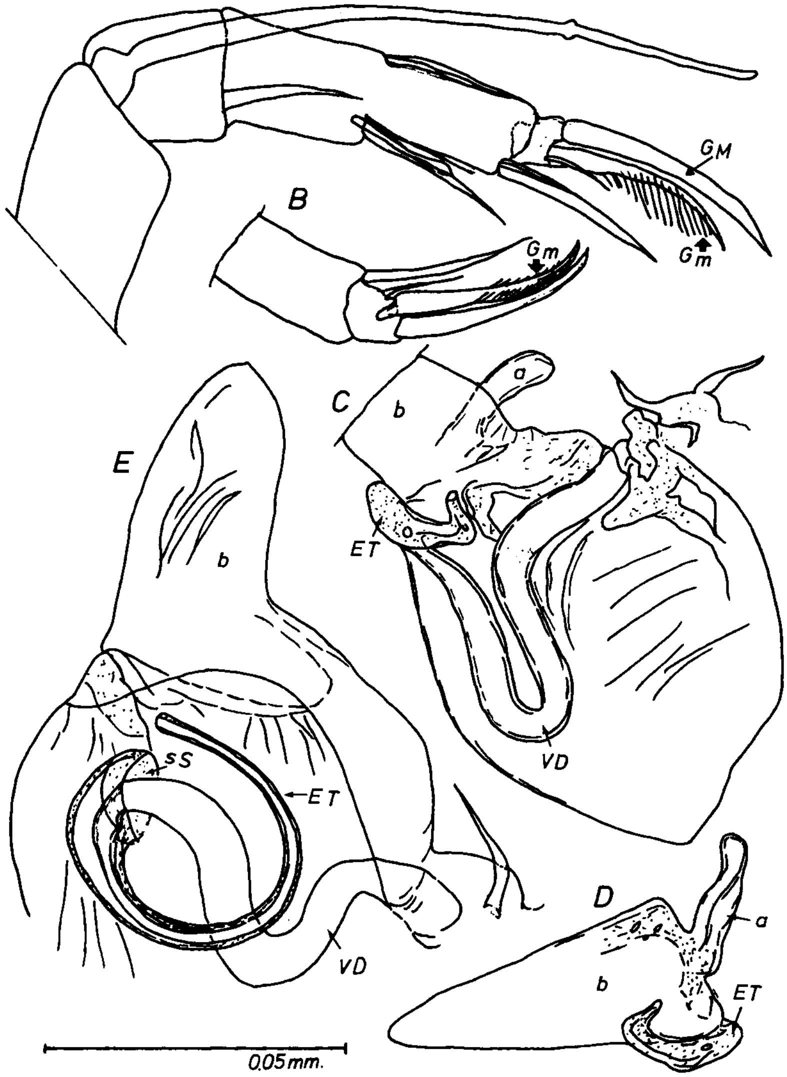
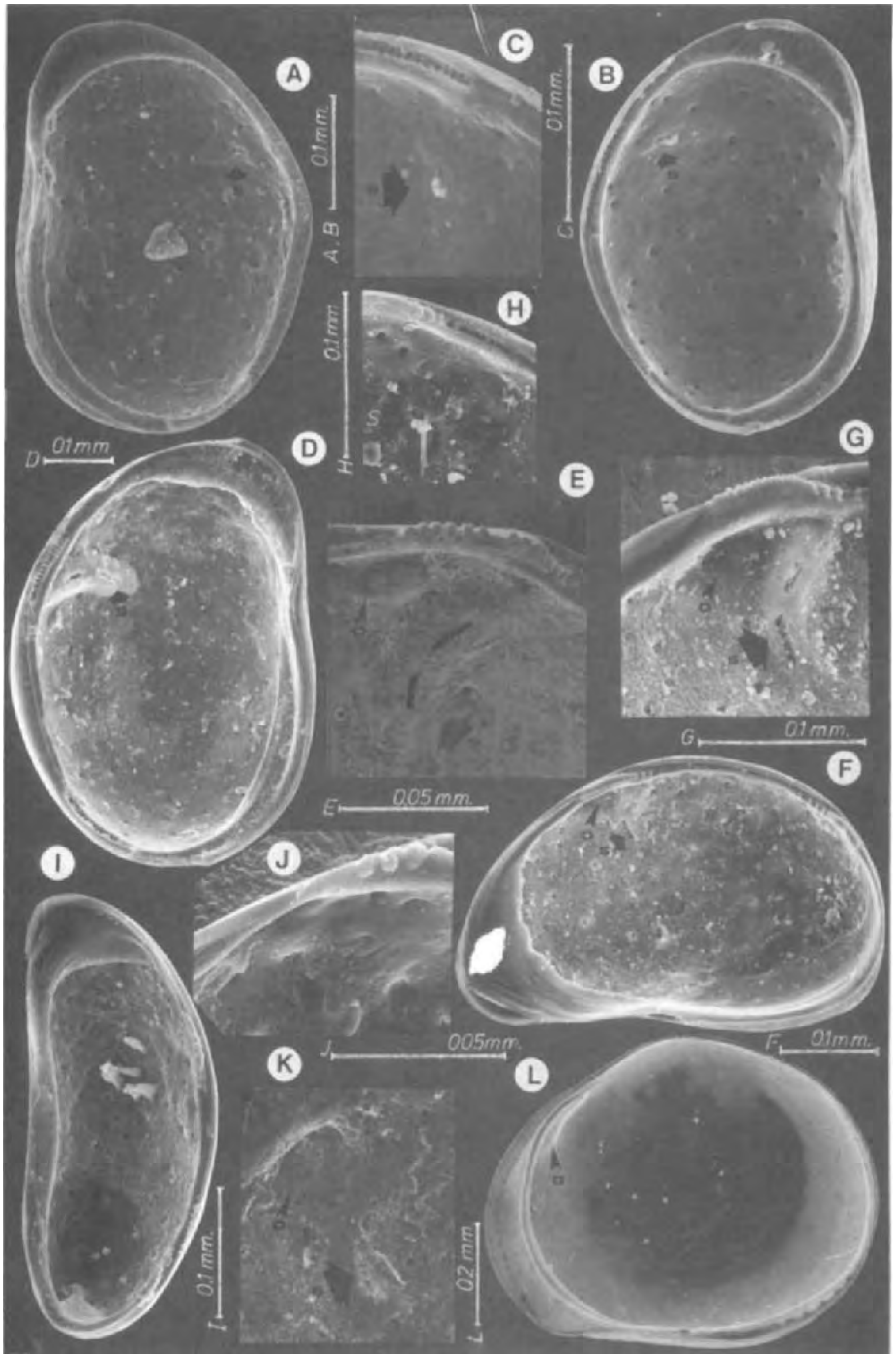


TEXT-FIG. 3—A–D. *Xestoleberis delamarei* (Banyuls/Mer): A. General view of second antenna ♂. B. Detail of the second antenna ♀. C, D. Details of the hemipenis (GM, Gm–distal claws of the antenna; a, b–distal lobes of the hemipenis; VD–vas deferens; ET–ejaculatory tube; sS–sclerotized sleeve). E. *Xestoleberis plana* (Argeles): Hemipenis in general view.

PLATE 3—Figs. A–C. *Xestoleberis prognata* n. sp. A. RV from inside with *X*.-spot. Upper Pliocene: Mount S. Nisola Stn. 53. B. LV from inside with *X*.-spot. Mount S. Nicola Stn. 53. C. Detail of the *X*.-spot area of the LV from inside. Figs. D, E. *Xestoleberis communis*. D. LV from inside with *X*.-spot. Banyuls/Mer. E. *X*.-spot and ocular lens of the RV from inside. Figs. F–H. *Xestoleberis* sp. gr. *communis* (Scario). F. RV from inside with *X*.-spot and ocular lens. G. Detail of the *X*.-spot and ocular lens of RV from inside. H. Detail of *X*.-spot with remnants of tissues in the LV from inside. Figs. I, J. *Xestoleberis parva* ♀ (Scario). I. RV from inside. J. Details of *X*.-spot. Fig. K. *Xestoleberis* sp. 1. Detail of the *X*.-spot and of the ocular lens of the RV from inside. Upper Miocene Cacela (Algarve), Portugal. Fig. L. *Notodromas persica* ♂. RV from inside with detail of the ocular lens. Neue Siedlersee (Austria). (s = *X*.-spot, o = lens).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Species.—*X. arcturi* Triebel, 1956; *X. galapagoensis* Gottwald, 1983; *X. delamarei* Hartmann, 1953; *X. costata* Hartmann, 1953; *X.* ? *xenomys* Barbeito-Gonzalez, 1971.

Genus Microxestoleberis G.W. Müller, 1894

(Pl. 4, figs. C–E; Pl. 2, fig. J)

A Xestoleberidid group characterised by its elongated valves and small shape (less than 400 μm). The hinge is adont and consists in a thin uncrenulated central bar in the left valve. The anterior marginal area appears large and with a reduced number of simple marginal pore-canals. The inner calcareous lamella is well developed.

The second antenna shows a dimorphic claw "Gm". The male claw is strongly sclerotized and pectinate as compared with that of the female which appears as a thin seta (see Müller, 1894, Pl. 39, figs. 45, 46).

Species.—Microxestoleberis nana Müller, 1894.

The Ocular Structures

The Median Eye

Most of the Xestoleberididae have a median, nauplius, eye formed by three ocelli (two lateral and a median one). Their main structure follows the model described by Nowikoff (1908) (see data in Hartmann, 1967; Andersson and Nilsson, 1981 and here Text-fig. 1 F). Basically, an ocellus is formed by a pair of corneal (lens) cells, several retinal cells, a refractive tapetum and a dark pigmented cup. The axons of the retinal cells form an efferent nerve.

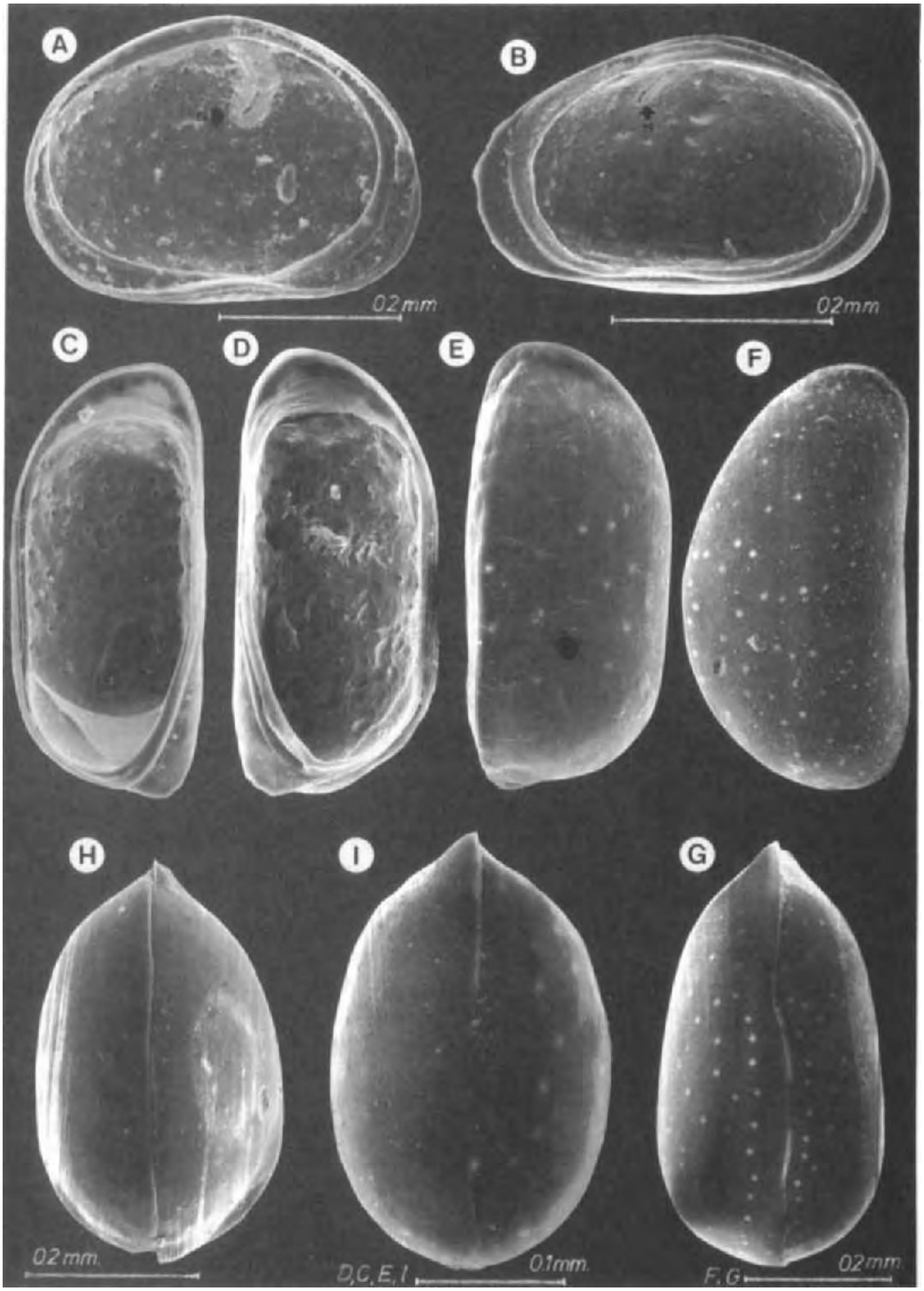
Species such as *Xestoleberis parva* (Text-fig. 2 G) have three ocelli grouped together but most of the Xestoleberididae species have lateral ocelli that are widely separated from the median one (*e.g. Xestoleberis decipiens,* Text-fig. 2 C; *X. plana,* Text-fig. 2 F).

Theoretically, with one median and two widely spaced laterally oriented ocelli the Xestoleberidids are able to see simultaneously a larger area than species with compact median eyes.

The Ocular Structures of the Carapace, Introductory Notes

We have already mentioned that many Xestoleberididae species display a lens on the carapace in front of the lateral eye, which is more or less well-defined as compared with the surrounding area. This lens is located within the procuticle of the outer calcified lamella and, consequently, the light rays are difracted when crossing the more dense medium and concentrated on the retinal cells. Theoretically, an ostracod biconvex lens such as one can find in some Xestoleberididae (*e.g.* species of the genus *Foveoleberis,* see further details) can be compared to a double prism (see Pl. 3, figs. F, G). The lens is surrounded by a clear ring which may play the role of a diaphragm. Theoretically, this helps once again to focus the light rays within the lateral ocellus. Also, at low magnification, the lenses of many Xestolberididae are visible as a translucent spot surrounded by an opaque milky calcitic area (*e.g.* Text-fig. 2 D). We believe that the crystals within the lens area are more tightly packed and have a position parallel to the surface of the valve, as compared with the surrounding area where the crystals should be more loosely packed and inner micro-voids should form. A similar situation can be observed in valves corroded by chemical and microbial

Plate 4—Fig. A. *Xestoleberis communis.* Left valve from inside (Banyuls/Mer). Fig. B. *Platyleberis profunda.* Right valve from inside. Upper Pliocene. Mount S. Nicola. Sample 53 (Sicily). Figs. C–E. *Microxestoleberis nana* ♀. C. LV from inside. D. RV from inside. E. LV from outside (Argeles). Figs. F, G. *Xestoleberis dispar* ♀. F. RV from outside. G. Carapace in dorsal view (Banyuls/Mer). Fig. H. *Xestoleberis xenomys* ♀. Carapace in dorsal view. Gulf of Taranto (Stn. 134 E). Fig. I. *Xestoleberis delamarei* ♂. Carapace in dorsal view (Banyuls/Mer). (xs = *X.*-spot).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agents as well as in the scars of the adductor muscles of the Darwinulidae or even in the "*X*.-spot" of some of the Xestoleberididae figured here (Pl. 5, fig. B; Pl. 2, figs. D, F). Finally, one can compare the carapace lenses of the Xestoleberididae with those of the corrective lenses used by humans (Text-fig. 1, fig. D) to concentrate and fix the light rays correctly on the retinal cells.

The "*Xestoleberis*-spot" is an intriguing structure which Whittaker, 1972 (quotation in Athersuch, 1976) has hypothesized as having a function connected with vision. We adopt here a similar opinion which is supported by the following arguments:

1–The largest "*X*.-spots" found by us always occur in photic zones *e.g.* within the *Xestoleberis communis* group. The littoral species have strongly developed spots while bathyal species living in aphotic habitats (*X. prognata* n. sp.) have a small "*X*.-spot" (see further details).

2–We found a fibrous structure which is inserted on the "*X*.-spot" on the valve of the *Xestoleberis* sp. group *communis* (Pl. 3, fig. H). We believe that this fibrous structure could be a ligament which fixes some of the lateral ocellar structures. Such a ligament exists in the human eye (see Text-fig. 1 C, M). One could argue that the "*X*.-spot" is a simple scar on to which a muscle is inserted. This muscle should in turn move other limbs and not be related to the lateral ocellus. It is improbable that this could be the case since the scars of the adductor and/or dorsal muscle (see Pl. 5, figs. C–E and Pl. 2, figs. H–K) in Xestoleberididae are smooth and sometimes protrude on the inner side of the calcareous lamella, whereas the "*X*.-spot" is always formed by a hollow spongy structure surrounded by a calcitic rim (see also Athersuch, 1976 and here Plate 1, figs. D, K).

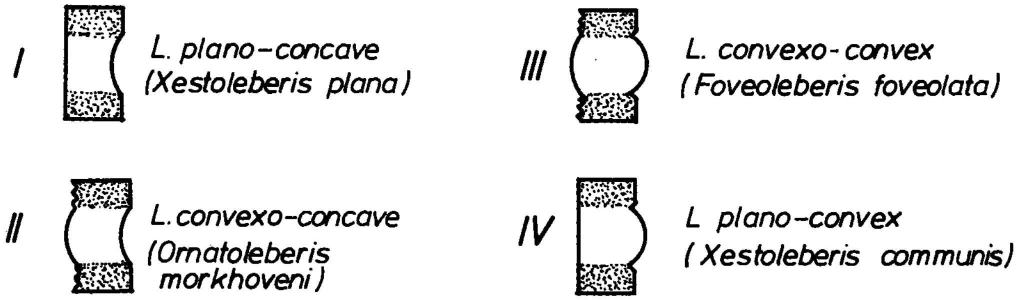
Description of the Ocular Structures of the Carapace of Xestoleberididae and Notodromadinae Taxa.

The most important data on the lenses and "*X*.-spots" of the Xestoleberididae and Notodromadinae are presented in Table 2. With the exception of the species of *Foveoleberis* and *Ornatoleberis*, all of the species recorded here have been examined by us using light and/or stereo-scanning microscopes. As our descriptions differ sometimes from the data already published, several comments will follow this table. The information presented in this section, as well as in the previous one, constitutes the data base for the discussions that follow in the next two chapters.

Table 2 shows that at least four types of lenses and two types of "*X*.-spots" have been recognised. Text-fig. 4 summarizes diagrammatically the main lens shapes. All possible combinations of lenses have been realized with the exceptions of the bi-concave one which, mechanically, would prove a very risky solution for an ostracod carapace since it normally does not focus light rays but disperses them. If one analyses Table 2 and Text-fig. 4, one gets the impression that in some cases the type of lenses and "*X*.-spot" do not vary chaotically but seem related to some supra-specific taxa. In fact, the plano-concave lens and the simple cell "*X*.-spot" occur mainly in the *Xestoleberis plana* group whereas the plano-convex lens type and the double-celled strongly protruding "*X*.-spot" are characteristic of the *Xestoleberis communis* group (see also the previous section on the systematics).

As compared with the literature data, our description of the ocular structures of *Xestoleberis delamarei* and *Xestoleberis galapagoensis* differ in some ways. Hartmann (1953) figured in the former species an ocular lens and/or a pigmented lateral ocellus in front of the "*X*.-spot" on the valves of both sexes. We examined living and fixed material collected in Banyuls/Mer on a beach close to those investigated by Hartmann and did not find such a structure. There is no evidence of a pigmented median eye and no trace of a well-structured lens (various figures in the text).

A female of *Xestoleberis galapagoensis* figured by Gottwald (1983, Fig. 44 E) displays two unstructured areas in front of the "*X*.-spot" which suggest the existence of ocular lenses in this interstitial species. Thanks to the kindness of Dr. Gottwald, we examined this species and on some valves and or carapaces we found variable areas of calcitic dissolution always around or in front



TEXT-FIG. 4—Diagrammatic scheme of the Xestoleberididae lenses.

TABLE 2—THE OCULAR STRUCTURES OF THE CARAPACE OF THE XESTOLEBERIDIDAE.

TAXON	LENS (O)	*X.*-SPOT (s)	FIGURES	REMARKS
Platyleberis n. g.				
P. profunda	ND	1 cell (MD)	5B; Pl. 1, A–D	†[1]
Microxestoleberis				
M. nana	ND	1 cell (WD) (sometimes none)	5A, B; Pl. 1, Y	†[1]
Xestoleberis				
gr. *communis*				
X. communis	plano-convex	2 cells (SD)	2E; 5A; Pl. 2, D, E	†[1]
X. sp. aff. *X. communis*	plano-convex + ring	2 cells (SD)	Pl. 2, F, G, H	†[1]
X. glabrescens	plano-convex	2 cells (SD)	6A, B	†[1]
X. prognata n. sp.	plano-convex	2 cells (WD)	Pl. 2, A–C	†[1]
gr. *plana*				
X. plana	plano-concave	1 cell (MD)	Pl. 25, 1 †[3]	†[1] Müller, 1894
X. dispar	plano-concave	1 cell (MD)	2D; Pl. 1, E, F	†[1]
X. parva	ND?	1 cell (WD)	Pl. 2, I, J	†[1] (for the lens see the text)
X. sp. 1(Nascimiento)	plano-concave	1 cell (MD)	Pl. 2, K	
gr. *arcturi*				
X. arcturi arcturi	NV	1 cell (WD)	Pl. 57, 27–30 †[3]	†[1] Triebel, 1956
X. galapagoensis	NV	1 cell (WD)	41, A †[3]	†[1] Gottwald, 1983
X. galapagoensis	NV	1 cell (WD)	44, A, C, E †[3]	†[1] Gottwald, 1983
X. delamarei	ND	1 cell (WD)	2, A, B; 6, F, I, J; Pl. 1, G, H, I, K	
Ornatoleberis				
O. morkhoveni	convexo-concave	1 cell (WD)	Pl. 1, 1–3, 5–7 †[3]	†[2] Keij, 1975
Foveoleberis				
F. foveolata	biconvex + ring	1 cell (WD)	Pl. 1, 1–3 †[3]	†[2] Malz, 1980
F. ymchenzi	biconvex + ring	1 cell (WD)	Pl. 1, 3; Pl. 2, 6–9 †[3]	†[2] Malz, 1980

†[1] — Outer surface of the carapace smooth; †[2] — Outer surface of the carapace markedly ornamented; †[3] — For figures see references mentioned in "Remarks".

ND— Not developed; NV—Not visible in normallight microscopy; WD—Weakly developed/MD—medially developed not protruding; SD — Stronglydeveloped protruding on the inner face of the valve.

of the "*X*.-spot". A similar case was also observed in a female valve of *Xestoleberis delamarei* (Text-fig. 2 B) with an opaque and milky frontal area around the "*X*.-spot". On one valve of *Xestoleberis delamarei* from Scario (Pl. 2, fig. K) we noticed a small tubercle but this was not an ocular structure as we did not find it on other valves of this species. *Xestoleberis parva* (Pl. 3, fig. J) presents a very poor imprint of the "*X*.-spot" (see arrow), the ocular lens which is not visible with light microscopy (neither transmitted nor reflected) appears in the SEM pictures as an unstructured area. We should consequently infer that this species has no true carapace lenses. It is worth mentioning that *X. parva* has a very thin, and translucent calcitic outer lamella, and the pigmentation of the epidermis is restricted to some very light coloured patches (Text-fig. 2 G). This species, which we found as a phytal dweller, resembles the interstitial *Xestoleberis* of the group *X. arcturi.* Even the surface dweller *Xestoleberis arcturi arcturi,* examined thanks to the kindness of Dr. Malz at the Forschungsinstitut Senckenberg, did not show carapace lenses.

A special comment should be made on the carapace lenses of the Notodromadinae. Fox (1966), Andersson and Nilsson (1981), gave a systematic description of these structures and reviewed the previous related literature. It is interesting to stress that *Notodromas monacha* Lilljeborg and *Notodromas persica* Guerney are neustonic species which swim with their dorsal side down near the surface of the water where the light is very strong. These species, unlike most of the Cypridacea, have dissociated lateral ocelli (Text-fig. 1 G, H) as in the Xestoleberididae. But as compared with the carapaces of this latter group, the two *Notodromas* species we examined display a sexual dimorphism of the lenses, *i.e.* the male has a pyriform lens (Text-fig. 1 H; Pl. 3, fig. L) which is slightly bi-convex whereas the female shows round lenses (Text-fig. 1 G).

EVOLUTIONARY PROBLEMS RELATED TO THE DEVELOPMENT OF OCULAR STRUCTURES IN XESTOLEBERIDIDAE

In the following section we shall discuss the pathways, origins and causes of the evolutionary changes of the ocular structures of the Xestoleberididae.

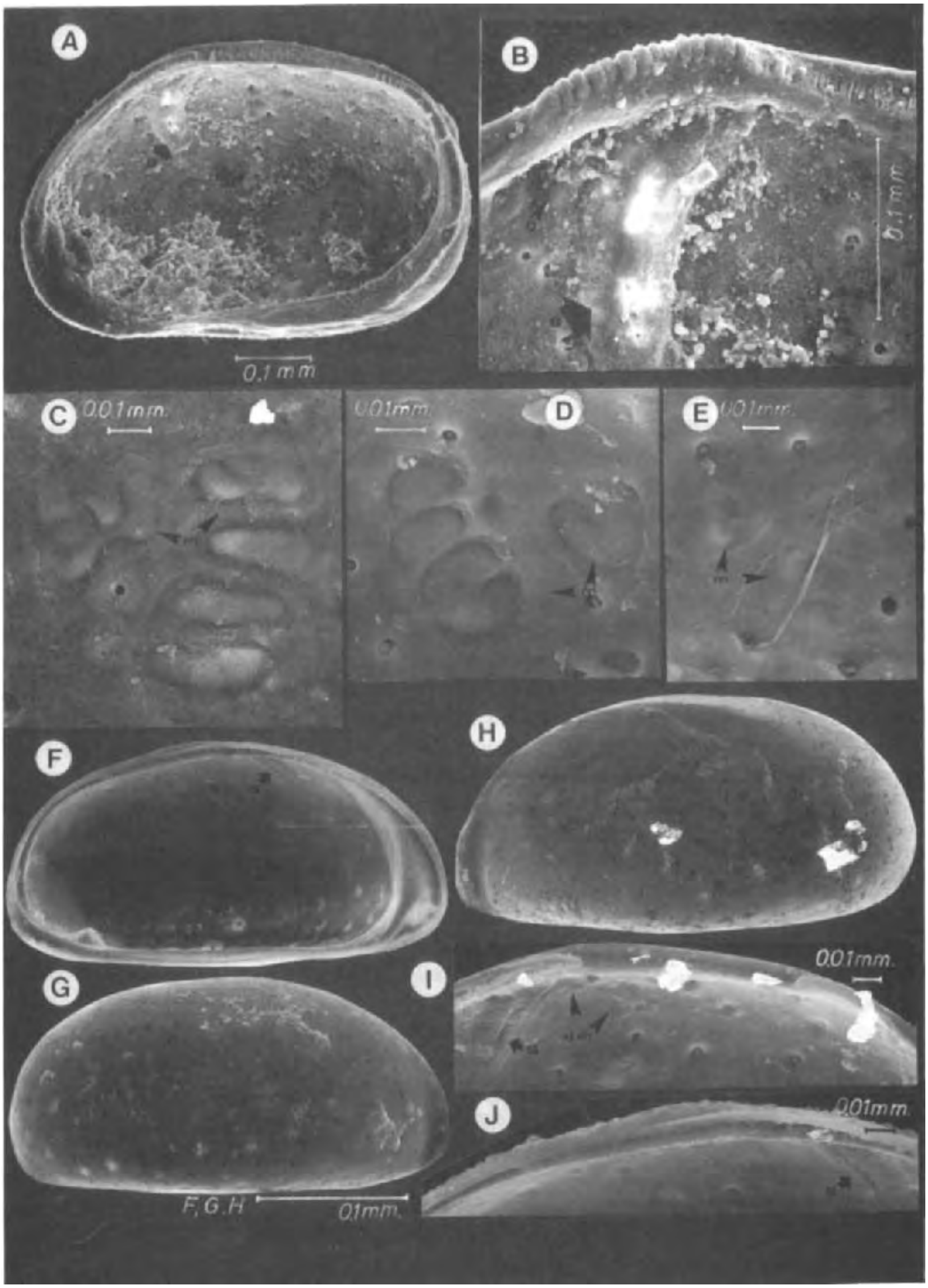
According to Seilacher (1970), any morphological structure is the product of a combination of three major types of forces: 1) Environmental forces (factors external to the organism, in response to which the latter produces a functional response), 2) Phylogenetic and genetic forces (*i.e.* internal factors that allow or inhibit the production of morphological variation), and 3) Structural forces (*i.e.* factors dependent on the constructional material of the organism that constrains or permits the production of a given structure).

From the morphological data presented in the previous sections we showed that the carapace lens and "*X*.-spot" do not display parallel developments, *e.g.* species with reduced lenses do not always show reduced "*X*.-spots" or, conversely, species with large lenses do not always have strong "*X*.-spots". This is why we shall discuss these two ocular structures separately.

Evolutionary Problems of the Lenses

That the carapace lens developed under the pressure of an environmental force, *i.e.* light in the photic marine zone, is without doubt. The convergent evolution of similar structures in the fresh-

PLATE 5—A, B. *Xestoleberis glabrescens.* A. RV from inside. B. Details of the *X*.-spot and of the ocular lens in the RV from inside. C-E. Central muscle-scars in Xestoleberididae. C. *Platyleberis profunda* in RV from inside (Saba Bank, Caribbean Sea). D. *Microxestoleberis nana* (Argeles) in LV from inside. E. *Xestoleberis delamarei* in RV from inside (Banyuls/Mer). F–J. *Xestoleberis delamarei* ♀ from Banyuls/Mer. F. LV from inside. G. RV from outside. H. LV from outside. I. Detail of the RV with *X*.–spot and dorsal muscle-scars. J. Detail of the *X*.-spot in the LV from inside. (s = *X*.-spot; m = adductor muscle-scars; dm = dorsal muscle scars; o = lens).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water Notodromadinae which live mainly below the air-water interface is a confirmation of the role of this external factor. We shall examine the pathways of the development of the lens in several Xestoleberididae groups living in shallow (photic) habitats; we will see that the development of lenses in these groups is also strongly dependent on internal and structural forces.

We noticed, in effect, that the Xestoleberididae developed two types of lenses, one with a concave face on the inner side of the carapace, the other with a convex face. Both of them seem to display the same function *i.e.* to focus the light and to increase the resolution of images on the eye (see Land, 1982 for a discussion).

It is not yet clear why some Xestoleberididae groups developed concave lenses and others convex ones. We are faced with the same dilemma concerning the two types of "*X*.-spots" (see below). But the development of the lens seems to have started within a phylogenetic group only after the animals acquired a certain type of organization of the inner limbs in some cases, or a certain structure of the carapace in others.

When the three ocelli are not dissociated, the animal receives light information from the median axis between the two open valves. There is no need of lenses on the lateral side of the carapace. Both Notodromadinae and Xestoleberididae have lateral ocelli that are dissociated from the median one with the perpendicular axis on the carapace wall. So it seems that in the case of the Xestoleberididae and Notodromadinae groups as compared with other Cypridacea and Cytheracea groups, the dissociation of the three ocelli occurred before the development of a lens. But this occurred only in some groups such as the Xestoleberididae in which genetic information could be expressed in its phenotype. One can hypothesize that the development of lenses is strongly dependent on internal forces that include both phylogenetic and genetic ones. Comparison between the Xestoleberididae and the Notodromadinae showed that the latter group developed a sexual dimorphism in the shape and size of the carapace lenses which never occurs in the former group. It is as if this type of information is not encoded in the genomic library of the Xestoleberididae.

But looking once again within the Xestoleberididae we observed that small littoral species with very thin carapaces such as *X. arcturi* Triebel or *X. parva* Müller, here figured, have very poorly developed lenses or no lenses at all. In these cases we believe that constructional constraints also play a role, *i.e.* in very thin carapace walls it is difficult to develop a concave lens. Much more important are the lenses of those species which have thick carapace walls and are strongly ornamented on their externally. Architectural problems (*i.e.* the outer ornamentation of the shell and the thickness of the wall) are probably also responsible for the development of strong lenses. Comparison of the ocular structures of representative of *Foveoleberis* Malz, *Uroleberis* Triebel and *Ornatoleberis* Keij will substantiate our contention.

Within *Foveoleberis,* if one examines the species described by Al-Furaih (1980, 1984) from the Upper Cretaceous Maastrichtian to Middle Palaeocene of Saudi Arabia, one finds the following series: *F. trapezium* Al-Furaih with a smooth shell surface and *F. ovata* Al-Furaih with a slightly pitted surface from Maastrichtian have no convexity of the lenses on the external side of the carapace. *F. oculata* Al-Furaih from the Middle Paleocene, which also has a strongly ornamented shell (large and deep pits) shows a well-developed convex lens. *Uroleberis parnensis* Apostolescu (see Triebel, 1958) from the Lutetian of the Paris Basin has a slightly pitted shell that has no outer lens convexity. The Recent *Ornatoleberis morkhoveni* Keij (Keij, 1975) which displays tubercles on the outer surface, has slight external convex lenses.

Malz (1980) describes, in the case of the well-ornamented *Foveoleberis foveolata* Malz and *F. ymchenzi* Malz, biconvex lenses protruding on both sides of the valve.

No lenses have been observed in the bathyal Xestoleberididae and the interstitial species of the group *X. arcturi.* In both cases, the environment is aphotic. From an evolutionary point of view the question arises whether the lack of lenses is due to regressive evolution or whether no evolutionary changes have occurred within the bathyal and interstitial *Xestoleberis* groups. The bathyal *Xestoleberis prognata* n. sp. (Pl. 1, figs. G, H) from Miocene and Pliocene deposits of the Mediterranean area may be related either to such xestoleberidids as the Maastrichtian species *Xestoleberis opinna* Schmidt (see figures in Brouwers and Hazel, 1978) or to species resembling *Xestoleberis communis* Müller (a living species from the Mediterranean) and *Xestoleberis glabrescens* Reuss from the Miocene (Badenian of the Vienna Basin (Paratethys). Our arguments on the phylogenetic affinities of those species derive from the general shape of the carapace and from the similarities in the structure and position of the hinge and shape of the inner calcareous lamella.

The cited species, distributed in littoral habitats, have a plano-convex carapace lens. If one accepts this possible phyletic relationship in the bathyal *X. prognata* n. sp. the lens has regressed so far as to disappear completely. This fact fits well within the paradigm that bathyal organisms display reduced ocular structures (Marshall, 1979). Nothing can be said on *Platyleberis profunda* (Breman) (Pl. 1, figs. A–F) as we do not know which, if any, are the related littoral species.

In the case of *X. delamarei* Hartmann (Pl. 5, figs. A–J), a blind interstitial species, we had the opportunity to compare its carapace structure with those of the close surface dweller *X. arcturi arcturi*. Both species have small and thin-walled carapaces and no lenses are detectable. This means that no evolutionary change occurred in the sub-surface habitat, an environment still exclusively inhabited by *X. delamarei*. This is an alternative situation to the well known paradigm which states that in sub-surface habitats, the exclusively interstitial dwellers that are either marine or limnic inhabitants underwent morphological reductions of the body limbs such as the eyes and/or carapaces (Hartmann, 1973; Maddocks, 1976).

The "*Xestoleberis*-spot"

The problems we discussed for the carapace lenses are essentially the same as those that occur in the case of the "*X*.-spot".

Very large "*X*.-spots" always occur in littoral dwellers, *e.g. X. communis* (Pl. 4, fig. A, Pl. 3, figs. D, E) and some species living along the Australian coast such as *X. kalgariensis* Hartmann, *X. quasirotunda* Hartmann, *X. bahialauraensis* Hartmann, *X. cedunaensis* Hartmann (Hartmann, 1978, 1979, 1981).

This suggests that environmental forces are of primary importance in the development of this structure. It is not yet clear why in some species such as *X. dispar* Müller (Text-fig. 2D; Pl. 4, figs. F, G; Pl. 2, figs. E, F), *X. pellucida* Müller and *X. intermedia* Brady & Robertson the "*X*.-spot" is formed mainly by a thin layer of calcite around a more or less deep hollow space; this thin rugose layer does not protrude markedly beyond the carapace wall as it does in the case of the group of species in which the "*X*.-spot" is very voluminous (the calcite layer around the hollow space protrudes markedly) as for example the case of *X. communis* species discussed here.

The thin-shelled *Xestoleberis* species show a poorly-developed "*X*.-spot" due to constructional constraints (*e.g. Hemixestoleberis duebeni* Hartmann, 1962 has no "*X*.-spot", *Xestoleberis arcturi* and *Xestoleberis parva* (Pl. 3, figs. I, J) have a very poorly developed "*X*.-spot", etc.). The bathyal species *X. prognata* n. sp. also has a reduced "*X*.-spot". We believe that in this case the aphotic environment is responsible for a reduction in the size of the "*X*.-spot".

A special situation is displayed by *Platyleberis profunda* (Breman). This bathyal species has a well-developed "*X*.-spot" as compared with that of *X. prognata* n. sp. One could hypothesize here that genetic internal constraints are strong enough to prevent a modification (reduction) of the "*X*.-spot".

In the case of *X. delamarei*, the "*X*.-spot" is as weakly developed as in the surface dweller homologue *X. arcturi arcturi*. Consequently, we do not have any evolutionary change as in the case of the carapace lens previously discussed.

The species of the genus *Microxestoleberis* also have a thin "*X*.-spot" but as we do not know of any surface species related to this interstitial species, we cannot decide on the evolutionary status of this character.

THE LIMITS ON THE USE OF THE OCULAR STRUCTURES OF XESTOLEBERIDIDAE IN PALAEOECOLOGICAL RECONSTRUCTION

Benson (1975) recognized that the deep sea cytherids, when compared with their littoral relatives, have no ocular tubercles or ocular spots. Benson (*op. cit.* and 1984) noted that the limits for the presence of an ocular tubercle is between 600 to 900 m in depth. Benson and other researchers, *e.g.* Steineck (1981), McKenzie and Peypouquet (1984) used this information to infer palaeodepths from ostracod structures.

In the case of the Xestoleberididae, we can use ocular structures for the reconstruction of palaeodepths only within certain limits.

1. The first thing is to identify the group of species (it would be best to identify phylogenetic lineages) in which ocular structures are known to occur and determine if they have evolved in progressive or regressive directions. We observed that in the case of the littoral Xestoleberididae living in the photic zone (less than 100 m depth), species with well calcified carapaces, of median size (400–700 μm carapace length) generally develop ocular structures and "*Xestoleberis*-spots". Such example are the Recent and fossil species of the *Xestoleberis* groups *X. plana, X. communis,* of *Uroleberis, Foveoleberis, Ornatoleberis,* etc. With this type of information we can therefore recognize shallow palaeohabitats (palaeodepths less than 100 m) which may be further checked with additional tests, *i.e.* the ostracod assemblage should be represented by other taxa normally living in shallow marine habitats such as representatives of Loxoconchidae, Leptocytheridae, Cytheromatidae) Paradoxostomatidae, etc. (see Hartmann, 1965, 1966–1975, 1981).

Some bathyal species with well-calcified carapaces such as *X. prognata* n. sp. belong to this group of Xestoleberididae. We observed that in this case the ocular structures are either reduced or absent. We can infer a palaeodepth, as suggested by Benson, deeper than 600 m.

Once again, it is important to check the ostracod assemblage with which the xestoleberidid species occur. For example, in the case of *X. prognata* n. sp. found by Benson (in Berggren *et al.*, 1976; Benson, 1976) in the Upper Miocene of southern Spain, the ostracod assemblage is typical of deep-sea habitats (*Bradleya dictyon, Henryhowella asperrima, Agrenocythere hazelae, Krithe* sp., *Bythocypris* sp., *Oblitacythereis ruggierii*).

The same may be true in the case of the Pliocene-Pleistocene section of Mount S. Nicola in Southwestern Sicily near Capo Rossello. This section, studied by one of us (G.B.), yielded an ostracod assemblage that can be considered typically upper bathyal with *Agrenocythere pliocenica, Oblitacythereis mediterranea, Paijenborchella solitaria, Quasibuntonia radiatopora, Bythoceratina scaberrima mediterranea, Henryhowella asperrima* and *Krithe* sp. This section shows a complete absence of contamination from shallower environments but 2 species of Xestoleberididae that are certainly deep water species (*P. profunda* and *X. prognata* n. sp.) were almost constantly present.

2. There are Xestoleberididae taxa known exclusively from one type of environment. As a rule of thumb, and until one can contradict this assertion, we can use fossil species of this category of Xestoleberididae for the identification of palaeohabitats or palaeodepths. This is the case for *Platyleberis profunda.* Until now this species has been found only in deep-water habitats of the Atlantic and Mediterranean at depths ranging from 700 to 1375 m (Breman, 1975; Nachite 1984; and this paper). The genus also occurs as fossil in the lower Oligocene of Moravia (Pokorný, 1981, and pers. comm.).

3. It is worth noting that the reduced size (carapace length less than 400 μm), pyriform shape, flat ventral side and absence of carapace lenses in xestoleberidids suggest that such carapaces occur, on the one hand, in the interstitial habitats at shallow depths and, on the other hand, in bathyal habitats. In this case, one can recognise the palaeohabitat or palaeodepth using the information provided by the associated fauna. Commonly, the interstitial xestoleberidids live together with representatives of typical interstitial Cytheracea such as microcytherids, Loxoconchidae of the genus *Tuberoloxoconcha* and/or with Polycopidae, etc. (see Hartmann 1953, 1954; Gottwald 1983; and Bonaduce and Danielopol in prep.). Bathyal xestoleberidids with pyriform and ventrally flattened carapaces occur together with representatives of the genera *Argilloceia, Bythoceratina scaberrima* group, *Bythocypris,* etc. (see *e.g.* McKenzie, 1982). One should be very careful in inferring also a bathyal and/or interstitial habitat from the reduced size of the "*X*.-spot". One should remember that even in surface littoral (shallow) environments, some Xestoleberididae (mostly those with thin carapace walls) have reduced or completely lack an "*X*.-spot" (*e.g. Semixestoleberis* species described by Hartmann, 1965, and the data presented in this paper on *Xestoleberis parva*).

THE INTEGRATION OF THIS OSTRACOD RESEARCH WITHIN A HUMANISTIC CULTURAL FRAMEWORK

In this communication we have demonstrated that the Ostracoda developed several types of carapace lenses. When one considers the historical development of the production of optical devices (*e.g.* the microscope), it is surprising to verify the analogies between biological lenses and man-made ones. In both cases one finds, for example, plano-convex and bi-convex lenses. It is interesting to remember that Nature has developed, within a phylogenetic line of Xestoleberididae, a convex-concave type of lens such as the one proposed by Leonardo da Vinci (Fig. 1E) for the functioning of the human eye (see Kemp, 1981, Fig. 95). The functional significance of the concave-convex lens which Leonardo proposed for the human eye was simply to reverse the image which arrives on the retina. The function of the ostracod lens is most probably to focus the image. We now know that Leonardo was wrong in his interpretation (Kemp, 1981), but it is a pleasure to recognize this analogy between the human imagination and the product of organic evolution.

CONCLUSIONS

The Xestoleberididae have been considered fairly homogeneous until now as far as their structure and habitat is concerned. Most of the past descriptions, except for a few relatively recent papers, do not pay attention to important characters such as the "*Xestoleberis*-spot" and hinge and lens structures. The discovery of deep-water species, previously considered contaminants from shallow environments, has demonstrated the need for a more detailed analysis of these structures and their interpretation in terms of function and the environment. Their discovery also poses problems concerning their phylogenesis, environmental origin and migration. We have been able to study the previously cited characters, define four different ocular structures within the family, correlate them with different environmental conditions and suggest different phylogenetic lineages. The species beloging to interstitial and deep-water environments show reduced ocular structures or their apparent absence. Near-shore surface-dwellering species generally show well-developed ocular structures with large lenses. We consider the so-called "*Xestoleberis*-spot" as a possible ligament scar for supporting some of the lateral ocellar structures. Its presence in deep-water species of Xestoleberididae suggests the migration and adaptation from a photic zone to deeper environments, with a reduction or disappearance of the lenses but the relict presence of the related ligament.

A similar evolutionary pathway does not occur within the *Xestoleberis arcturi* group represented by surface littoral and interstitial dwellers. Here, even surface species display reduced "*X.*-spots" and the lenses of the carapace are lacking (not visible). We have shown that the different solutions that the Xestoleberididae have adopted towards the development and/or regression of the different ocular structures of the carapace depend on the interplay of external (environmental) and internal (mainly genetic and phylogenetic) causes as well as on constructional material constraints.

Following Benson's pioneer work (1975), in recent years palaeontologists have used the ocular structures of the carapace (*i.e.* the eye tubercle) for the identification of palaeodepths and photic and/or aphotic habitats. We have shown here that the Xestoleberididae can also be used as palaeoindicators, but only within certain defined limits.

In the last section, we have shown that there are surprising similarities between a carapace lens of the type defined for the ostracod Xestoleberidae and the human lens as imagined by Leonardo da Vinci and discussed by Kemp (1981). With this example, we believe it is also possible to relate ostracod morphology within a humanistic framework thereby stimulating the interests of a wider and more interdisciplinary audience.

The aim of this contribution is therefore to point out that the Xestoleberididae ostracods are well worth better and more intensive study for scientific, philosophical and practical purposes, bearing in mind different lines of research that include the study of their systematics, functional morphology, ecology/palaeoecology and evolutionary biology.

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A Preliminary Account of the Distribution of Ostracoda in Recent Reef and Reef Associated Environments in the Pulau Seribu or Thousand Island Group, Java Sea

ROBIN C. WHATLEY AND KAREN WATSON
University College of Wales, Aberystwyth, Wales

ABSTRACT

Thirteen samples taken from seven distinct environments on and around the reef complex of Pulau Pari in the Pulau Seribu, Java Sea, yielded 141 species of podocopid and platycopid Ostracoda belonging to 49 genera. The environments sampled represent all the major niches available to ostracods in Pulau Pari. These are, from seaward to landward, fore reef, reef slope, outer reef flat, lagoon, intertidal mangrove, intertidal and supratidal. The influence of the environment is seen in the distribution of the fauna. Some taxa are either restricted to or are only dominant in, certain environments. For example, the Bairdiidae achieve their maximum diversity and incidence on the reef while such genera as *Renaudcypris* and *Hansacypris* are effectively confined to the intertidal zone. Other taxa such as *Loxoconcha, Xestoleberis* and *Ornatoleberis,* considered at the generic level, exhibit a catholic environmental tolerance, although individual species of these taxa are much more restricted in their distribution. The environmental distribution of the Pulau Pari fauna is compared with reef and reef associated faunas described from elsewhere. No other fauna, however, seems to have been comprehensively studied from a reef complex presenting similar environments to those occurring in Pulau Pari.

INTRODUCTION

The association between Ostracoda and reef environments goes back to the lower Palaeozoic (Warshauer and Smosna, 1977). Despite this, relatively few studies have been published on this association. A review of some of these and a comparison of their results with that of the present study is made below.

This paper because of its preliminary nature confines itself for the most part to a consideration of the distribution and diversity of genera on a recent reef in the Java Sea.

The study, which is partly supported by Robertson Research Singapore, is based on a series of sediment samples collected by Miss Penny Turner of the Dept. of Geology, Aston University (who is also partly supported by RRS). The material was not chemically preserved and, therefore, the ostracods are all "dead". Only limited ecological data is available although it is hoped to obtain more information on mean salinities and temperatures in due course.

The only previous study of ostracods from the Pulau Seribu known to the authors is by Keij (1974, 1975) who first described *Triebelina pustulata* and *Ornatoleberis morkhoveni* from the area.

LOCATION AND PHYSIOGRAPHY

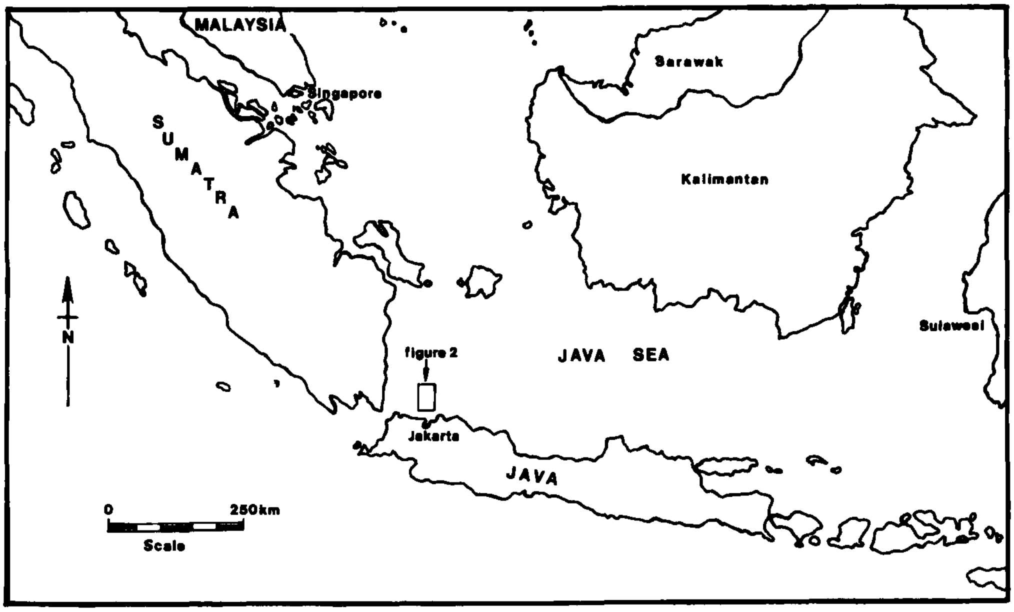
The Pulau Seribu (latitude 5° 35′S, longitude 106° 35′E, are a group of small coral reefs which commence 25 km from the north Java coast and extend in an approximate N-S chain for around 40 km. (Text-fig. 1). A general description of the Pulau Seribu, also known as the Thousand Island Group, is given by Cook and Saito (1982). The reefs have also been described by Scrutton (1976, 1978).

The reefs are situated on the NNE-SSW trending Seribu High, a structural high in the northwest Java Sea Basin which separates the Sunda sub-basin to the west and the Arjuna sub-basin to the east. Although a deep channel to the south separates the Pulau Seribu from the Java mainland, the reefs are situated on a shallow shelf ranging in depth between 30–40 m. The reefs rise up steeply from the sea floor; with slopes of the order 70–75°. At the surface, the reefs vary in size and shape but many tend to be elongated in an approximately east-west direction. They range in length from 50 m to 5 km (Text-fig. 2). Cook and Saito (1982) suggest that the reefs in the Pulau Seribu can be categorized as "platform, platform lagoonal and elongate platform types" following Maxwell's (1968) classification of reef types within the Great Barrier reef.

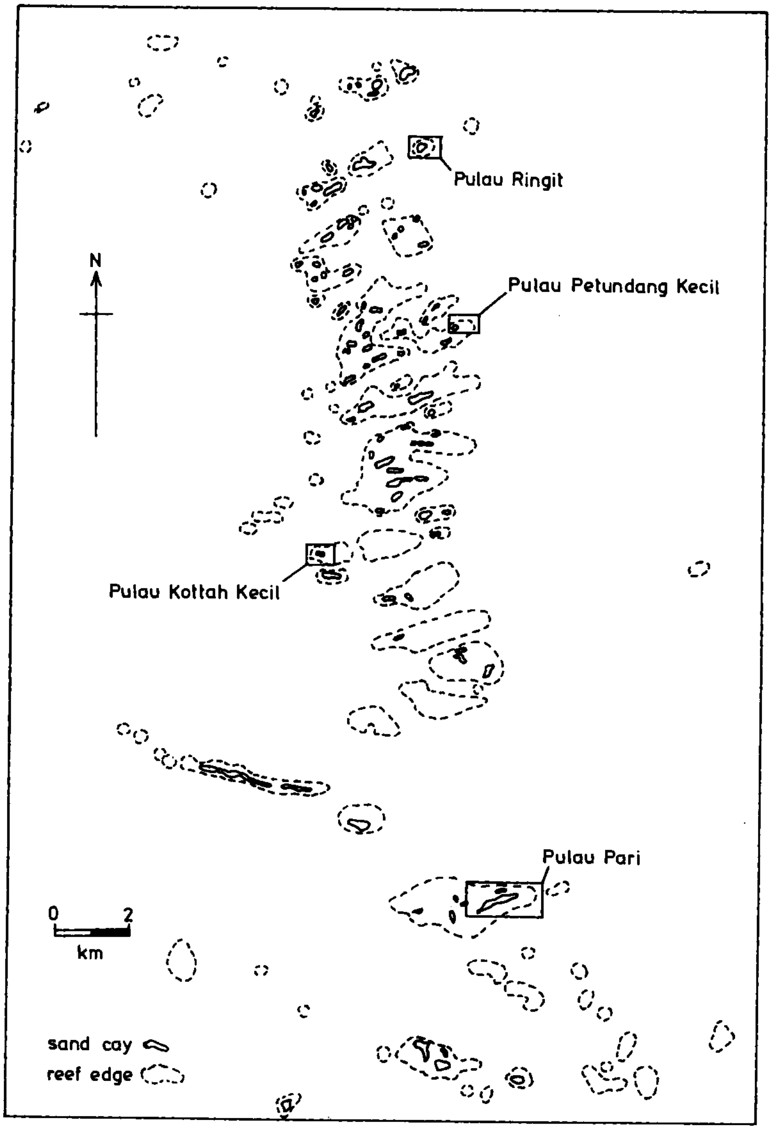
We are studying the Ostracoda of four of the reefs, which from north to south are: Pulau Ringit, Pulau Petondang Kecil, Pulau Kottah Kecil and Pulau Pari (Text-fig. 2). The present study is, however, concerned solely with Pulau Pari.

Pulau Pari

Text-figure 3 shows the reef complex associated with Pulau Pari. It comprises a complex of five cays (low lying islands or emergent "reefs" of sand or coral) surrounded by a reef. Although Pulau Pari cay itself is only some 2.8 km by 0.5 km the entire complex is approximately 8 km long by



TEXT-FIG. 1—Regional setting of the Pulau Seribu.

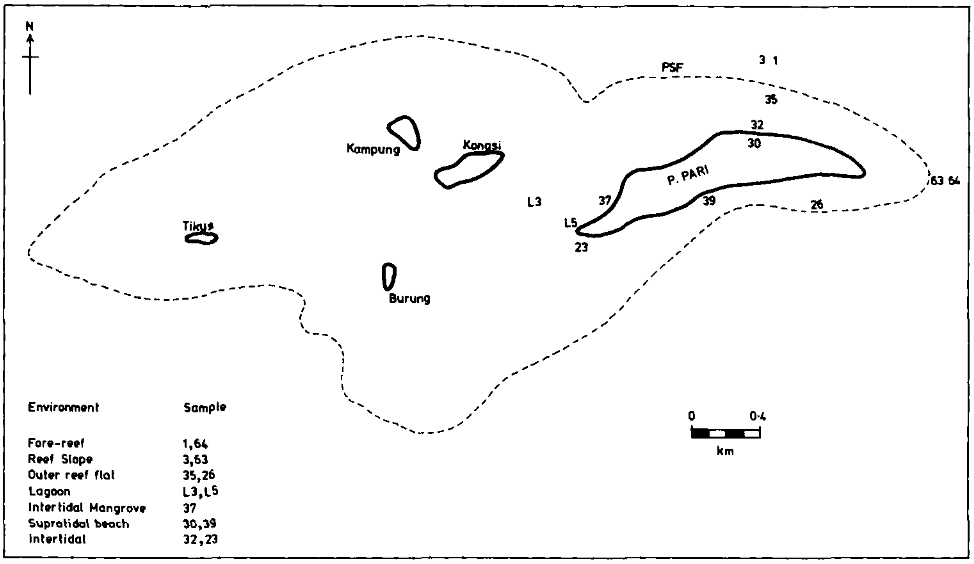


TEXT-FIG. 2—The reefs of the Pulau Seribu.

(at its widest) 4 km. The complex is aligned east-west. Along the north side of the reef the slope is much shallower than on the south side and coral growth less vigorous. On the south side the reef is more protected and coral growth is very vigorous, giving rise to a steep slope.

The lagoon associated with Pulau Pari is considered mature in that it contains well established mangroves, particularly northeast of the island.

Although a total of 30 sediment samples are available to us from Pulau Pari, only 13 have been processed in time for the study. Their positions are given in Text-fig. 3. The remaining samples from Pulau Pari and the other islands will be studied in due course.



TEXT-FIG. 3—The reef complex of Pulau Pari indicating sample localities.

THE ENVIRONMENTS SAMPLED

Text-figure 4 represents in diagrammatic form the various reef and reef associated environments which have been sampled in this study of Pulau Pari. The seven different environments are described in turn:

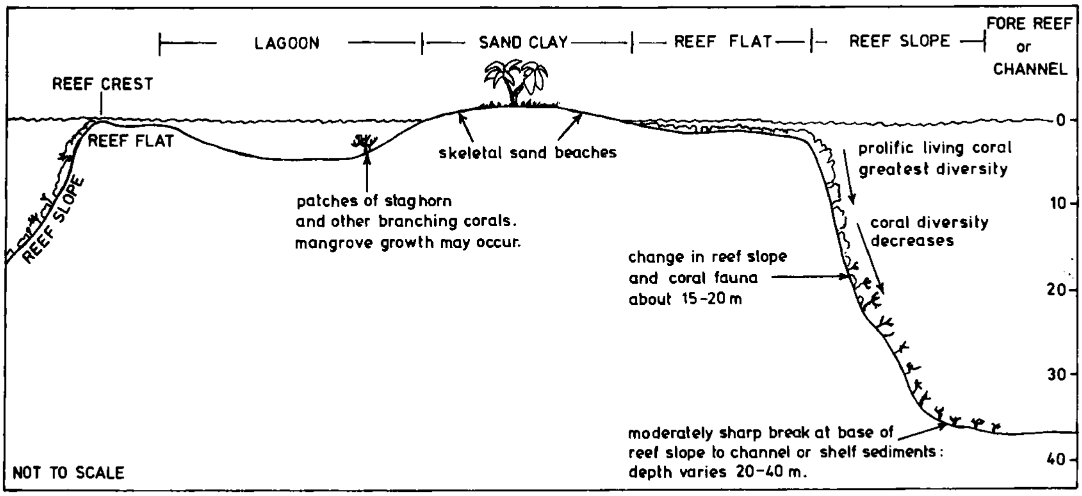
Fore reef: Sample 1 (depth 20 m)
Sample 64 (depth 31 m)

This environment, on the seaward side of the reef slope provides the deepest water (20–40 m) in the study. The substrate is of medium-coarse skeletal sands and gravels, and the sea-bottom flat and featureless. Grain size increases towards the base of the reef slope where sea fans (Gorgonaria) begin to appear.

Reef slope: Sample 3 (depth 10 m)
Sample 63 (depth 10 m)

From the "growing edge" of the reef down to the sea-floor there is a steep slope of some 70–75°. Coral diversity declines downslope and from almost 100% cover there is a gradual decrease as living coral gives way to areas of dead coral and pockets of sediment. The coral assemblages change with depth to those more tolerant of reduced light intensity. At a depth of between 15–20 m colonial corals give way to a fauna dominated by sea whips and sea fans. At around the same level there is a general easing off in the reef slope and the slope is covered with more and more sekeltal sand and gravel and larger fragments of dead coral from higher up the reef slope. This trend continues to the base of the slope with all forms of flora and fauna becoming rarer. The sediments of the reef slope are largely coral, mollusc and algal in their derivation. They are poorly sorted and unabraded. According to Cook and Saito (1982) the skeletal debris is usually composed of the following:

coral	50–85%
molluscs	5–30%



TEXT-FIG. 4—Diagrammatic section through a typical reef of the Pulau Seribu (adapted from Scrutton, 1976).

Halimeda	0–50%
red algae	0–3%
echinoids	1–5%
foraminifera	1% maximum

Reef flat: Sample 26 (depth 1.5 m)
Sample 35 (depth 0.6 m)

This is an area of rather uniform shallows floored by skeletal sand. Maximum depth is some 3 metres and while parts of the reef may be emergent at low spring tides, it is usually covered by about 1m minimum of water. In the more sheltered areas the sediment is fine sand; elsewhere it is medium to coarse-grained with large fragments of molluscan and coral debris. Patchy coral growth occurs although coral diversity is low, reflecting diminution in oxygen and nutrient levels relative to the "growing edge". The individual grains are often abraded and range in shape from angular to subrounded. According to Cook and Saito (1982) their composition is usually as follows:

corals	50–80%
molluscs	20–40%
echinoids	
green algae	rarely exceeding 2% each
foraminifera	

The reef flat abounds in animal life. Apart from corals, holothurians, fish, molluscs, echinoderms, crustaceans and marine worms are all abundant and diverse.

Lagoon: Sample L3 (depth 1 m; some coral growth)
Sample L5 (depth 2 m; rich in algae)

There is a well developed lagoon on the northwest side of Pulau Pari cay. The sediment is medium grained skeletal sand grading to fine grained sandy muds with carbonaceous material in deeper parts. This supports some mangrove growth and also patches of "Stagshorn" and other coral. The water depth is variable but probably does not exceed a few metres. The deepest sample available to us was taken at 2 m. As there is no freshwater run off from the cay, the salinity of the lagoon and the intertidal mangrove, given high evaporation, is probably in excess of that of the open sea.

Intertidal Mangrove: Sample 37

Particularly on the northwest shore of Pulau Pari cay, well established mangroves occur in the intertidal zone. The sediment is a fine grained dark organic-rich mud.

Intertidal: Samples 23, 32.

The environment is an intertidal sandy beach composed of medium to coarse skeletal sands, well sorted and abraded.

Supratidal: Samples 30, 39.

These two samples were collected above maximum high water mark on sandy beaches. Sediment type as for the intertidal zone.

METHODS

The sediment samples were collected by hand, either by snorkel or scuba diving, during the winter of 1983. Sediment was scooped from a shallow surface layer into a plastic bag (Turner, pers comm., 1984). In the laboratory, samples were washed over a 230 mesh/inch sieve and the dried samples split into 30, 60 and 100 mesh/inch fractions. A count of ostracods from a known weight of each fraction of each sample was made. The count was then recalculated, dependent on the amount of each fraction picked, to yield the total number of ostracods in the whole sample. Because grain size varied enormously in the samples, from coral rubble to find muddy sands, it was impractical to pick equal volumes of sediment from each. For this reason the total number of individuals from each sample has been standardized to represent the number of ostracods recovered from 100 g of sediment. The authors are fully aware, however, that this to a certain extent is dependent on sedimentation rate.

THE DISTRIBUTION OF THE OSTRACODA

The 13 samples yielded a total of 49 genera and 141 species. The distribution of the taxa among the 7 environments studied is given in Table 1. This also shows the number of species belonging to each genus and the number of individual specimens of each genus (standardised to 100 g sediment) recovered from each envrionment. The figures in brackets in Table 1 represent the precentage abundance of each genus in each envrionment.

Table 1 illustrates that both diversity and incidence are very variable. For example, incidence of individuals per 100 g sediment is higher on the outer reef flat and in the lagoon than elsewhere. Generic and specific diversity is highest on the reef slope and in the lagoon.

Data from Table 1 is synthesized in Table 2. This clearly demonstrates the different diversity patterns of the various environments. Since the faunas of the intertidal and supratidal environments are probably and certainly derived respectively, they can largely be ignored. The diversity of the fore-reef samples is surprisingly low but this is probably a reflection of the low incidence which itself is probably due to the coarse nature of the sediment. The high diversity of the reef slope, however, is apparent despite the relatively low incidence. Unfortunately, there has not been sufficient time to undertake a population age structure analysis (Whatley, 1983) of the faunas to determine which species are autochthonous to which environment. However, the faunas of the lagoon and intertidal mangrove and to a larger extent the outer reef flat, seem to be composed in the main of species whose age structure is suggestive of a biocoenosis.

TABLE 1—THE NUMERICAL AND PERCENTAGE ABUNDANCE DISTRIBUTION OF GENERA IN THE 7 ENVIRONMENTS SAMPLED AT PULAU PARI (NUMBER OF INDIVIDUALS STANDARDIZED TO REPRESENT RECOVERY FROM 100G. SEDIMENT).

	SAMPLE STATIONS						
GENERA (No. of species)	1, 64 Fore-reef	3, 63 Reef slope	35, 26 Outer Reef flat	L3, L5 Lagoon	37 Intertidal mangrove	32, 23 Intertidal	30, 39 Supratidal
Bairdoppilata (2)		14(2.2)	5(0.05)				
Neonesidea (10)	8(10.5)	78(12.1)	209(2.2)	100(4.6)		3(4.5)	
Paranesidea (8)	12(15.8)	90(13.9)	115(1.2)	94(4.4)	3(1.1)	2(3.0)	1(3.3)
Triebelina (4)	3(3.9)	24(3.7)	75(0.8)	3(0.1)		1(1.5)	
Anchistrocheles (4)	1(1.3)	6(0.9)	22(0.2)	5(0.2)		1(1.5)	
Paracypris (1)		1(0.2)	1(0.01)				
Renaudcypris (1)			56(0.6)	5(0.2)	110(40.0)	25(37.9)	4(13.3)
Hansacypris (2)					69(25.1)		
Propontocypris (9)	1(1.3)	3(0.5)	73(0.8)	125(5.8)	3(1.1)	9(13.6)	1(3.3)
Bythoceratina (1)	2(2.6)	13(2.0)					
Cythere? (1)		2(0.3)					
Hulingsina (1)	1(0.2)	369(3.9)	27(1.3)			1(1.5)	
Neocyprideis (2)				113(5.2)	5(1.8)		
Cytherura (2)	1(1.3)			4(0.2)			
Eucytherura (2)		4(0.6)					
Hemicytherura (1)		2(0.3)					
Semicytherura (1)	1(1.3)						
Cytheropteron (2)	3(3.9)						
Paracytheridea (2)	1(1.3)	18(2.8)	207(2.2)	4(0.2)		1(1.5)	
Ambostracon (3)	1(1.3)	24(3.7)	442(4.6)	112(5.2)	18(6.5)	1(1.5)	1(3.3)
Caudites (3)	2(2.6)	19(2.9)	814(8.5)	148(6.9)	7(2.5)	1(1.5)	
Jugosocythereis (2)	1(1.3)	12(1.9)	217(2.3)	33(1.5)	5(1.8)	1(1.5)	4(13.3)
Mutilus (2)	5(6.6)	71(11.0)	380(4.0)	22(1.0)	3(1.1)		
Neobuntonia (1)	1(1.3)						
Quadracythere (1)		22(3.4)	844(8.8)	108(5.0)			1(3.3)
Hemikrithe? (1)		2(0.3)	52(0.5)	4(0.2)			
Parakrithella (2)	2(2.6)	6(0.9)					
Callistocythere (5)	1(1.3)	17(2.6)	1399(14.6)	42(1.9)	2(0.7)	1(1.5)	1(3.3)
Tanella (5)	1(1.3)	4(0.6)	622(6.5)	57(2.6)		11(16.7)	
Cytheromorpha (1)		1(0.2)		64(3.0)			
Loxoconcha (10)	8(10.5)	60(9.3)	484(5.1)	298(13.8)	6(9.1)	4(1.5)	2(6.7)
Loxoconchella (2)		5(0.8)		8(0.4)			
Touroconcha (2)		15(2.3)	70(0.7)	16(0.7)			
Paradoxostoma (2)				15(0.7)	1(0.4)		
Pellucistoma (1)				5(0.2)	2(0.7)		
Coquimba (1)	4(5.3)	1(0.2)					
Hemicytheridea (1)		6(0.9)	52(0.5)	12(0.6)			
Kotoracythere (1)	7(9.2)	1(0.2)	259(2.7)				
Psammocythere? (1)		2(0.3)					
Neomonoceratina (5)		2(0.3)		23(1.1)			
Alocopocythere (2)		14(2.2)		11(0.5)			
Cletocythereis (1)		7(1.1)		12(0.6)			
Pistocythereis? (2)				20(0.9)	4(1.5)		
Ruggieria (2)				12(0.6)		1(1.5)	
Trachyleberis? (1)		4(0.6)					
Xestoleberis (16)	3(3.9)	61(9.4)	1176(12.3)	267(12.4)	18(6.5)	6(9.1)	6(20.0)
Ornatoleberis (3)	3(3.9)	14(2.2)	1421(14.9)	57(2.6)	2(0.7)	2(3.0)	7(23.3)
Cytherella (1)				4(0.2)			
Cytherelloidea (5)		10(1.5)	129(1.6)				
Gen. Indet (1)		4(0.6)					

TABLE 2—SELECTED STATISTICS ON THE DISTRIBUTION OF OSTRACOD GENERA, SPECIES AND INDIVIDUALS, PULAU PARI.

	SAMPLE STATIONS						
ENVIRONMENT	1, 64 Fore-reef	3, 63 Reef slope	35, 26 Outer	L3, L5 Lagoon	37 Intertidal Mangrove	32, 23 Intertidal	30,39 Supratidal
No. of individuals†	76	646	9,552	2,154	275	66	30
No. of genera	23	38	25	33	18	17	10
No. of species	32	74	60	67	30	26	16
% made up by most abundant species	9.2	10.1	12.6	7.7	38.5	37.9	16.7
% made up by 3 most abundant species.	26.3	26.2	29.1	21.7	63.6	56.8	40.0

† *Standardized to represent total no. of individuals recovered from 100 g sediment.*

The relative abundance of the 31 most important genera is given in Text-fig. 5. The relative abundances are expressed in percentages of the total population of each environment. Text-figure 5 illustrates that the faunas of certain environments are dominated by certain genera. For example, although *Neonesidea* and particularly *Paranesidea* are widely distributed throughout the entire area, they clearly dominate on the reef. The same is true of *Triebelina,* and to a lesser extent *Mutilus.*

Renaudcypris clearly exhibits its preference for environments of a restricted nature away from the open sea. *Hansacypris* is similar but restricted to the intertidal mangrove. Both *Xestoleberis* and *Ornatoleberis* are ubiquitously distributed as is *Loxoconcha.* The distribution of *Caudites* and *Ambostracon* is somewhat similar.

The degree to which genera are restricted to environments is outlined below:

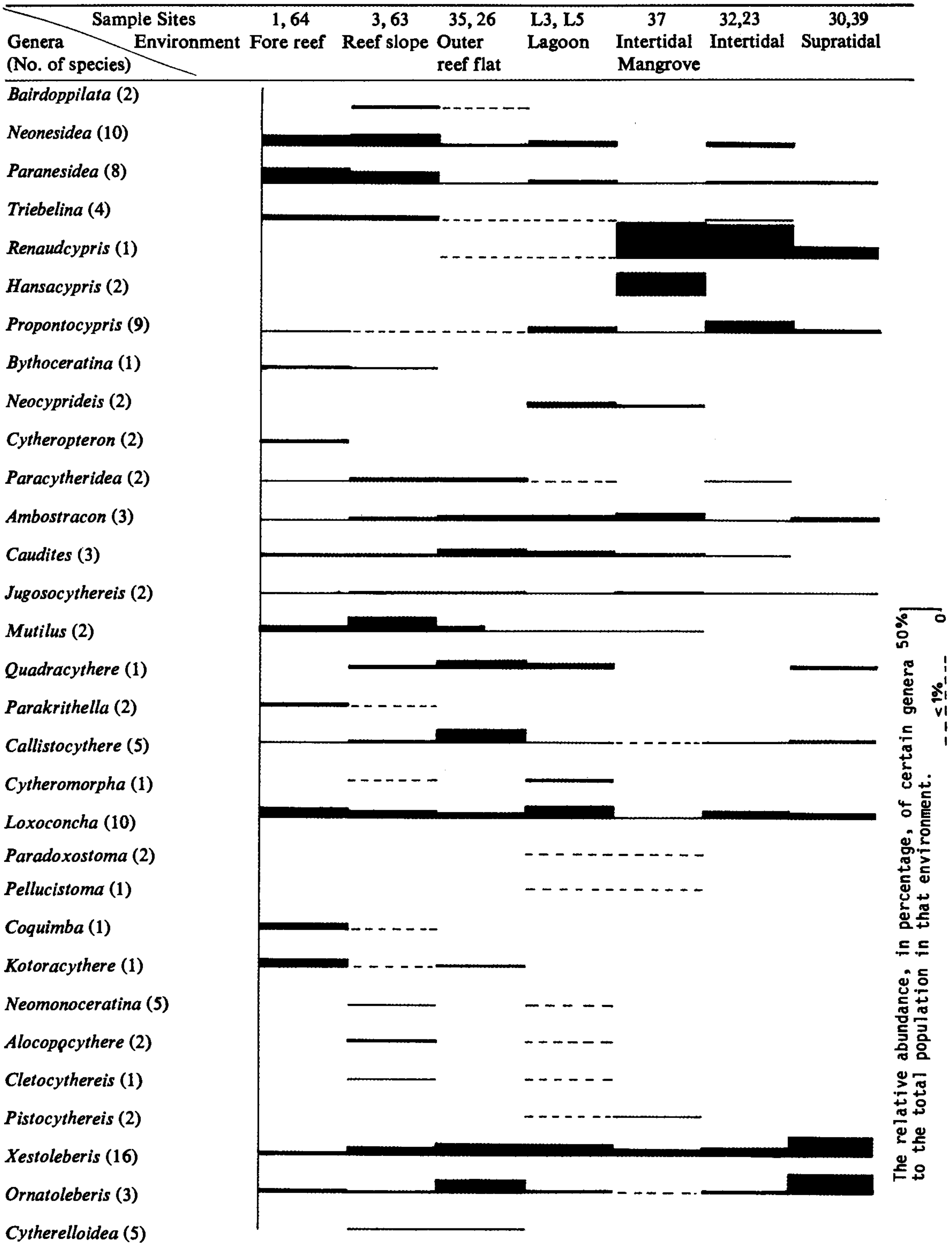
Only one species of the 141 is ubiquitous, that being a very abundant species of *Ambostracon.* No less than 48 species, however, are confined to a single environment as shown in Table 6.

TABLE 3—SPECIES CONFINED TO A SINGLE ENVIRONMENT.

Environment:	Genus	
Intertidal mangrove	*Hansacypris* 2 spp.	(25.1%)
Lagoon	*Cytherella* 1 sp.	(0.2%)
Reef slope	*Eucytherura* 2 spp.	(0.6%)
	Hemicytherura 1 sp.	(0.3%)
	Gen. indet. 1 sp.	(0.6%)
	Trachyleberis 1 sp.	(0.6%)
Fore reef	*Semicytherura* 1 sp.	(1.3%)
	Neobuntonia 1 sp.	(1.3%)
	Cytheropteron 2 spp.	(3.9%)

TABLE 4—GENERA WHICH OCCUR IN ONLY TWO (USUALLY SIMILAR) ENVIRONMENTS.

Genus	Environments
Neocyprideis *Paradoxostoma* *Pellucistoma* *Pistocythereis?*	Lagoon and intertidal mangrove only
Cytheromorpha	Lagoon and reef slope (very rare in latter)
Paracypris *Cytherelloidea*	Reef slope and outer reef flat
Parakrithella *Coquimba*	Reef slope and fore reef



TEXT-FIG. 5—The environmental distribution, in terms of relative abundance of selected genera, on Pulau Pari.

TABLE 5—UBIQUITOUS GENERA.

Paranesidea	*Callistocythere*
Propontocypris	*Loxoconcha*
Ambostracon	*Xestoleberis*
Jugosocythereis	*Ornatoleberis*

TABLE 6—SPECIES CONFINED TO A SINGLE ENVIRONMENT.

Fore reef	Reef slope	Outer reef flat	Lagoon	Intertidal mangrove	Intertidal
Semicytherura 1sp.	*Bairdoppilata* 1sp.	*Paranesidea* 1sp	*Cytheurura* 1sp.	*Hansacypris* 2 spp.	*Neonesidea* 2 spp.
Cytherura 1sp.	*Paranesidea* 1sp.	*Propontocypris* 1sp.	*Tanella* 1sp.	*Propontocypris* 1sp.	*Triebelina* 1sp.
Cytheropteron 2 spp.	*Triebelina* 1sp.	*Callistocythere* 1sp.	*Loxoconcha* 1sp.	*Tanella* 2 spp.	
Neobuntonia 1sp.	*Cythere*? 1sp.	*Cytherelloidea* 1sp.	*Loxoconchella* 1sp.	*Loxoconcha* 1sp.	
Neocyprideis 1sp.	*Eucytherura* 2 spp.		*Paradoxostoma* 1sp.	*Paradoxostoma* 1sp.	
Loxoconcha 1sp.	*Hemicytherura* 1sp.		*Neomonoceratina* 4 spp.		
	Gen. indet 1sp.		*Pistocythereis*? 1sp.		
	Loxoconchella 1sp.		*Ruggieria*? 1sp.		
	Psammocythere? 1sp.		*Cytherella* 1sp.		
	Neomonoceratina 1sp.				
	Cytherelloidea 3 spp.				

Despite the preliminary nature of the study, a considerable degree of environmental endemism is shown by the fauna of the Pulau Pari reef complex. The degree to which this is more widely applicable to the complex as a whole will be tested when the study is complete.

COMPARISON WITH OTHER REEF FAUNAS

Relatively few studies have been made of the Ostracoda of reef and reef-associated environments and even fewer are directly applicable to the present study. This is either because the nature of the reef body studied is not comparable with Pulau Pari or the descriptions of the environments sampled are such that comparisons between the results are difficult or impossible to make.

A considerable number of ostracod taxa have been described from reef environments but relatively few comprehensive studies of the ecological distribution of Ostracoda in reefs have been made. The majority of these have been carried out in the Caribbean/Gulf of Mexico region. These include Tressler, 1949; Puri and Hulings, 1957; Kornicker, 1958, 1961, 1964; Puri, 1960; Pokorny, 1968; Van den Bold, 1974, 1977; Krutak, 1974, 1982; Krutak and Rickles, 1979; Maddocks, 1974; Teeter, 1975; Keij, 1974, 1975, 1976; Palacios-Fest and Gio-Argaez, 1979.

Neither the reefs nor the reef-associated environments studied in the Caribbean/Gulf of Mexico are directly comparable to Pulau Pari and few are closely similar. Nonetheless, certain aspects of the distribution of the Ostrăcoda are common between the two areas. For example, there are many references to the enhanced diversity and incidence of Bairdiidae in immediate association with coral bioherms and adjacent detrital carbonates (Puri, 1960; Puri and Hulings, 1957; Maddocks, 1974; Teeter, 1975; Keij, 1974). Other than the Bairdiidae, the reef and reef-associated faunas of the Caribbean have many other genera which are also prominent in such environments in the Java Sea. These incude *Jugosocythereis, Caudites, Loxoconcha, Mutilus, Propontocypris, Paracytheridea, Hemicytherura, Xestoleberis* and *Cytherelloidea.*

Teeter (1975) in his study of the Holocene marine Ostracoda from offshore Belize encountered many faunal assemblages which in their generic composition resemble those of the present study. For example, the fauna inabiting the barrier rim, reef flat and apron of the reef flat was dominated by *Bairdoppilata, Triebelina, Loxoconcha* and *Xestoleberis* and also included *Quadracythere, Cytherura* and *Paracytheridea.* Referring to the fauna of these environments Teeter (p. 414) states "The ostracod diversity attains a maximum and, inversely, the dominance shows a marked decrease in the shallow, stable, carbonate-platform environment. Especially striking is the very high diversity of the barrier rim, attributable perhaps to the numerous niches available in complex organic reef associations. The decreased dominance reflects the rising competition between members of the association". Teeter could equally well have been referring to the faunas of the present study from the reef slope (Tables 1, 2, Text-fig. 5).

The back reef lagoon described by Teeter, with water depths between 6 and 60 m cannot be used as a standard of comparison with that of Pulau Pari with a depth of some 2 m.

The most comprehensive study of a Pacific reef is by Allison and Holden (1971) who described the distribution of the Recent Ostracoda of Clipperton Island in the eastern Pacific. The two lagoons are not comparable since that of Clipperton Island is non-marine and inhabited by freshwater cyprids. It is instructive, however, to compare the distribution of the Ostracoda across the Clipperton Island reef profile (Allison and Holden, 1971, p. 171, Table 1) with Text-fig. 5 and Table 1 of the present study. Both incidence and diversity are higher in the present study but in both studies the Bairdiidae are dominant on the seaward side of the reef. *Mutilus* is well represented in both profiles as is *Paracytheridea. Loxoconcha,* a dominant at Pulau Pari is unaccountably absent at Clipperton Island which also lacks *Ornatoleberis* and where *Xestoleberis* is much less diverse. The low diversity of the Clipperton Island fauna is probably due to the isolation of the island from adjacent bodies of shallow water.

The importance of the Bairdiidae in reef environments is not confined to Recent examples. The association is of considerable antiquity extending back to at least the Carboniferous (Bless, 1983). It was certainly very well established in the Upper Triassic of the littoral of the Tethys (Kristan-Tollmann *et al.*, 1980) and has been subsequently documented by many authors in the Cainozoic but particularly in the Upper Cretaceous (Pokorný, 1977; Babinot and Colin, 1983).

Envoi

The strong environmental control imposed on the distribution of Ostracoda in reef and near reef situations has considerable importance with respect to hydrocarbon exploration. Reefs and other carbonate build-ups are, in many areas, important hydrocarbon reservoirs. Krutak (1982) has commented on the importance in this respect, of ostracods in the Gulf Coast Basin. Similarly, Scrutton (1976, 1978) has referred to the importance of the study of the modern reefs in the Java Sea with respect to achieving a better understanding of their oil bearing Miocene counterparts in Indonesia. It is hoped that, when the present study is completed, it will provide data of considerable value in oilfield exploration.

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Distribution of Recent Ostracoda in Ise and Mikawa Bays, Pacific Coast of Central Japan

ANNE-MARIE BODERGAT AND NORIYUKI IKEYA
Université Claude-Bernard, Lyon I, France and Shizuoka University, Japan

ABSTRACT

The relationship between shallow marine environments and ostracod species in Ise and Mikawa Bays on the Pacific coast of central Japan is discussed on the basis of 28 surface sediment samples collected in summer, 1984.

The distribution of benthonic ostracod species is influenced by various parameters of the marine environment. Among them the salinity and the distribution of sediment materials are especially important elements that strongly characterize habitats of benthonic organisms in the bay.

In this study the distribution of the main ostracod associations is also considered in relation to several other environmental parameters. Particular attention is paid to the effects of water pollution on the environment and the ostracod fauna, since the bay areas we investigated are located close to large industrial cities.

INTRODUCTION

The Japanese Archipelago is located on the eastern side of the Asian Continent and is composed of four large and several thousands of small islands aligned from north to south over a distance of some 2,000 km. It is in the Temperate Zone, where the warm Kuroshio Current runs northward from the southern Pacific and the cold Oyashio Current runs southward from the north Pacific.

The wide variety of Recent ostracod species found in the sea areas around this archipelago form unique faunas which differ somewhat from those in other areas. In terms of ostracod biogeography these areas constitute an independent domain called the Japonic Realm (Benson, 1964). Ostracoda from seas around Japan were first investigated by the Challenger Expedition (Brady, 1880). Since then a number of studies have been made by Kajiyama (1912, 1913), Hanai (1957–), Ishizaki (1968–), Schornikov (1969–), Okubo (1975–), Hiruta (1975–), Ikeya and Hanai (1982), Frydl (1982), Abe (1983), etc., which have contributed to clarification of the Ostracoda found a round Japan. The areas investigated so far, however, are only a small part of the sea areas around the Japanese Archipelago whose long shorelines mean that a large number of sea areas have not yet been studied in terms of ostracod faunas. Taking this slow development of ostracod studies into account, it is assumed that the 250 or so Recent ostracod species known to us at present from areas around the Japanese Archipelago will be doubled by future studies in this field. We have also discovered a number of genera and species hitherto unknown as well as some not previously reported from Japan. These new taxa will be described later.

The study of Ostracoda has recently advanced from merely reporting sporadic discoveries of local occurrences to defining the distribution areas of each species. This, in turn, has opened the way for the discussion of speciation processes. However, clarification of speciation processes calls for a large amount of data. In areas around the Japanese Archipelago, however, data on the occurrence of ostracod species are too scarce, partly because of the short history of their study. There is now a definite need to collect more data in order to understand better the Japonic Realm ostracod faunas as well as to enable us to discuss the specific relationships between this and other areas.

The purpose of this study is to clarify the distribution of Recent ostracod species in Ise and the adjacent Mikawa Bay on the Pacific coast of central Japan. This kind of study will enable us to make precise statements about the autoecology of the ostracod species, as well as about the extent to which the environmental parameters influence the species associations.

According to Yoshimura (1934), the large bays around Japan are classified into two types on the basis of their depth; namely, bays with depths of more than 1,000 m, such as Sagami and Suruga Bays, and those with depths of less than 100 m. The latter are classified into two further types: 1) Bays deeper than 50 m with steep shores and less developed tidal flats and deltas, such as Aomori Bay and the Inland Sea, and 2) Those that have depths of less than 50 m with shoals and well developed tidal flats and deltas. Examples of these include Tokyo, Osaka, Ise, and Mikawa Bays, the last two being the objects of this research.

Ise and Mikawa Bays have recently been noted for primary and secondary water pollution caused by waste water discharged from Nagoya, a huge industrial centre which is located behind these two bays. Among the various environmental factors, the distribution of sediment materials is of particular importance, since it strongly affects the abundance and faunal composition of osttracod associations. Attention is also paid to seasonal changes in the environment which, through changes in the constituents of the sediments, affect the ostracod fauna in each station investigated.

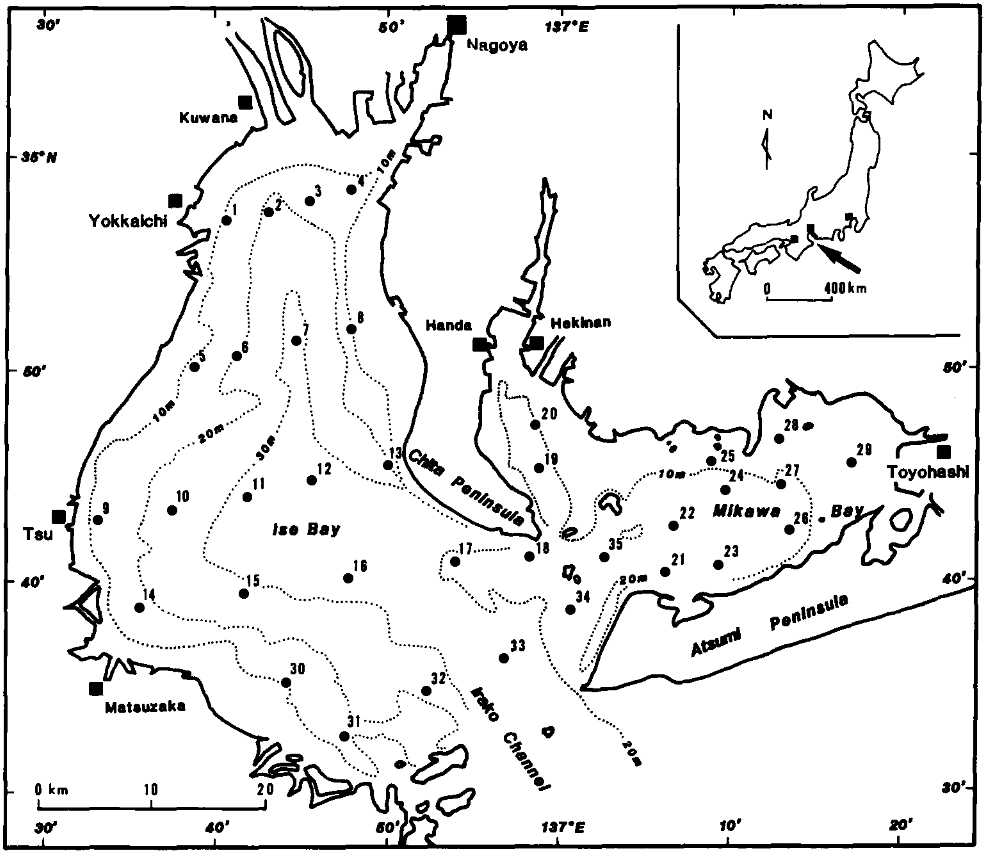
DESCRIPTION OF THE AREAS STUDIED

Ise and Mikawa Bays, like Tokyo, Osaka, and Hakata Bays, are typical examples of the inner bays of Japan in which eutrophication has been notable in recent years. One thing that all these inner bays have in common is that large cities and industrial areas are located in their catchment areas, and thus the discharge load of waste water from these areas is extremely large.

Ise and Mikawa Bays are also typical inner bays of Japan from the geographical point of view in that: 1) They have relatively large areas (Ise Bay has an area of 1,620 km^2 and that of Mikawa Bay is 510 km^2). 2) They are not very deep and the centres of these bays form a furrow (The average depth of Ise Bay is 19 m, while that of Mikawa Bay is 9 m). 3) Large amounts of fresh water from rivers flow into these bays. The total amount of fresh water flowing in annually reaches 80% of the volume of each bay (Saijo, 1984). 4) The mouths of these bays are scattered with islands, and the channels are narrow. Thus the bays are half-closed, and the exchange of water with the open sea is limited (Text-fig. 1).

Sediments: Mud dominates the bottom sediments in all parts of the bays except the mouths and coastal parts. Coarse materials increase towards the mouth of both bays, and gravel is distributed around the basement which is composed of Tertiary and Pre-Tertiary rocks and is exposed in the channel part. Distribution of the bottom surface sediments based on grain size analysis is shown in Text-fig. 2. In this research we also classified the bottom sediments into seven types based on the particles which were left on a 200 mesh sieve (see the sediments types IV and Text-figs. 2 and 3).

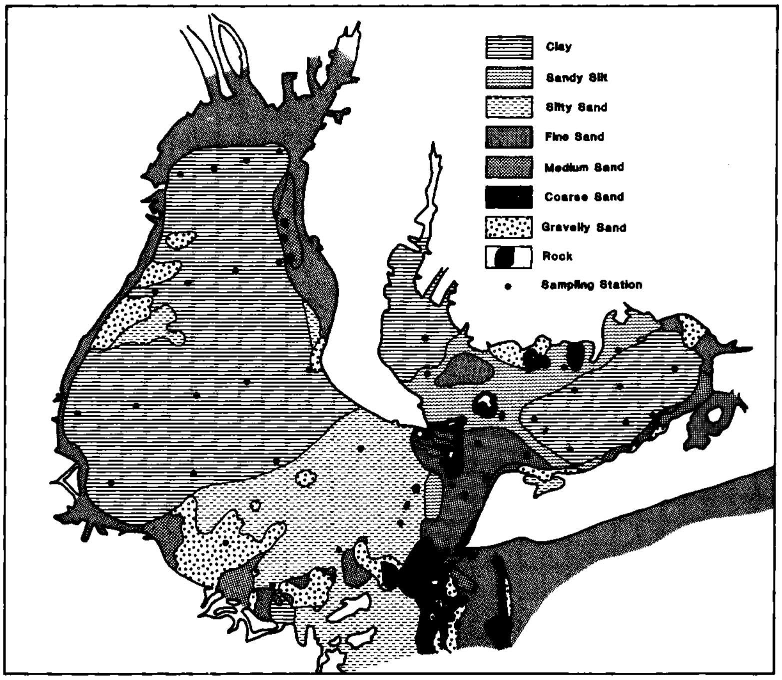
Currents: Two kinds of water current exist in these bays; namely, the tidal current which changes periodically twice a day and the residual current, which is the mean of all the currents. The tidal



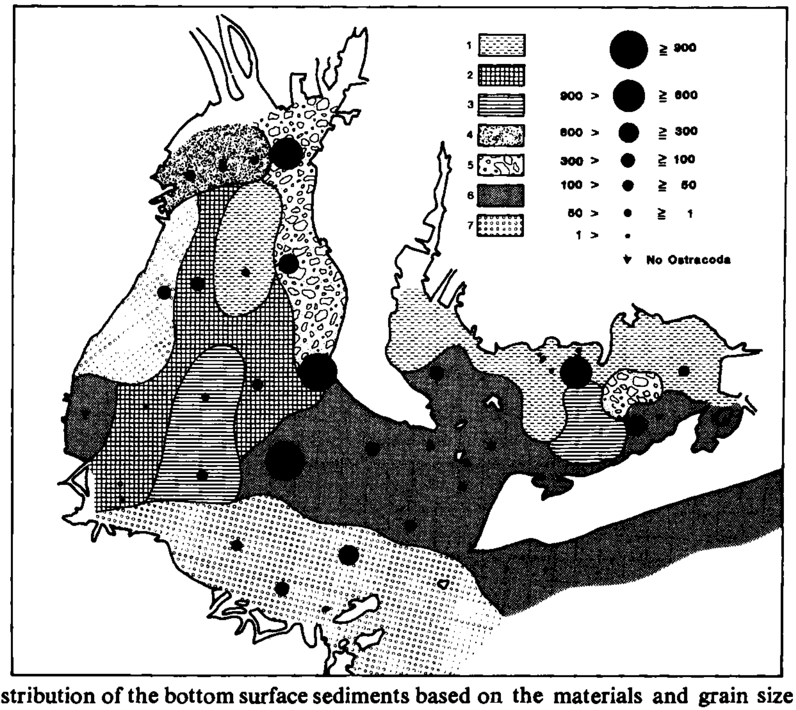
TEXT-FIG. 1—Physiography of Ise and Mikawa Bays and sampling station locations.

current, which flows in from the open sea through Irako Channel reaches speeds of as much as 2 kts around the channel. It then branches into Ise and Mikawa Bays, and the current speed decreases to 0.4 kt and 0.2 kt, respectively, towards the head of each bay. The main part of the tidal current in Ise Bay runs along the Chita Peninsula, and the western part of this bay forms a counter current area. Another branch, which passes through the Morozaki and Nakayama Channels, enters Mikawa Bay, and then further divides into two streams, one of which runs towards the north and the other towards the east. The residual current, although its velocity (about 0.1 kt) and constancy are not great, is important because of its effect on the formation of water masses and distribution of substances in the bay. This current is evident in summer, but not in winter. Roughly speaking, a counterclockwise circular current is seen in the southern half of Ise Bay, and a clockwise current in the northern half; whereas in Mikawa Bay a counterclockwise current is found in the central and inner parts, and an outward stream near the mouth of the bay. In addition, a vertical circulation has been observed near the mouth which flows inward in the bottom layer and outward in the upper layer of water (Unoki, 1978).

Temperature and Chlorinity: The two bays resemble each other with respect to seasonal changes in the water temperature and the chlorinity. In winter the upper and lower water layers in these bays are well-mixed and thus the water temperature is slightly higher in the lower layer than in the upper, *i.e.*, inversion of water temperature takes place. However, inversion is not observed in the water density. Isopleths representing 17 ‰ and 19 ‰ chlorinity are used as indices of the limits of open sea influence and land drainage, respectively. In spring stratification develops slowly in the water in the bays; in May the isopleth representing 17 ‰ chlorinity moves to the mouths of the



TEXT-FIG. 2—Distribution of the bottom surface sediments based on grain size analysis (after Aichi Fisheries Experimental Station, 1970).



TEXT-FIG. 3—Distribution of the bottom surface sediments based on the materials and grain size of the particles which were left on a 200-mesh sieve (1: Diatom facies, 2: Diatom and pellet facies, 3: Pellet facies, 4: Fine biogenic facies, 5: Coarse biogenic facies, 6: Fine to medium sand facies, 7: Coarse sand facies). Circles indicate the total number of ostracod specimens per unit sample (1cc).

bays. In summer stratification reaches its peak. Both the isopleths representing the water temperature and those representing the chlorinity become parallel to the water surface in the bay. The top layers down to 10 m deep are all occupied by water with a high temperature and low chlorinity (17 ‰). In autumn, stratification is promptly destroyed, an event which takes place in September (Unoki, 1984).

Transparency: The transparency is used as an index of marine pollution, *i.e.*, it is closely related to the amount of chlorophyll produced by phytoplankton which causes secondary pollution of the sea water. In these areas the transparency increases in winter and decreases in summer, and it decreases towards the head of the bay. The isopleths of transparency are similar to those of chlorinity. Transparency in these areas has decreased radically from 6 m to 3 m over the decade from 1961 to 1971. In 1980 as many as 98 occurrences of red tide blooms were observed, lasting for 297 days in total. Occurrences of red tide blooms have been increasing in the last decade, and are now 2.7 to 4 times as common as a decade ago. Sekiguchi (1975) reported that species of the genus *Conodiscus* dominate among the diatoms which cause red tide blooms. Concentrations of more than 0.1 ppm inorganic nitrogen and more than 0.015 ppm inorganic phosphorous are used as indicators of the occurrence of red tides (Unoki, 1984).

Low oxygen water mass: In summer the oxygen concentration decreases, not only since oxygen transport from the upper to the lower layer is prevented by the stratification, but also because organic substances dropping from the upper layer decompose. This phenomenon has been particularly notable in Mikawa Bay where the size of the low oxygen water mass has been increasing year after year, sometimes covering even the whole bay.

MATERIALS AND TECHNIQUES OF STUDY

During the "84–R–5" Cruise by the research vessel "Seisui-maru", a Mie University, Faculty of Fishery, on June 2nd (Stations 1–13) and 3rd (Stations 14–35) 1984, 35 sediment samples were collected in Ise and Mikawa Bays. The sediment samples were collected by a Smith-McIntyre grab sampler (32 × 35 cm in surface; 18 cm in maximum depth) at stations disposed all over the bays at intervals of 3 to 10 km, so that they represent practically all parts of the bays. In this study we examined 23 samples from Ise Bay and 5 from Mikawa Bay (Text-fig. 1). About 500 cc was taken from the surface part of each muddy or sandy sediment sample, stained with Rose Bengal, washed immediately through a 200–mesh sieve (74 μm openings), and then dried. We tried to collect at least 200 specimens of ostracod individuals at each station, though this object was not achieved at all the stations. Living individuals were easily distinguished by the reddish coloured soft parts when stained with Rose Bengal. The volume of each surface sediment sample was measured in order to calculate the numbers of individuals and species per cubic centimetre. It should be noted that the volumes measured are those of the dried samples. The volumes of the raw samples were not measured exactly. It is expected, however, that the dried sample volumes, in combination with the sediment types in these sea areas which we studied before, will be of use in estimating the population density of each ostracod species.

All the ostracod specimens used in this study are deposited in the Institute of Geosciences, Faculty of Science, Shizuoka University.

THE SEDIMENT TYPES

To benthonic organisms the bottom surface sediment characteristics, which form their habitats, are of particular importance. In most ecological studies the sediments are classified on the basis of particle size. Sediment grain size distribution in a particular sea area is the net result of various physical agencies and is one of the fundamental parameters of the environment which reflect certain aspects of the hydrographic conditions. However, the sediment composition is no less important to the benthonic organisms than the grain size distribution.

In this research we identified the constituent components of the particles retained on a 200-mesh sieve (74 μm opening), and recognized seven sediment types on the basis of their component substances and grain size distribution (Text-fig. 3). We also discuss the relationship between the sediment types classified by this method and the ostracod species distributions.

The component substances of the sediments and their approximate amounts are summarized in Table 1. Below are brief descriptions of the seven sediment types.

I) Coarse biogenic facies (Stations 4, 8, 13 and 27): This facies is distributed along the eastern coast of Ise Bay and the eastern part of Mikawa Bay. The main components of this facies include coarse grains, molluscan shells and shell fragments, fragments of fish bone, spines and plates of echinoderms. Pellets and rock fragments are also found, although they are not abundant; the former increase slightly towards the head of the bay, and the latter towards the mouth. The foraminifers inhabiting this facies include the agglutinated *Trochammina hadai* which increases towards the head of the bay, and the calcareous Miliolid species and *Nonionella stella* which increase towards the mouth. At station 13, which is close to the mouth of the bay, a small number of planktonic foraminifers are also found.

II) Fine biogenic facies (Stations 1, 2 and 3): This facies is distributed in the innermost parts of Ise Bay. Its components, like those of the previous facies, include minute fragments of molluscs, fish, and echinoderms. Pellets and diatom frustules are commonly found as well. Only two species of foraminifers, *Trochammina hadai* and *Haplophragmoides* sp., both agglutinating forms, inhabit this facies.

III) Diatom facies (Stations 7, 20, 22, 25, 28 and 29): This facies is distributed along the northern coast of Mikawa Bay and in the northern part of Ise Bay. Pelagic diatom frustules, mainly *Coscinodiscus* spp., are its major component, while minute fragments of echinoderms, gastropods, pelecypods, and fish bone are minor constituents. Pellets and rock fragments are almost never found; instead mica and plant fragments, which easily become suspended in water, occur in large quantities. Among the foraminifers, *Trochammina hadai* is found at all the stations except station 20. Miliolid species, although in very small numbers, are present at all the stations.

IV) Pellet facies (Stations 11, 15, 23 and 24): This facies is found in the deep central parts of Ise and Mikawa Bays. The major components are rugby-football-shaped particles of three different sizes, the first large (0.8–0.4 mm in major axis, 0.5–0.2 mm in minor axis), the second medium (0.6–0.2 mm in major axis, 0.3–0.1 mm in minor axis), and the third small (0.1–0.2 mm in major axis, 0.05–0.1 mm in minor axis). Although the pellet sources are not identified, the first two forms are probably attributable to polychaetes or gastropods (Schafer, 1953), whereas the last one, which is dominant in station 15, is likely to be from copepods because of its size (Sekiguchi, 1975). Fragments of echinoderms, gastropods, pelecypods, and fish bone are common, although much less in quantity than the pellets. Diatoms, plant fragments, mica, and other pelagic materials are almost non-existent. Medium grained quartz and schist fragments are also present at station 15. Of the foraminifers, *Trochammina hadai* is the only species found at station 11, whereas Miliolid species and *Nonionella* sp. are present at station 15.

V) Diatom and pellet facies (Stations 6, 10, 12 and 14): This facies is widely distributed on the outer side of the pellet facies in Ise Bay. Pellets produced on the bottom and diatom frustules produced in the water column occur in almost equal amounts. Calcareous biogenic materials are not present in significant amounts. Mica and rock fragments are found in small amounts at station

TABLE 1—LIST OF THE SAMPLING LOCATIONS, THE DEPTHS, AND THE BOTTOM CHARACTERS OF THE STATIONS

Station No.	N. Lat.	E. Long.	Depth (m)	Bottom characters													
				I	II	III	IV	V	VI	VII			VIII	IX	X	XI	
										p	a	c				M	R
1	34°57.10′	136°40.49′	9.3	M	++	++	+	—	—	—	•	—	+	+	+	++	—
2	34°57.62′	136°42.72′	21.8	M	++	++	+	—	—	—	+	+	+	+	•	—	—
3	34°57.94′	136°45.05′	17.6	M	++	+	+	—	—	—	•	—	+	+	—	—	—
4	34°58.26′	136°47.36′	12.5	M	+	++	++	—	—	—	+	+	•	++	•	•	—
5	34°50.07′	136°38.46′	9.5	*1 gM	•	•	•	—	—	—	—	—	—	—	—	—	++
6	34°50.57′	136°40.90′	19.0	M	+	•	+	—	—	—	•	•	++	++	—	•	•
7	34°51.20′	136°44.40′	31.3	M	—	•	•	—	—	—	•	•	++	•	—	—	—
8	34°51.71′	136°47.47′	17.5	M	++	++	++	—	—	—	•	•	+	+	—	•	•
9	34°42.65′	136°33.16′	11.7	M	—	•	•	—	—	—	+	—	+	+	•	++	•
10	34°43.21′	136°37.36′	24.3	M	•	•	+	—	—	—	•	—	++	++	+	•	•
11	34°43.75′	136°41.57′	29.9	M	•	•	•	—	—	—	+	—	•	++	—	•	•
12	34°44.41′	136°45.68′	33.0	M	+	+	•	—	—	—	•	•	++	+	•	•	•
13	34°45.13′	136°49.85′	28.0	*2 sM	++	•	++	—	—	•	•	+	•	•	•	+	+
14	34°38.58′	136°35.74′	19.5	M	•	•	•	—	—	—	•	—	++	++	•	+	•
15	34°39.07′	136°41.54′	29.3	sM	+	+	+	—	—	—	—	•	•	++	—	•	+
16	34°39.90′	136°47.55′	33.3	sM	•	•	•	—	—	—	•	•	•	•	•	++	+
17	34°40.48′	136°53.57′	19.1	fs	+	•	•	—	—	—	•	•	—	•	—	+	++
18	34°40.60′	136°58.11′	10.3	fs	•	•	•	—	—	—	—	•	—	—	—	+	++
19	34°45.07′	136°58.63′	12.0	*5 fs	•	•	—	—	—	—	•	•	—	—	—	++	++
20	34°47.40′	136°58.09′	11.9	*5 M	+	+	+	—	—	—	•	•	++	—	—	++	•
21	34°40.22′	137°05.31′	12.5	fs	+	+	+	—	—	—	•	•	—	—	—	+	++
22	34°42.46′	137°65.08′	17.0	M	+	+	•	—	—	—	+	•	++	•	•	++	•
23	34°41.23′	137°09.79′	12.8	M	•	++	+	—	—	—	—	—	•	++	—	—	—
24	34°43.55′	137°09.23′	13.0	M	—	+	•	—	—	—	+	—	+	++	—	—	—
25	34°45.51′	137°08.53′	8.5	M	•	+	+	—	—	—	++	•	++	•	+	+	•
26	34°42.12′	137°13.20′	10.0	M	•	+	•	—	—	—	++	—	—	+	•	+	++
27	34°44.43′	137°12.89′	9.5	M	+	++	+	—	—	—	+	—	+	+	+	—	•
28	34°46.43′	137°12.40′	6.0	M	—	•	+	—	—	—	++	•	++	—	+	+	+
29	34°45.44′	137°16.70′	6.7	M	•	•	•	—	—	—	+	•	++	—	+	+	•
30	34°35.63′	136°44.47′	15.3	fs,G	•	+	•	+	+	—	—	•	•	—	—	—	++
31	34°32.23′	136°47.29′	22.1	*1 sMG	•	+	•	—	+	—	—	•	—	•	+	•	++
32	34°34.28′	136°51.89′	22.4	*2,3 fs	+	+	+	—	+	—	•	+	—	•	—	+	++
33	34°36.18′	136°56.19′	32.9	*2 fs	•	•	•	—	—	•	—	+	—	—	—	+	++
34	34°38.15′	137°00.34′	12.4	fs	+	•	•	—	—	—	—	++	—	—	—	+	++
35	34°40.61′	137°02.24′	13.4	*3,4 fs	•	•	•	—	—	—	—	+	—	—	—	+	++

++, abundant; +, common; •, rare; —, non.

I: Macroscopic observations. M: Mud, gM: Gravelly mud, sM: Sandy mud, fs: Fine sand, G: Gravel. *1: Living polychaetes were abundant. *2: Living echinoderms were abundant. *3: Living gastropods and pelecypods were abundant. *4: Living ophiuroids were abundant. *5: The transparency of water was less than 1m because of red tide blooms. II-XI: Microscopic observations. II: Fragments of spines and plates of echinoderms; III: Shells of molluscs (gastropods, scaphopods, and pelecypods), fragments of them, and juveniles; IV: Fish bones, vertebral columns and parts of skeletons of small fish, and scales of fish; V: Fragments of thoracics; VI: Spicules of cornacuspongids; VII: Foraminifers (p: planktonic, a: agglutinated, c: calcareous test); VIII: Diatom frustules; IX: Pellets excreted probably by invertebrates, such as polychaetes, gastropods, and copepods; X: Fragments of plants; XI: Rock fragments. (M: Mica fragments, R: Quartz particles and fragments of gneiss, schists, etc.)

14, which is close to the coast, but do not occur at any other station. Of the foraminifers, the agglutinated *Trochammina hadai* is dominant at all the stations. Calcareous forms are very rare and are only seen in *Nonionella* sp. and Miliolid species at stations 6 and 12.

VI) Fine to medium sand facies (Stations 9, 16, 17, 18, 19, 21, 26, 33, 34 and 35): This facies is widely distributed in the coastal part of Mikawa Bay along the Atsumi and Chita Peninsulas, around the mouth of this bay (Morozaki and Nakayama Channels), the eastern part of the mouth and the western part of Ise Bay. Calcareous biogenic materials are rare. Fine to medium grained sands made of rock fragments are the major component together with abundant mica fragments. Of the agglutinated foraminifers, *Trochammina hadai*, is rare at stations 17, 19 and 21 although at station 26 it is abundant. Of the calcareous foraminifers, the Miliolidae-*Nonionella* assemblage is dominant at station 19, whereas the *Ammonia-Elphidium* assemblage dominates the other locations near the mouth of the bay. Tests of calcareous foraminifers are particularly abundant at stations 34, 35 and 36, which are located in the channel area.

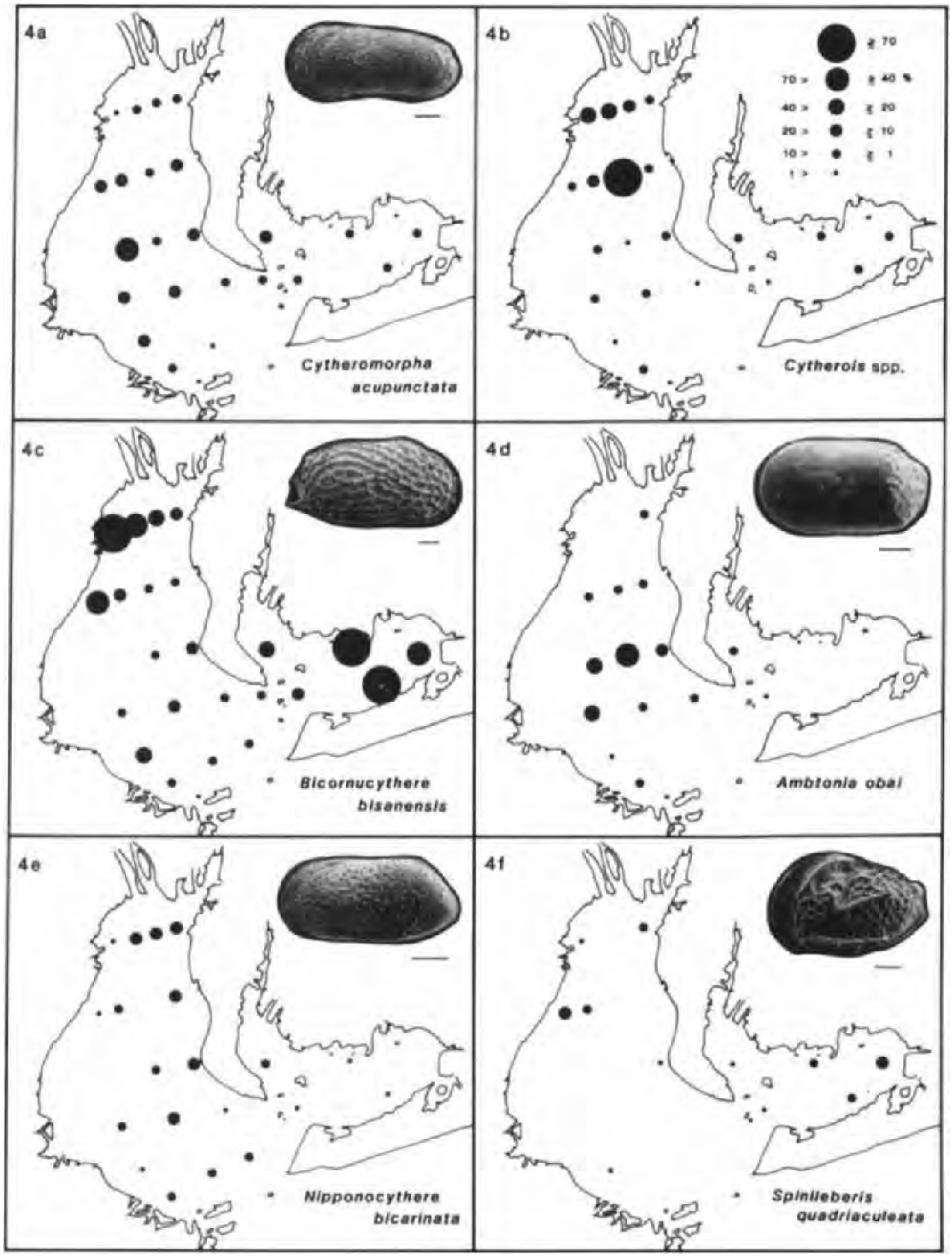
VII) Coarse sand facies (Stations 5, 30, 31 and 32): This facies is distributed along the western coast of the inner part of Ise Bay and in the western part of the mouth of the bay. Rock fragments are present in large amounts but mica is not abundant. Calcareous biogenic materials are extremely rare at station 5, whereas molluscan shell fragments, although not abundant, are commonly found at the mouth of the bay. Sponge spicules occur at three stations near the mouth of the bay. Large quantities of Balanus fragments are found at station 30. Fragments of echinoderms, gastropods, pelecypods, and fish bones are all abundant at station 32. Foraminifers are found only at stations near the mouth of the bay. A number of species are identified including Miliolid species, *Ammonia beccarii*, and some oceanic species such as *Cibicides lobatulus, Hanzawaia nipponica*, and *Rosalina* sp.

DISTRIBUTION OF OSTRACODS IN RELATION TO ENVIRONMENTAL PARAMETERS

Ostracods were examined at 23 stations in Ise Bay and 5 in Mikawa Bay, out of a total of 35 sampling stations in these bays. Station 9, in the western part of Ise Bay, was barren of ostracods and only one ostracod was found at stations 10 and 14 respectively, in spite of the large quantity of sediment examined. At all other stations significant numbers of ostracod individuals were collected.

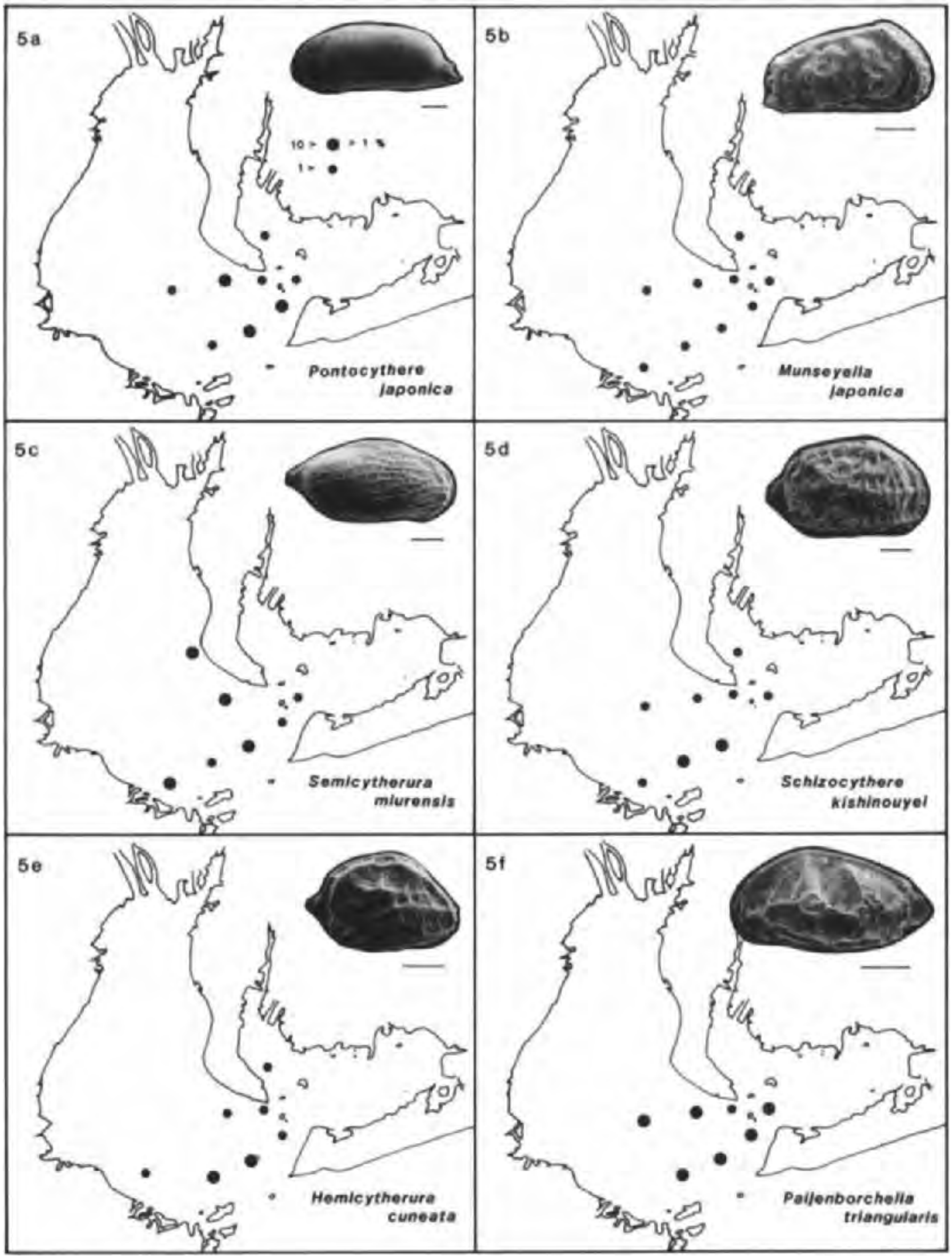
A total of 63 genera and 127 species were recognized, and living and dead specimens were distinguished as well. The total number of specimens per unit volume (1cc) from each station are shown in Text-fig. 3. Distribution maps of 12 species that are characteristic of these bays are shown in Text-figs. 4 and 5. It is apparent from Text-figs. 4 and 5 that some ostracod species are distributed all over the bays, while others are restricted to either the inner parts, deep areas in the centre, shallow coastal regions, or the mouth of the bay. It is interesting to see that the occurrences of some taxa are characteristically concentrated in particular areas.

Among the various environmental parameters, the grain size distribution and composition of the bottom sediment, salinity of water, spreading of terrestrial materials, etc. have often been referred to by some researchers (Ishizaki, 1968–1971) as major elements that determine or influence ostracod distribution. We must remember, however, that the distribution of carapaces of any particular species ultimately preserved in the bottom sediments may not necessarily reflect the distribution of the individuals of that species during life. Clarification, by reference to the hydrographic conditions, is needed on whether carapaces in the sediments belonged to autochthonous individuals or were transported from neighbouring areas.



TEXT–FIG. 4—Distribution of the six species characteristic of the bays. 4a: *Cytheromorpha acupunctata* (Brady, 1880), left valve male (St. 6), IGSU-O-486. 4b: *Cytherois* spp. 4c: *Bicornucythere bisanensis* (Okubo, 1975), right valve female (St. 1), IGSU-O-487. 4d: *Ambtonia Obai* (Ishizaki, 1971), left valve female (St. 11), IGSU-O-488. 4e: *Nipponocythere bicarinata* (Brady, 1880), left valve male (St. 8), IGSU-O-489. 4f: *Spinileberis quadriaculeata* (Brady, 1880), left valve female (St. 26), IGSU-O-490. (Bars below the figures of species indicate 100 microns respectively.)

Circles indicate the percentage of individual specimens of the species for all ostracod specimens obtained from the station.



TEXT-FIG. 5—Distribution of the six species characteristic of the channel area. 5a: *Pontocythere japonica* (Hanai, 1959), left valve male (St. 34), IGSU-O-491. 5b: *Munseyella japonica* (Hanai, 1957), right valve female (St. 32), IGSU-O-492. 5c: *Semicytherura miurensis* (Hanai, 1957), right valve male (St. 31), IGSU-O-493. 5d: *Schizocythere kishinouyei* (Kajiyama, 1913), right valve female (St. 36), IGSU-O-494. 5e: *Hemicytherura cuneata* (Hanai, 1957), right valve female (St. 32), IGSU-O-495. 5f: *Paijenborchella triangularis* (Hanai, 1970), left valve male (St. 34), IGSU-O-496. (Bars below the figures of species indicate 100 microns respectivelly.)

Circles indicate the percentage of individual specimens of the species for all ostracod specimens obtained from the station.

Substrate: According to observations by Ishizaki (1968–1971), the distribution of some ostracod species is not restricted by the bottom surface sediment types; it even seems to be independent of the distribution of the sediment types. Some examples of such ubiquitous species were in fact found in this research as well.

One must remember, however, that both Ishizaki's work and this research describe the distribution of ostracod species in terms of the total number of ostracod individuals of each species, including both living and dead specimens, which may not necessarily reflect the distribution of the living individuals of that species. Carapaces of dead individuals of certain species inhabiting seaweeds on rocky shores and sandy shallow bottoms are transported by water currents, sorted with the sediment materials, and then deposited at various places. Carapaces of dead individuals are thus dispersed over wide areas extending far beyond those of living individuals, although their occurrence becomes sparser as distance increases from the living habitat. In the area studied *Cytherois uranouchiensis, C. nakanoumiensis,* and many juvenile valves of *Loxoconcha modesta* are among the species that show such a tendency; they are distributed over wide areas without being restricted by the bottom sediments. However, attention must be drawn to the numerous valves of *Cytherois* spp. concentrated at station 7 (Text-fig. 4b). These species inhabit the seaweed zone on rocky shores but not the muddy bottoms of central areas of the bay. Since their valves are thin and light they were probably carried in suspension like diatom frustules and deposited by currents in the central area of the bay. If so, they also fit into the postulated relationship with the sediment types in our classification. Transportation of ostracod valves has already been pointed out by Kontrovitz (1975) and Kontrovitz and Nicolich (1979).

Some individuals of certain benthonic species that are found in great abundance at particular stations, such as *Bicornucythere bisanensis, Cytheromorpha acupunctata, Ambtonia obai, Nipponocythere bicarinata,* and *Spinileberis quadriaculeata,* prove to have been transported from their native habitats giving them an extended distribution area which is seemingly independent of sediment type. In such cases one can specify the living habitats of these species and their characteristic sediment types to some extent, since individuals, particularly living ones, are abundant in some places and rare at others to which they have been transported. The five species listed here are all characteristic of muddy-fine sediments of inner bays.

Bicornucythere bisanensis, as pointed out by Abe (1983), inhabits mainly mud-rich sediments in inner bays where the bottom currents are weak enough to allow deposition of a flocculent layer on the bottom. In fact, this species is most densely concentrated in the innermost parts of these bays (Text-fig. 4c). *Cytheromorpha acupunctata* and *Ambtonia obai* are distributed in deeper areas in the centre of the bay, where the mud content is higher. *Nipponocythere bicarinata* is distributed all over these bays, whereas *Spinileberis quadriaculeata* is concentrated in shallow areas along the coast, where the mud content is not so high. The former, in comparison with the latter, tends to be more densely distributed in areas where the sediment grain size is slightly larger. The latter is restricted to the inner parts of both bays which are exposed to land drainage flowing in, suggesting that this species is more adapted to a brackish environment.

Both *Pistocythereis bradyi* and *P. bradyformis* are found on muddy sand but have different distribution areas, the former occurring in the inner parts of the bay, the latter near the mouth. No living specimens of these two species have been found and the living habitats are not yet known.

Pontocythere spp. and *Callistocythere* spp. are distributed at stations near the mouth and the channels of the bays, where the sand content is high. This agrees with the results of previous research conducted in other areas.

Semicytherura miurensis, Schizocythere kishinouyei, Hemicytherura cuneata, Paijenborchella triangularis, Munseyella japonica, etc. are also found exclusively at places near the mouth of the bay where the sand content is high.

The numbers of living and dead specimens taken as a whole, indicate the net results of the environmental parameters at that place. It is expected that this will provide information which will be useful in dealing with fossil ostracod assemblages.

Marine and terrestrial influences: The influence of water flowing in from rivers is particularly significant in these bays, compared with that of marine water which is introduced only through the narrow mouths of the bays. Fresh water and various other substances carried in by rivers are mixed with sea water and cause changes in the water and bottom sediments. The extent to which these changes take place is not constant, but varies from one place to another in the bay. Distribution of ostracod species is also diverse, of course, in correspondence with the variations in the environment. Occurrence of both marine and brackish species at any one place is considered to indicate that the place is under the influence of both marine water and land drainage. This has already been suggested by Wagner (1957), Rosenfeld (1979), Bodergat (1983), and Maddocks and Locklin (1982).

The amount of land drainage introduced is particularly large near the head of the bay and the mouths of rivers along the coast, and its influence is assumed to be most significant. However, almost no fresh water ostracod species have been found which would have been transported by rivers. The brackish water species inhabiting these areas include *Bicornucythere bisanensis* and *Spinileberis quadriaculeata*. The maximum numbers of *Cytheromorpha acupunctata* and *Ambtonia obai*, which have been regarded as brackish water species, were found at stations 11 and 12, respectively. These stations are all located in the deep area in the centre of the bay which is not under the direct influence of river water. The fact that no living specimens were found at these stations might imply that the carapaces found there were transported from the neighbouring areas and deposited there.

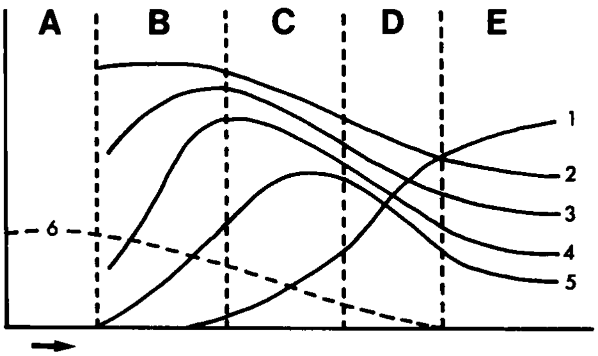
The distribution patterns of *Nipponocythere bicarinata, Pistocythereis bradyi,* and *Trachyleberis niitsumai* are similar to each other. They are concentrated near the head of the bay, but found all over the bay as well although extremely rare near the mouth of the bay. We assume that these species are characteristic of the inner bays where the salinity is lower than in normal marine water.

According to Hanai (personal communication), *Krithe* sp. has a natatory life style. This species is densely distributed along the eastern coast of Ise Bay, which forms the route of marine water flowing into the bay. This species is smaller in size than those from offshore bottom sediments, and is likely to be a new species that has adapted to shallow sea environments.

As for *Trachyleberis scabrocuneata* and *Pistocythereis bradyformis,* Ishizaki (1968 and 1971) has found a large number of individuals in muddy bottom sediments in bays. In the areas we studied, however, their distribution is restricted to the mouth of the bay which is under the influence of marine water, and does not include the inner parts of the bay. The species listed in Text-figure. 5 are considered to be those under strong influence of marine water.

Industrialization: Water pollution has been particularly notable in recent years because of rapid urbanization and industrialization. With the increase in water pollution, the number of species (S) and population density (D), as well as the number of individuals (I) over the number of species (S) of the benthonic organisms, increase moderately until the amount of precipitation of the polluting substances on the sea bottom reaches some limit. Once this limit is reached, however, (S) decreases first, followed by (D), while the ratio (I)/(S) increases. Further increase in precipitation of the polluting substances causes a radical decrease in both (S) and (D), as well as some decrease in the ratio (I)/(S). Still further increase in pollution makes habitation by living organisms totally impossible (Kitamori, 1984) (Text-fig. 6).

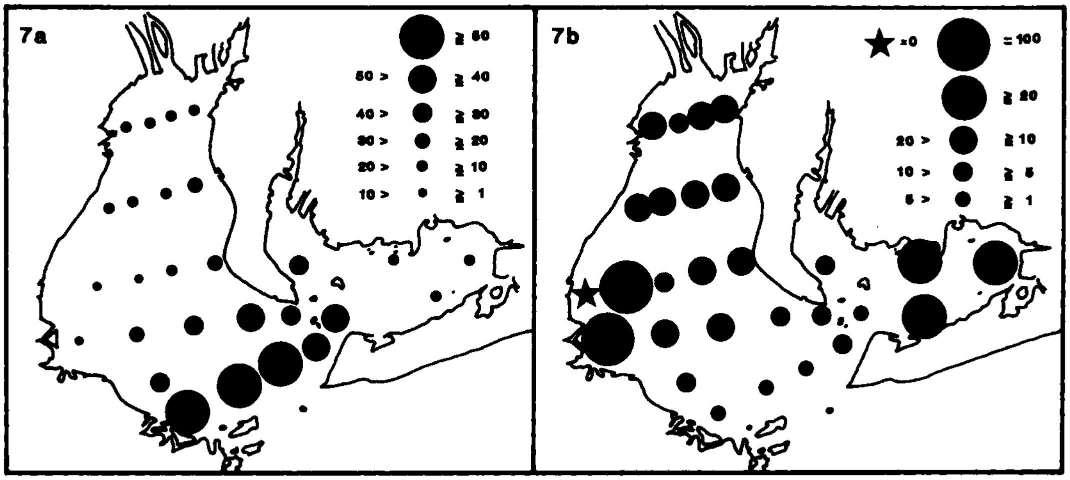
The benthonic organisms include polychaetes, molluscs, crustaceans, echinoderms, and so forth; among these, the first two are dominant on the muddy bottom in the inner bay. It is generally assumed that the polychaetes are quite resistant to pollution, while the crustaceans are rather sensitive and have low tolerance. Iwaki *et al.* (1976) referred to the polychaete *Paraprionospio pi-*



TEXT-FIG. 6—Schematic diagram showing the transitions in the benthonic faunas in relation to the degree of organic pollution (After Kitamori, 1984). A: azoic area, B: pollution area, C: over-trophic area, D: eutrophic area, E: normal marine area, 1: percentage of Crustacea, 2: percentage of Polychaetes, 3: number of individuals/species, 4: number of individuals, 5: number of species, 6: amount of contaminants in sediment. Arrow shows distance from the outlet of waste water.

nata as an index of the extent of pollution in this bay. According to their report, with the increase in water pollution this species has expanded its distribution area continuously since 1946 until it covered the whole area in 1968. Large sized pellets, probably from the polychaetes, are found more or less at all the stations except those in the channel area. They are particularly abundant in the deeper area in the centre of the bay where the bottom sediments are composed almost exclusively of pellets. Large amounts of pellets are found also near the mouths of rivers, which are adjacent to large cities.

Crustaceans are supposed to be very sensitive to water pollution. Although we do not have data on crustaceans in general in this area, nevertheless, we have tried to interpret the distribution of the ostracods, which are one class of Crustacea, in relation to water pollution. The first observation concerns the number of ostracod species at various stations (Text-fig. 7a). More species are distributed around the mouth of Ise Bay and along the western coast of the Chita Peninsula which is on the route of marine water flowing into the bay than elsewhere. On the other hand, less variety of species is seen as the distance increases from the route of the marine water. This probably means that the more marine water flows in, the slower the pollution tends to be. It also suggests that pollution is already higher in the northern and western parts of Ise Bay and in all parts of Mikawa Bay. Secondly, the population densities at different locations (Text-fig. 3) proved to be parallel with the number of species at most stations, but unexpected high productivities were also observed at some stations against this general tendency. The fact that station 28 in Mikawa Bay is free from pollution may be because there is no river flowing in near this station and the bottom is rocky in this area. The low population densities in the channel areas, through which marine water flows in, may be attributed to the coarseness of the component particles of the bottom sediments. Finally, comparison of the ratio of the number of individuals (I) over the number of species (S), which is the simplest index of diversity between different stations (Text-fig. 7b) makes it clear which parts of this area are most polluted. The inner part of Mikawa Bay and the western part of Ise Bay are shown to be polluted on this basis. Three of the stations in the latter area are the most polluted and are devoid of living organisms. Not only are ostracod valves almost never found, but fragments of other organisms are also missing in these areas. This map also suggests that normal marine environments which are free from pollution are still preserved around the mouth of these bays and in the channel area.



TEXT-FIG. 7—Distributions of the number of species and the diversity index. 7a: Distribution of the number of species. 7b: Distribution of the diversity index based on the total number of individuals compared with the total number of ostracod species.

It may be said that *Cytheromorpha acupunctata,* which is relatively abundant in polluted areas, is more resistant to pollution than the other ostracod species. Rosenfeld and Ortal (1982) has already presented an analogous interpretation with respect to other ostracod species from polluted areas.

Another source of pollution was detected at station 13. Microscopic observation of sediment samples from this station, although washed with water before observation, revealed some dark spots which are probably oil stains. This may be another example of the type of pollution reported by Kaesler, Smith and Whatley (1979).

More calamitous to the ostracod populations may be the industrial waste water which contains high concentrations of heavy metals. Accumulation of these metals, judging from the sedimentation rates determined by 210 Pb, has been increasing since 1960 (Sue *et al.*, 1982). Chromium, zinc, copper, lead, and other metal contents are higher in the inner parts of the bay. It is possible, in effect, that these metals have their source not only in the industrial wastes but also in detritus materials carried by the rivers flowing into the bay. Nevertheless, it is interesting to note that the ostracod productivity is lowest where the concentration of either zinc, lead, chromium, or copper is highest. At present, however, we can only infer the relationship between the ostracod associations and the accumulation of heavy metals from the industrial sources, on the basis of what we have known about these two. Direct evidence of the response of the ostracods to the industrial pollution is very poor. So far, only Bodergat (1978) has demonstrated this in the case of the abnormally high cerium content in the Gulf of Marseille which is attributed to an accidental exposure to industrial drainage.

CONCLUSIONS

All the ostracod species distributed in this region are those characteristic of the warm Kuroshio current. They are classified into five groups on the basis of their patterns of distribution in the bays: 1) The species which are evenly distributed all over the bays (*e.g. Nipponocythere bicarinata* and *Cytheromorpha acupunctata*), 2) Those that are concentrated in the channel area (*e.g. Pontocythere* spp., *Callistocythere* spp., *Munseyella japonica,* etc.), 3) Those that are concentrated in the inner parts but are distributed all over the bay as well (*e.g. Bicornucythere bisanensis*), 4) Those that are restricted to the inner parts of the bay (*e.g. Spinileberis quadriaculeata*), 5) Those that are concentrated in the deeper area in the centre of the bay (*e.g. Ambtonia obai* and *Cytherois* spp.)

The distribution patterns of the species listed here do not necessarily reflect the habitats of living individuals of these species, since it is very likely that some individuals were transported from their native habitats to other places after death. However, it seems reasonable to assume that the places where any particular species is densely distributed are also main habitats of that species. One exception to this rule of thumb involves *Cytherois* spp., which behave like diatom frustules. They are dispersed all over the bay, but are deposited mostly in particular areas where the water current is stagnant.

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Preliminary Study on the Ecology of Ostracods from the Moat of a Coral Reef off Sesoko Island, Okinawa, Japan

RYOICHI TABUKI AND TOMOHIDE NOHARA
University of the Ryukyus, Nishihara, Okinawa, Japan

ABSTRACT

The authors studied the ecology of intertidal and subtidal ostracods living in the moat of a coral reef off Sesoko Island, Okinawa Japan. Here, the preliminary results on the species composition of ostracods and its seasonal change are shown in relation to substrates (green algae, *Ulva pertusa*; red algae, *Jania decussato-dichotoma*; filamentous algae on gravels; sand) and water depth.

INTRODUCTION

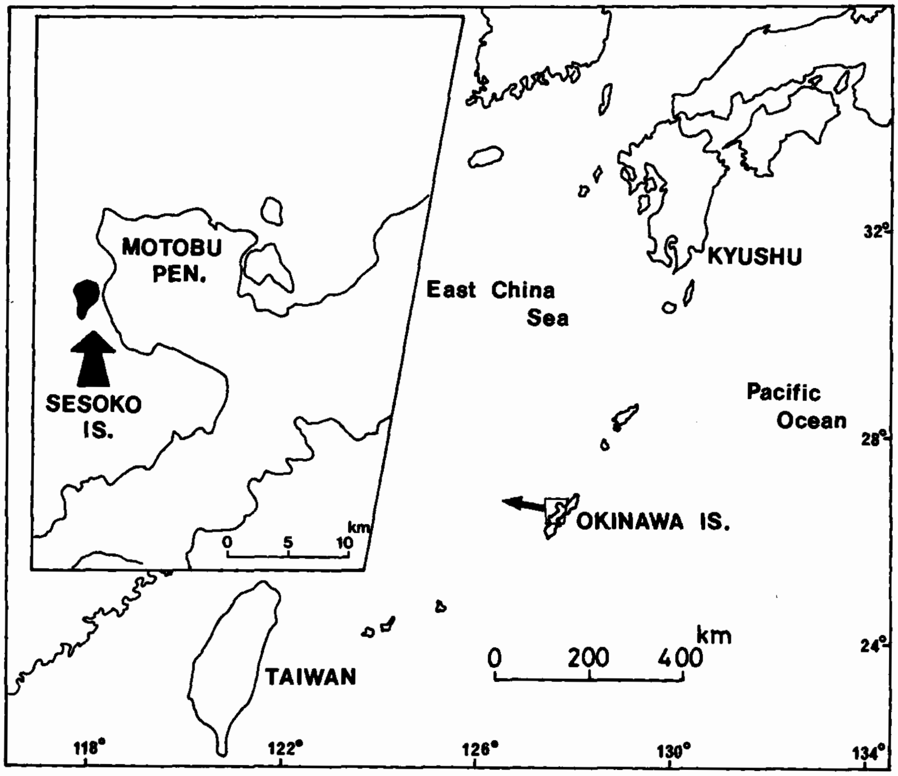
The ecology of ostracods in the intertidal and subtidal zones has been studied mainly in temperate areas (Theisen, 1966; Williams, 1969; Whatley and Wall, 1975; Skaumal, 1977; etc.) with little attention devoted to subtropical areas. Since May 1984, the authors have been investigating the ecology of intertidal and subtidal ostracods living in the moat in the inner area of a coral reef off Sesoko Island, Okinawa.

As part of an ongoing study of the ecology of subtropical ostracods, we will present the preliminary results of relationships of species composition and its seasonal change to substrates, particularly sea weeds which are thought to be important habitats for ostracods, and water depth.

STUDY AREA

Okinawa Island is the largest and central island of the Ryukyu Islands which extend between Kyushu of Japan and Taiwan (Text-fig. 1). Since it is situated at about 26 to 27 degrees north latitude, and is directly influenced by the Kuroshio Warm Current which flows west of the island, Okinawa Island has a subtropical climate.

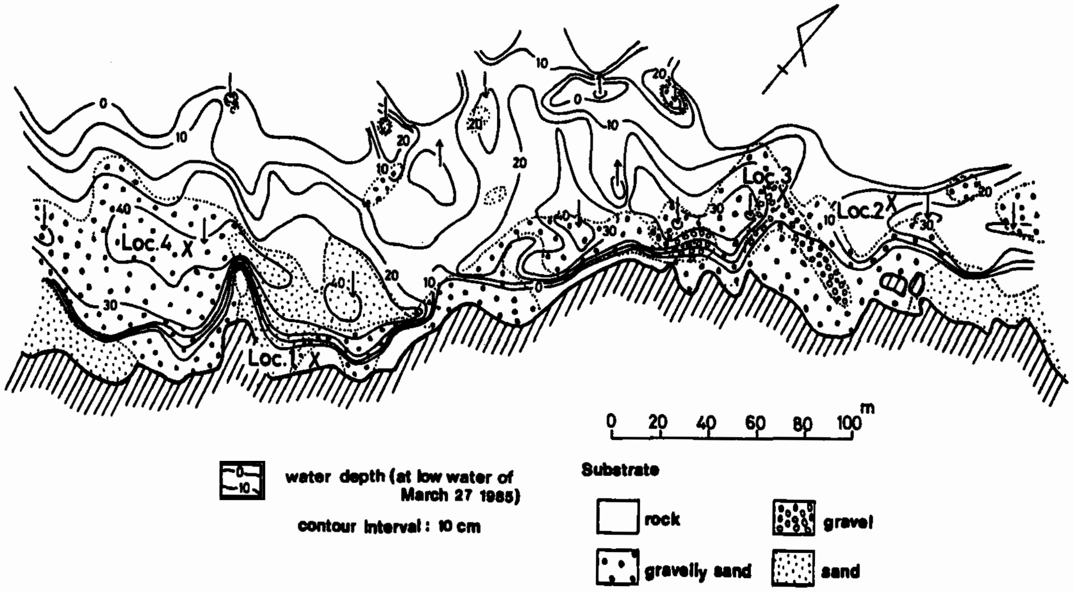
Sesoko Island is 0.5 kilometers west of the Motobu Peninsula of Okinawa Island (Text-fig. 1). Marine terraces which are composed of Quaternary limestone are developed at four or five elevation levels on the island. A fringing reef surrounds it. The reef is particularly developed off the northwestern coast of the island, where it extends prominently toward the open sea, and in the inner area of the reef, reef flat and moat, are well developed. The moat is crescent-shaped with a maximum width of about 200 meters in its middle. At low water of spring tide, the moat is nearly isolated from the open sea by the exposed reef flat, and the margins of the moat are exposed to air; the tidal range in the study area is about 2.0 meters at maximum spring tide, and about 0.1 meter at minimum neap tide.



TEXT-FIG. 1—Location map of Sesoko Island.

The study area occupies the northeastern part of the moat where abundant sea weeds and sea grasses grow. Text-fig. 2 shows the topography and substrates of the study area and is based on preliminary data obtained by the authors form November 1984 to April 1985. In the moat, there is a deep area extending almost parallel to the shore line where loose sediments such as gravel and sand are accumulated. Macroalgae and sea grasses are distributed widely in the moat. There were many species and numbers of individuals in spring, but from spring to summer they decreased gradually and, in autumn, only three species could be found; those were *Ulva pertusa* (green algae), *Jania decussato-dichotoma* (red algae) and *Thalassia hemprichii* (sea grass). Text-fig. 3 shows the distributions of these three species in the northern part of the study area from November to December 1984.

Water temperature and salinity were measured for coastal water at Sesoko Marine Science Center, University of the Ryukyus, located on the eastern coast of Sesoko Island. There, the mean monthly maximum temperature of 1982 was 28.6°C in August and the mean monthly minimum was 20.1°C in February. The mean salinity ranged from 34.6 to 35.3 ‰ (Nakamura 1983).



TEXT-FIG. 2—Topography and substrates of the study area. The location of sampling localities is shown on the map. The part with oblique lines indicates the lowest marine terrace.

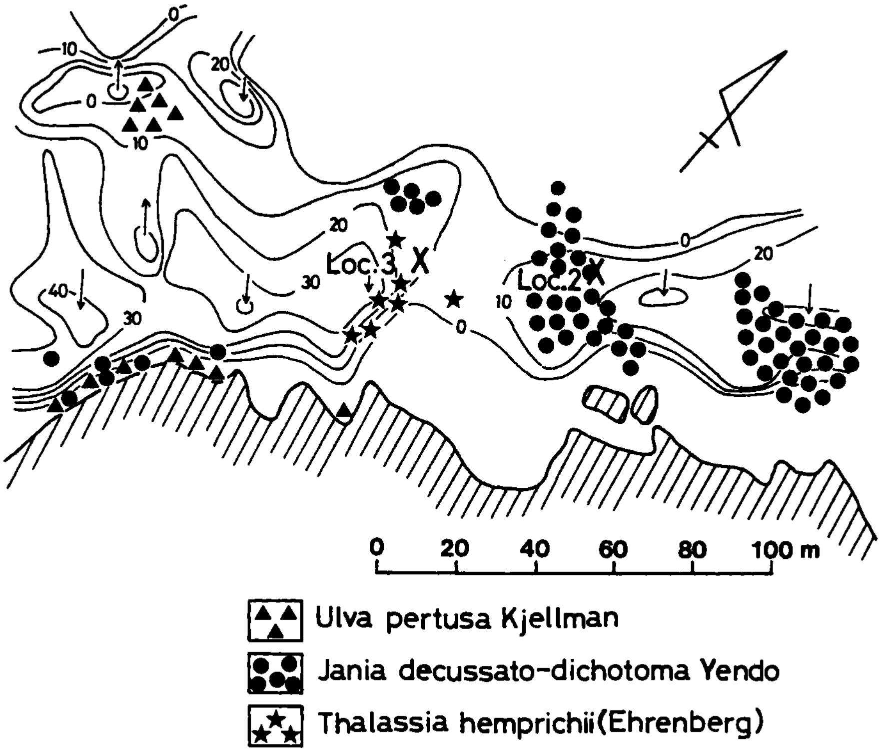
METHODS

Sampling localities 1 to 4 are shown in Text-fig. 2. Localities 1 to 3 are located in the lower part of the intertidal zone, and locality 4 is in the subtidal zone. *Ulva* samples were collected in the tide pool of locality 1, and *Jania* samples were collected on the rock platform of locality 2. *Ulva* has smooth and flat fronds. *Jania* gives a hemisphere-like appearance as the product of complex intergrowth of filamentous plant bodies. At localities 3 and 4, we collected the gravels on which filamentous algae were growing. Filamentous algae grow densely on some cobble to boulder size gravels and on parts of rock, and trap sand grains. They are frequently found to be covered with a thin sand layer. There seems to be no marked decrease of filamentous algae at any particular season. Samples were collected with surrounding sea water by means of plastic bags and agitated in the bags with a 10% solution of formaline. Then the contents in the bags were put through a Taylor's 425 mesh sieve. The remains in the sieve were dried up and partitioned into samples which contained approximately 200 ostracods.

RESULTS

We selected 16 samples among the monthly samples which were collected since May 1984.

Thirty-eight species of Podocopa and two species of Myodocopa were identified but the Myodocopa are not listed in Table 1. As a whole, the genera *Xestoleberis, Paradoxostoma* and *Loxoconiculum* were predominant in the samples from the moat. *Xestoleberis* cf. *X. hanaii* and *X.* sp. A were dominant species, and *Loxocorniculum* sp. A, *Paradoxostoma* sp. B, *P.* sp. C and *P.* sp. D also occurred abundantly.



TEXT-FIG. 3—Distribution of representative macroalgae and sea grasses in the northern part of the study area during the period from November to December, 1984.

Table 2 represents the number of individuals per species per unit sample. Ostracod species in this list are divided into two species groups; one group relevant to the nature of the substrates or the water depth, and the other group which has no distinct relation to particular substrates or water depth or which occurs infrequently. The boundary between these two groups is drawn between *Paradoxostoma lunatum* and *Hermanites* sp.

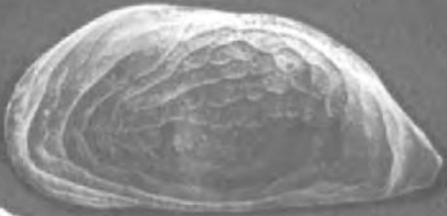
Among the former group, the upper four species from *Semicytherura*? sp. to *Aurila* sp. occur mainly from the *Ulva* samples from locality 1. *Paradoxostoma* sp. E is confined to the intertidal samples. The following five species of *Paradoxostoma* are characteristically found in the *Jania* samples, locality 2. The species from *Xestoleberis* cf. *X. sagamiensis* to *Paradoxostoma lunatum* are found at localities 2 to 4, and, in particular, the last three species are characteistic in the filamentous algae samples at localities 3 and 4.

Some species show prominent increase in individual number at particular seasons. *Paradoxo-*

PLATE 1—Figs. 1, 2. *Perissocytheridea inabai* Okubo, 1983. 1. Lateral view of right valve (Loc. 1, sample 0521). ×80. 2. Lateral view of left valve (Loc. 1, sample 0521). ×80. Figs. 3, 4. *Pectocythere*? sp. 3. Lateral view of right valve (Loc. 1, sample 0817). ×105. 4. Lateral view of left valve (Loc. 1, sample 0817). ×105. Figs. 5, 6. *Aurila* sp. 5. Lateral view of right valve (Loc. 1, sample 0817). ×75. 6. Lateral view of left valve (Loc. 1, sample 0817). ×75. Figs. 7, 8. *Hermanites* sp. 7. Lateral view of right valve (Loc. 2, sample 0521). ×80. 8. Late ralview of left valve (Loc. 2, sample 0521). ×80. Figs. 9, 10. *Callistocythere* sp. A. 9. Lateral view of right valve (Loc. 3, sample 1109). ×105. 10. Lateral view of left valve (Loc. 3, sample 1109). ×105. Figs. 11, 12. *Loxoconcha* (*Loxoconcha*) *uranouchiensis* Ishizaki, 1968. 11. Lateral view of right valve (Loc. 1, sample 0817). ×105. 12. Lateral view of left valve (Loc. 1, sample 0817). ×105. Figs. 13, 14. *Loxocorniculum* sp. A. 13. Lateral view of right valve (Loc. 1, sample 0817). ×105. 14. Lateral view of left valve (Loc. 1, sample 0817). ×105.

Plate 1


1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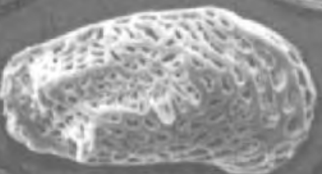
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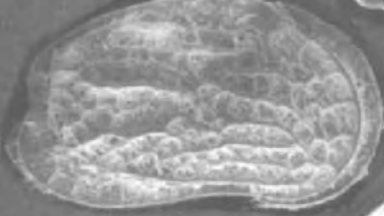
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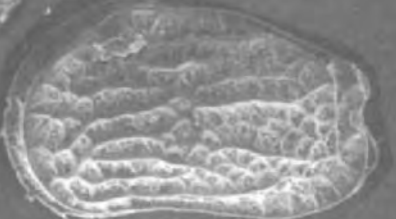
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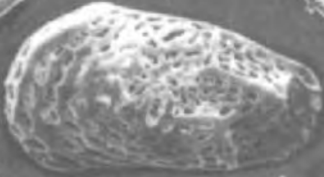
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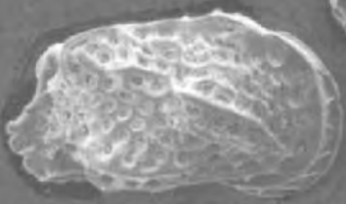
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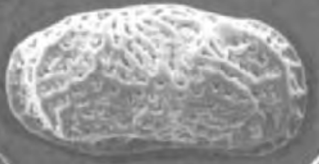
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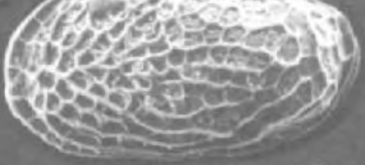
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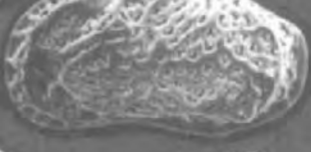
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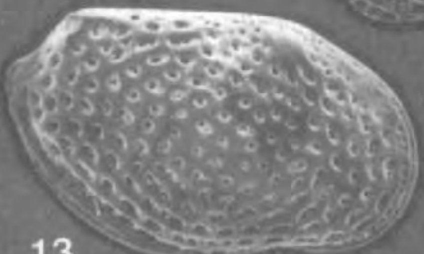
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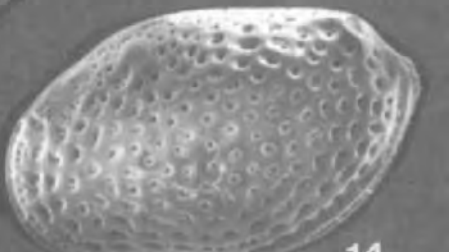
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TABLE 1—LIST OF LIVING OSTRACOD SPECIES FROM THE MOAT OF SESOKO ISLAND. SAMPING LOCALITIES ARE ARRANGED FROM HIGHER TO LOWER LEVELS; LOCALITIES 2 AND 3 ARE ALMOST AT THE SAME LEVEL, AND LOCALITY 1 IS SOMEWHAT HIGHER IN LEVEL. SAMPLING NUMBERS ARE REPRESENTED BY SAMPLING DATES.

localities	Loc. 1 (Ulva)				Loc. 2 (Jania)				Loc. 3 (f. algae)				Loc. 4 (f. algae)			
species / samples	0817	1221	0221	0521	0815	1109	0221	0521	0816	1109	0221	0521	0922	1109	0222	0521
Neonesidea sp.				1		2		2			1		2			
Propontocypris (Propontocypris) sp.	1															
P. (Ekpontocypris) sp.				1	1								1		1	
Perissocytheridea inabai Okubo, 1983				1						1		3				4
Pectocythere? sp.		2		2	3		1	2		3	6	1	9		3	5
Callistocythere sp. A								2	3	31	15	13	1	23	2	
C. sp. B	8			2				1		1						
C. sp. C												1				
Aurila sp.	14	11	2						5	1	1					
Aurila? sp.														2	5	
Coquimba sp.											1					
Hermanites sp.	6		1		14	2	1	2	20	9	1	2	5	3	1	2
Eucythere sp.					1											
Semicytherura? miurensis (Hanai, 1957)											3				1	
S. ? sp.	2	1	4	52						1	1					
Paracytheridea sp.													1			
Loxoconcha (Loxoconcha) uranouchiensis Ishizaki, 1968								1	3	12	45	83	17		4	28
L. (L.) sp.			1													
Loxocorniculum sp. A	47				66	4			208	64	25		13	23	2	1
L. sp. B	2															
L. sp. C					1	3				6	1	9	5	6	3	4
Xestoleberis setouchiensis Okubo, 1979	1	3	2		1			2			8	9	3	3	6	
X. cf. *X. hanaii* Ishizaki, 1968	148	101	100	145	73	16	77	34	9	38	67	103	50	45	135	69
X. cf. *X. sagamiensis* Kajiyama, 1913							9	3		2	13	3		18	49	19
X. sp. A	16	25	7		11	29	124	158	8	80	45	80	136	153	68	68
X. sp. B	4		1	6	1	2	3	3	2	3	5	15				
X. sp. C								1		1	3	4				
Paradoxostoma affine Okubo, 1977						1		8								6
P. lunatum Okubo, 1977								1				1		6	6	2
P. cf. *P. gibberum* Schornikov, 1975					15	2				11	4					
P. sp. A	2		3	1		2	5	4	1					1	1	
P. sp. B	7				36	143	15	45								
P. sp. C	5	113	34	6		2	2			2	1	1	1		2	
P. sp. D	6	1	1	1	14	142	17	3	1	43	7		21	20		4
P. sp. E	4		1	4			1		2	1						
P. sp. F	3					19	9	12		27	15	30	27	2	15	43
P. sp. G						1									3	
P. sp. H										1						
total number of individuals	276	257	157	222	237	370	264	284	262	338	268	358	292	305	307	269

stoma sp. C occurs abundantly in the December sample at locality 1, and *P.* sp. B and *P.* sp. D attain a maximum individual number in the November sample at locality 2. Unfortunately, we could not take a sample of *Ulva* in November, because the plant bodies were too few and small to be collected. It is likely that these three species of *Paradoxostoma* occur in great abundance at the same time. *Paradoxostoma* sp. A and *P.* sp. F, both of which are also characteristic in the *Jania* samples as well as *P.* sp. B and *P.* sp. D, occur in great abundance in February. *Hermanites* sp. and *Loxocorniculum* sp. A show a distinct abundance in the August samples, but this tendency is not clear in the subtidal samples at locality 4. It seems that the patterns of seasonal change in individual number of some species are not the same at all localities. This is well represented by the occurrences of the two dominant species of *Xestoleberis*. For example, *X.* cf. *X. hanaii* attains a maximum individual number in the December sample at locality 1, and in the February samples at localities 2 and 4, and in the May sample at locality 3. It is important to note that the ratio of adults to juveniles in individual number ranges about from 10 to 45% in the samples at locality 1, and as contrasted with this result, in the samples of other localities, adults show only a very small ratio, generally less than 10%, or are not found. At present, however, we can not decide the cause of this difference of age structure of *Xestoleberis* cf. *X. hanaii* in those localities.

The seasonal range of the total individual number per unit sample is much wider in the intertidal samples at locality 1 to 3 than in the subtidal samples at locality 4. This results from the marked

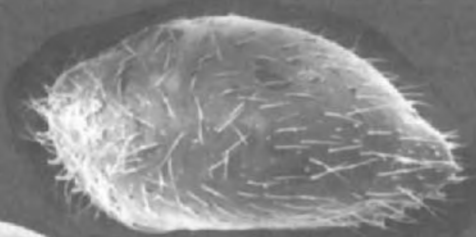
TABLE 2—LIST OF OSTRACOD SPECIES REPRESENTING THE NUMBER OF INDIVIDUALS PER UNIT SAMPLE. THE AMOUNT OF UNIT SAMPLE WAS DECIDED SO THAT ABOUT SEVERAL HUNDRED OSTRACODS COULD BE COLLECTED FROM IT; THE UNIT SAMPLE IS THE PLANT SAMPLE OF 50 GRAMS IN WET WEIGHT FOR MACROALGAE, AND IS THE PLANT SAMPLE FROM ABOUT 100 CM² IN SUPERSCRIPT SURFACE AREA OF GRAVEL FOR FILAMENTOUS ALGAE.

localities	Loc. 1 (*Ulva*)				Loc. 2 (*Jania*)				Loc. 3 (f. algae)				Loc. 4 (f. algae)			
species / samples	0817	1221	0221	0521	0815	1109	0221	0521	0816	1109	0221	0521	0922	1109	0222	0521
Semicytherura? sp.	4	5	5	16						2	0					
Callistocythere sp. B	18			1				3		2						
Paradoxostoma sp. C	11	513	46	2		5	21			3	0	1	2		2	
Aurila sp.	31	50	3						21	2	0					
Paradoxostoma sp. E	9		1	1			11		9	2						
P. sp. B	16				44	330	160	141								
P. sp. A	4		4	0		5	53	13	4					2	1	
P. sp. D	13	5	1	0	17	328	181	9	4	69	1		34	32		4
P. sp. E	7					44	117	38		43	3	32	43	3	16	46
P. affins Okubo, 1977						2		25								6
Xestoleberis cf. *X. sagamiensis* Kajiyama, 1913							96	9		3	3	3		29	52	20
Paradoxostoma cf. *P. gibberum* Schornikov, 1975					18	5				18	1					
Loxocorniculum sp. C					1	7				10	0	10	8	10	3	4
Callistocythere sp. A								6	13	50	3	14	2	37	2	
Loxoconcha (Loxoconcha) uranouchiensis Ishizaki, 1968								3	13	19	9	89	27		4	30
Paradoxostoma lunatum Okubo, 1977								3				1		10	6	2
Hermanites sp.	13		1		17	5	11	6	85	14	0	2	8	5	1	2
Loxocorniculum sp. A	104				80	9			888	102	5		21	37	2	1
Xestoleberis cf. *X. hanaii* Ishizaki, 1968	329	459	135	45	88	37	819	107	38	61	13	110	80	72	144	74
X. sp. A	36	114	9		13	67	1319	496	34	128	9	86	218	245	73	73
X. sp. B	9		1	2	1	5	32	9	9	5	1	16				15
X. setouchiensis Okubo, 1979	2	14	3		1			6			2	10	5	5	6	
Pectocythere? sp. A		9		1	4		11	6		5	1	1	14		3	5
Loxocorniculum sp. B	4															
Propontocypris (Propontocypris) sp.	2															
Loxoconcha (Loxoconcha) sp.			1													
Neonesidea sp.				0		5		6			0		3			
Propontocypris (Ekpropontocypris) sp.				0	1								2		1	
Eucytherura sp.					1											
Xestoleberis sp. C								3		2	1	4				
Paradoxostoma sp. G						2									3	
P. sp. H										2						
Callistocythere sp. C												1				
Coquimba sp.											0					
Perissocytheridea inabai Okubo, 1983				0						2		3			4	
Semicytherura? miurensis (Hanai, 1957)											1				1	
Aurila? sp.														3	5	
Paracytheridea sp.													2			
number of individuals per unit sample	612	1169	210	68	286	856	2831	889	1118	544	53	383	469	490	325	286

seasonal changes in the individual number of several species in the intertidal samples; examples of such species are *Paradoxostoma* sp. C at locality 1 and *Loxocorniculum* sp. A at locality 3. This wider range of individual number in the intertidal samples may reflect the influence of greater fluctuations of environmental factors on ostracods found there.

We have been collecting surface sand samples at irregular intervals near locality 4 by means of a soil-net sampler, since September 1984. We were unable to collect living ostracods from sand samples until January 1985. We also found some living ostracods from the sand sample in February 1985, and were able to collect about 50 ostracods alive from the sand sample in June 1985. Only three species were recognized (in order of dominance): *Loxoconcha uranouchiensis*, *Perissocytheridea inabai* and *Xestoleberis* sp. A. It is probable that the species composition of ostracods from the sand area is rather different from that of the sea plant samples, and that the density of ostracods is very low in the sand area.

Plate 2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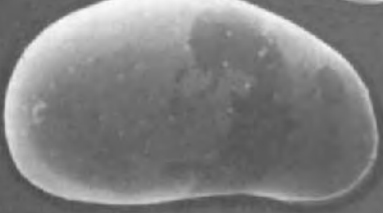
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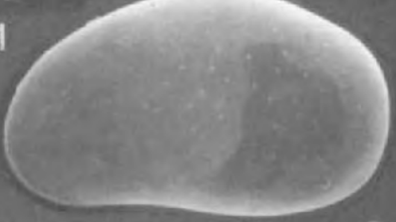
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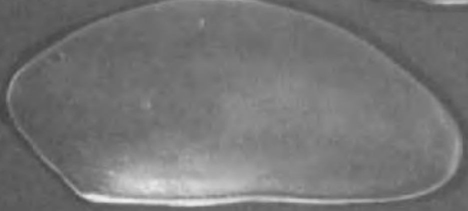
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CONCLUSIONS

Among the ostracods from the moat, there were many species which showed a distinct areal or seasonal change in their occurrences, so that the species composition of ostracods from the moat was greatly changeable areally and seasonally.

The moat is situated landward in the coral reef area and is considerably isolated from the open sea at low water. This peculiar situation results in the highly variable water temperature, salinity, and strength and direction of water movement. On the other hand, the moat is protected from the direct influence of the open sea such as strong wave action, and sea weeds and sea grasses, which are thought to be important habitats for ostracods, flourish there.

The marked areal and seasonal changes in species composition of ostracods from the moat may be the product of adaptation to this characteristic environment of the moat.

In the future, we are going to study the life cycles of ostracod species and observe and measure physical, chemical, and biological environmental factors. We may also take into consideration the migration of ostracods, which was emphasized by Whatley and Wall (1975), within the moat and from other areas into the moat.

ACKNOWLEDGEMENTS

The authors would like to thank the students of our department, the staff of Sesoko Marine Science Center of University of the Ryukyus and Mr. Shinya Matsuda of University of the Ryukyus for their help in many ways in the course of this study. The authors are deeply indebted to Professor Ernest H. Williams of University of Puerto Rico, Puerto Rico, for reading the manuscript.

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PLATE 2—Fig. 1. *Neonesidea* sp. Lateral view of left immature valve (Loc. 3, sample 0221). ×75. Figs. 2, 3. *Xestoleberis* cf. *X. hanaii* Ishizaki, 1968. 2. Lateral view of right valve (Loc. 1, sample 0817). ×80. 3. Lateral view of left valve (Loc. 1, sample 0817). ×80. Figs. 4, 5. *Xestoleberis* sp. A. 4. Lateral view of right valve (Loc. 2, sample 0521). ×180. 5. Lateral view of left valve (Loc. 2, sample 0521). ×180. Figs. 6, 7. *Xestoleberis* cf. *X. sagamiensis* Kajiyama, 1913. 6. Lateral view of right valve (Loc. 2, sample 0521). ×80. 7. Lateral view of left valve (Loc. 2, sample 0521). ×80. Fig. 8. *Paradoxostoma* sp. A. Lateral view of right valve (Loc. 2, sample 0221). ×105. Fig. 9. *Paradoxostoma* sp. B. Lateral view of right valve (Loc. 2, sample 1109). ×105. Fig. 10. *Paradoxostoma* sp. C. Lateral view of right valve (Loc. 1, sample 1221). ×80. Fig. 11. *Paradoxostoma* sp. D. Lateral view of right valve (Loc. 2, sample 0815). ×105. Fig. 12. *Paradoxostoma affine* Okubo, 1977. Lateral view of right valve (Loc. 2, sample 0521). ×80.

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Podocopid Ostracods of Brisbane Water, Near Sydney, South-Eastern Australia

CHRISTOPHER BENTLEY
Canberra C.A.E., Canberra, Australia

ABSTRACT

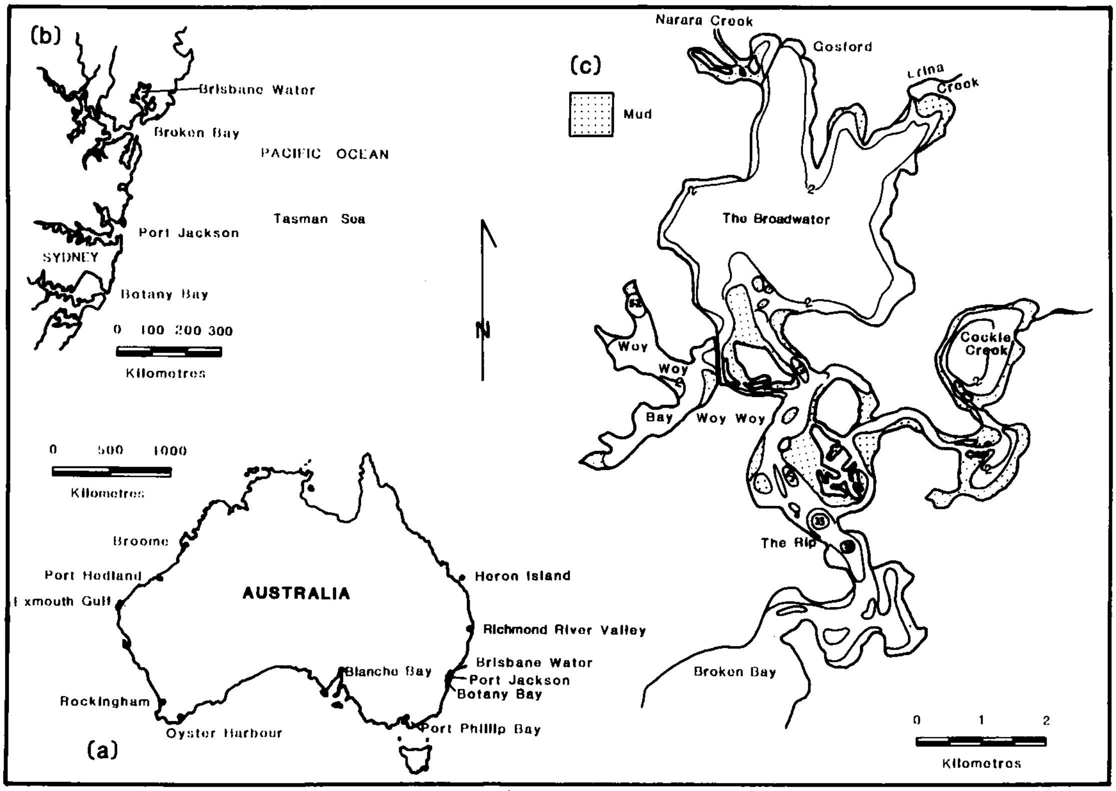
The distribution of ostracods in Brisbane Water is controlled firstly by substrate type and secondly by salinity. The fauna of Brisbane Water (fifty-one species in thirty-eight genera is more closely related to that of Heron Island than to that of Port Phillip Bay. For Botany Bay to the south the reverse is true. This is in agreement with Hartmann's (1981) idea of the East Coast of Australia as a "large tropical-subtropical transition zone". One new genus (*Mckenziartia*) is described.

Fifty one species in thirty-eight genera of podocopid ostracod were found in Brisbane Water (see species list). They represent fifteen families—Bairdiidae, Bythocytheridae, Osticytheridae, Cytheromatidae, Hemicytheridae, Krithidae, Leptocytheridae, Loxoconchidae, Paradoxastomatidae, Pectocytheridae, Trachyleberididae, Xestoleberididae, Pontocyprididae and Candonidae. The Trachyleberididae, with eleven genera, dominate the fauna in terms of number of genera, with the Bythocytheridae (seven genera) and Hemicytheridae (five genera) next in rank. The remaining families have one or two genera each. In numbers of individuals it is the Osticytheridae (*Osticythere*), Bairdiidae (*Neonesidea*), Xestoleberididae (*Xestoleberis*) and Trachyleberididae (*Ponticocythereis*) which dominate, each with hundreds of individuals.

Brisbane Water itself is an estuary in a drowned valley (see Text-fig. 1). It consists of a broad shallow area known as the Broadwater, smaller shallow areas to either side (Cockle Creek and Woy Woy Bay) and narrow channels connecting them to Broken Bay and thence to the ocean. The maior channel has been excavated to a depth of thirty-five metres at its narrowest point by tidal currents, which reach velocities of 1.70 m/sec.

Previous work in the immediate vicinity has been scant. To the south, Brady (1880) collected ostracods in Port Jackson. The fauna of Botany Bay was examined by Urbaczewski (1977, unpub.). McKenzie (1967) described a fauna from Port Phillip Bay, near Melbourne. He has also described Tertiary Ostracoda from Victoria (1974) and South Australia (1979). To the north, the fauna of Heron Island was studied by Labutis (1977, unpub.). Hartmann has described ostracods collected at many points around the Australian coast (1978, 1979, 1980, 1981, 1982). McKenzie and Pickett (1984) described faunas from the Pleistocene of the Richmond River valley, north of the study area. One new genus, *Papillatabairdia*, has been described from Brisbane Water (Bentley, 1981) and a second (*Mckenziartia*) is described herein.

The sediments of Brisbane Water range from clean quartz and shell fragment sands in the tidal channels to faecal pellet muds in the broad shallow areas, mud flats and channel edges, with



TEXT-FIG. 1—(a) Map of Australia showing the points at which specimens referred to *Mckenziartia portjacksonensis* have been found; (b) Location of Brisbane Water with regard to Sydney, Port Jackson and Botany Bay; (c) Bathymetric map of Brisbane Water, with mud banks shaded.

admixtures between these substrate types at their boundaries and in the less strongly flowing channels. The greatest diversity of ostracods is found in the muddy sands (86.5% of total species). The fauna in the clean sands (51.4%) is comparable in number to that found in the most populous of the muds (range 5.4 to 54%).

Six ostracod assemblages can be distinguished, the apparent primary distribution factor being substrate type. These assemblages have been named for the substrate type, with the mud assemblages being further separated and named for their location.

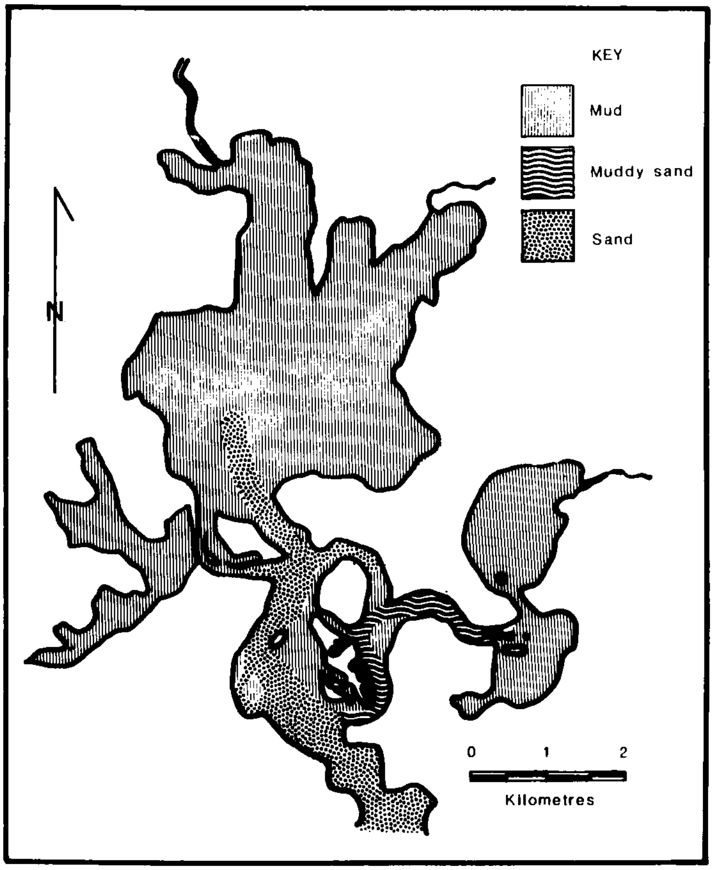
A second factor which affects the ostracod fauna in a more general way than substrate type is salinity or degree of marine influence. This is obviously strongest near the tidal race of the Rip and decreases as distance from the Rip increases. This correlates generally with substrate type, the sandier substrates corresponding to more nearly marine conditions and the muds correlating with the lower salinities due to the input of fresh water from the creeks and towns. The salinity range found in Brisbane Water is from 30.2 parts per thousand near the Rip to 24.2 parts per thousand near Gosford.

The SAND assemblage contains nineteen genera (51% of the total genera), one of which (*Baltraella* sp.) does not occur in any other assemblage. This group is dominated by trachyleberid genera.

The MUDDY SAND assemblage contains thirty-two genera (86.5%), seven of which are unique to this faunule. These are *Keijia* sp., *Australimoosella* sp., *Cytheropteron* sp., *Bythocythere*

TABLE 1.—SPECIES LIST.

Actinocythereis cf. *scutigera costata* Hartmann, 1978
Actinocythereis? sp.
Alocopocythere reticulata indoaustralica Hartmann, 1978
Australimoosella sp.
Baltraella sp.
Bythoceratina sp.
Bythocythere sp.
Callistocythere puri McKenzie, 1967
Callistocythere sp. 1
Callistocythere sp. 2
Caudites cf. *litusorienticola* Hartmann, 1981
C. scolipicula Hartmann, 1981
Cletocythereis australis Malz, 1980
Cytheralison pravacauda Hornibrook, 1952
Cytheropteron sp.
Echinocythereis sp.
Hanaiceratina sp.
Hemicytheridea reticulata Kingma, 1948
Hemicytherinid sp.
"Hiltermannicythere" bassiouni reticulata Hartmann, 1979
Keijella sp.
Keijia sp.
Loxoconcha australis minor Hartmann, 1979
L. abditicostata Hartmann, 1981
L. trita McKenzie, 1967
Loxoconcha sp.
Loxoconchella pulchra McKenzie, 1967
Maddocksella sp.
Mckenziartia portjacksonensis (McKenzie, 1967)
Neonesidea cf. *amygdaloides* (Brady, 1865)
Osticythere baragwanathi (Chapman, Crespin and Keble, 1928)
Papillatabairdia dentata Bentley, 1981
Paracytheroma caudata Hartmann, 1978
P. sudaustralis McKenzie, 1978
Paradoxastoma sp.
Parakrithella australis McKenzie, 1967
Ponticocythereis militaris (Brady, 1866)
Quasibradleya sp.
Schlerochilus sp.
Semicytherura? sp. 1
Semicytherura? sp. 2
Serratocythere sp. 1
Serratocythere sp. 2
Tasmanocypris setigera McKenzie, 1979
Trachyleberid sp. 1
Trachyleberid sp. 2
Trachyleberis sp.
Xestoleberis briggsi McKenzie, 1967
X. olivacea Brady, 1898
X. setigera Brady, 1880
X. tigrina Brady, 1866



TEXT-FIG. 2—Map showing distribution of substrate types in Brisbane Water.

sp., *Bythoceratina* sp., *Hanaiceratina* sp. and *Schlerochilus* sp. Trachyleberid and bythocytherid species dominate this assemblage.

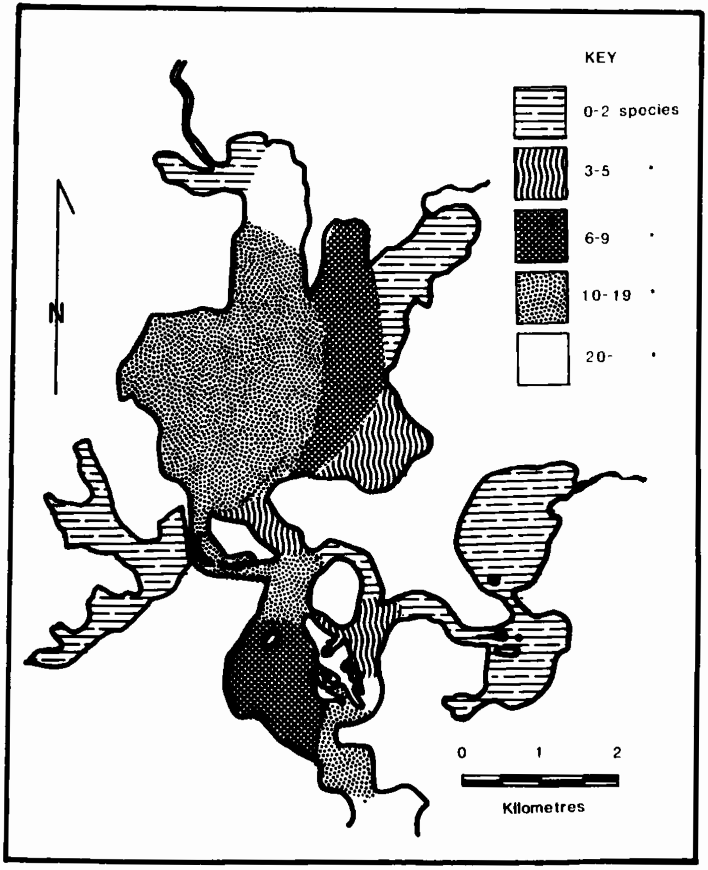
The MUD assemblages vary greatly in the number of genera they contain. The most diverse is the GOSFORD mud assemblage which contains twenty genera (54%), two of which (*Paradoxastoma* sp. and *Actinocythereis* cf. *scutigera costata*) are unrepresented elsewhere. Trachyleberid and hemicytherid genera form the best represented groups here. The trachyleberids are less dominant than in the sandy assemblages.

The CHANNEL-SIDE mud assemblage contains eight genera (21.6%) which come from seven families.

The BROADWATER mud assemblage which contains five genera (13.5%), is the one which covers the largest area. Its five genera represent five families. The bythocytherids and hemicytherids which were common in the faunules above are absent.

The CREEK mud assemblage contains only two genera, *Semicytherura*? sp. and *Osticythere baragwanathi*, which represent the Cytheruridae and the Osticytheridae. The water in the two creeks (Narara and Erina Creeks) ranges from fresh to brackish, according to the tide and the weather. This greatly restricts the viable fauna.

The most widely occurring species were *Osticythere baragwanathi* (in all assemblages), *Loxoconcha trita* McKenzie, 1967, *Callistocythere* spp. and leguminocytherid sp. (in all but the creek mud assemblage). The bythocytherid and hemicytherid genera are restricted to the sandier assemblages and the Gosford assemblage. The trachyleberids are also restricted in other than those assemblages.

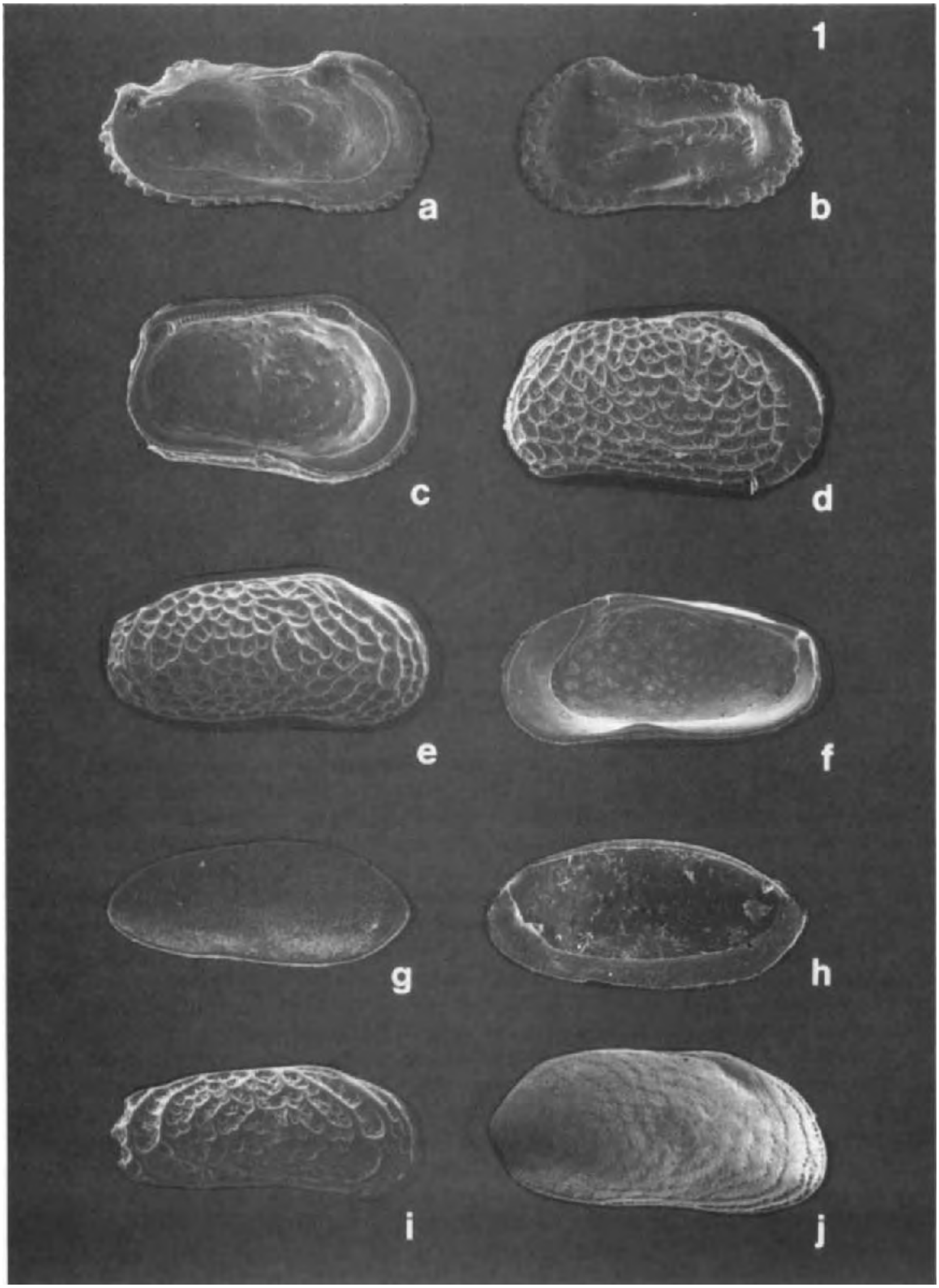


TEXT-FIG. 3—Map showing number of species found per sample.

Other environmental factors investigated (dissolved oxygen, pH and water temperature) appeared to have little bearing on the distribution of ostracods in Brisbane Water, as the assemblages covered all levels of these variables. Dissolved oxygen had a range of 7.0 to 10.1 parts per thousand. The range of pH was from 5.1 to 7.4, while water temperature in March 1978 had a range of 25 to 27 degrees.

Comparison of the various faunules using the Jaccard coefficient indicates that the Gosford faunule has strong affinities with virtually all assemblages, none of which appears to be closely related to any but the Gosford assemblage. This assemblage appears then as an amalgam of all the others and may well be a favourable site for deposition of ostracod valves, rather than an inhabited area.

Use of the Jaccard coefficient on faunal lists for Heron Island, Brisbane Water, Botany Bay and Port Phillip Bay has shown that the closest ties are between the faunas which are closest geographically. Apart from this the Brisbane Water fauna shows more affinity to the Heron Island fauna than to the Port Phillip Bay fauna, while for Botany Bay the reverse is true. This seems to be in agreement with Hartmann's statement (1981) that the East Coast of Australia represents a "large tropical-subtropical transition zone".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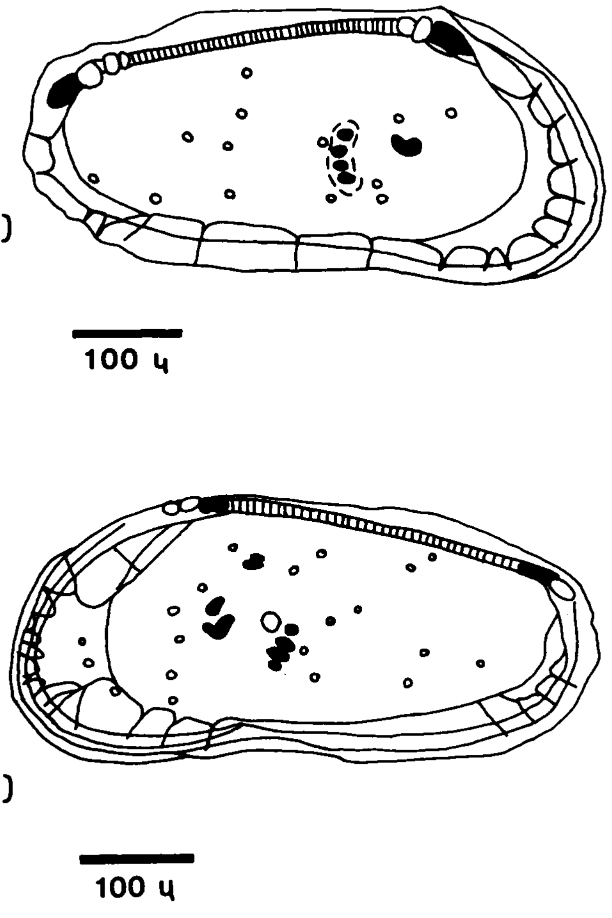
SYSTEMATICS

Family PECTOCYTHERIDAE Hanai, 1957

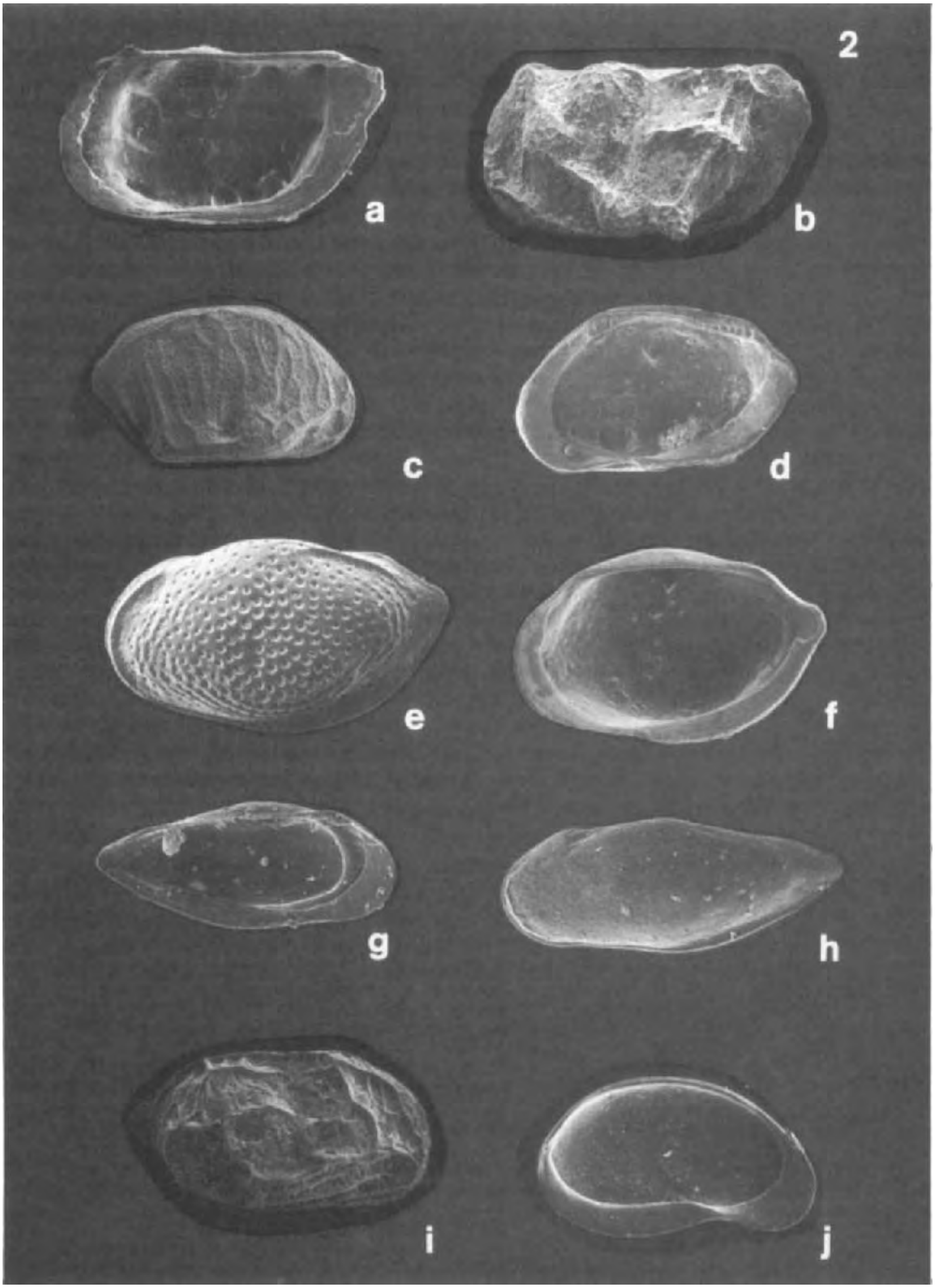
Genus MCKENZIARTIA Labutis and Bentley, n. gen.

Cythere demissa BRADY, 1880, p. 66, Pl. 12, fig. 7a-j (not *demissa*).
Hemicytheridea MCKENZIE, 1964, p. 448–453.
"*Hemicytheridea*" MCKENZIE, 1967, p. 85, figs. 3i-j, Pl. 12, fig. 6.
Pectocythere? HARTMANN, 1978, p. 143–144, figs. 605–618, Pl. 14, figs. 4–11, 14.
Pectocythere HARTMANN, 1980, p. 122–123, Pl. 5, fig. 17.



TEXT-FIG. 4—Internal views of valves of *Mckenziartia portjacksonensis* in transmitted light. (a) from McKenzie (1967) specimen NMV J76, female left valve; (b) from Bentley (1978) specimen FO5, male right valve, showing variability in the anterior vestibule.

PLATE 1—Figs. a, b. *Actinocythereis* cf. *scutigera costata* Hartmann. (a) male internal LV, ×90, CB511; (b) female external LV, ×85, CB510. Figs. c, d. *Osticythere baragwanathi* (Chapman, Crespin and Keble). (c) female internal LV, ×80, CB1217; (d) male external RV, ×85, CB1218. Figs. e, f. *Mckenziartia portjacksonensis* (McKenzie). (e) female external RV, ×95, CB719; (f) male internal RV, ×100, CB1218. Figs. g, h. *Paradoxastoma* sp. (g) left lateral view of carapace, ×130, CB1108; (h) internal RV, ×120, CB1207. Fig. i. *Keijia* sp., external RV, ×135, CB1303. Fig. j. *Australimoosella* sp., female external RV, ×100, CB917.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Type species.—Mckenziartia portjacksonensis (McKenzie, 1967)

Etymology.—For Dr. K. G. McKenzie, who first described the type species of the genus.

Diagnosis.—Pectocytherid genus of small to medium size, characterized by elongate oval shape, rounded posteriorly, coarsely reticulate ornament with a crescentic fossa in the central muscle scar region, concave anteriorly, and a pentodont hinge.

Description.—A pectocytherid genus of medium size; elongate oval in lateral view; anterior rounded, somewhat downturned, venter weakly concave, posterior rounded to slightly truncate, dorsum straight, sloping posteriorly from anterior cardinal angle; greatest height anteromedial; valve surface strongly reticulate with concentric ridges anteriorly and posteriorly, oblique ridges anteriorly, with characteristic crescentic fossa in muscle scar area, concave anteriorly. In dorsal view, tapering anteriorly, ends rounded. Internally: inner lamella broad anteriorly; anterior vestibule deep, narrow to broad; posterior vestibule elongate, shallow; marginal pore canals few, scattered, simple, occasionally branching; moderate number of open normal pore canals; central muscle scars comprising four adductor scars in subvertical row, two frontal scars, large rounded fulcral scar, up to two dorsal scars; sexual dimorphism distinct, males longer and lower than females.

Discussion.—Mckenziartia n. gen. can be distinguished most easily from other pectocytherid ostracods by the crescentic fossa over the central muscle field and by its rounded posterior. It lacks the marginal denticles of *Arculacythereis* Hartmann, 1980 and *Dampiercythere* Hartmann, 1978; the marginal denticles and slight posterior alae of *Morkhovenia* Teeter, 1975; the truncate posterior and the posterior spines of *Keijia* Teeter, 1975 and *Munseyella* Van den Bold, 1957. The straight hinge bar of *Mckenziartia* n. gen. differs from that of *Tanella* Kingma, 1948, which is arcuate.

This genus has been recorded from many points around the Australian coast (see Fig. 1a; McKenzie, 1964, 1967, 1984; Hartmann 1978, 1980) and from New Zealand (Hornibrook 1952, p. 13, 17, 21). The specimen figured by Hartmann (1978, Fig. 605) and one of those figured by McKenzie (1967, Fig. 3) have broad anterior vestibules while those from Heron Island (Labutis, 1977, unpubl.), Botany Bay (Urbaczewski, 1977, unpubl.) and Brisbane Water (Bentley, 1978, unpubl.) have the narrower anterior vestibule. The other specimen figured by McKenzie (1967, Fig. 3j) is midway between the two conditions. It therefore appears that this character is variable within the species, perhaps analogous to the variability shown in species of *Krithe* and *Parakrithe* (McKenzie and Peypouquet, 1984) which appears to be a response to dissolved oxygen levels. Possibly *Mckenziartia* may also be useful in this fashion.

In Brisbane Water it occurs in all except the creek and the sand assemblages, in waters ranging from near fresh to almost marine. It occurs on the continental shelf between Curtis Island and Heron Island (Labutis, 1977). Hartmann (1978) found it on hard sandy substrates in north Western Australia.

The genus is at present monotypic. For description of the appendages see Hartmann (1978).

PLATE 2—Figs. a, b. *Bythoceratina* sp. (a) internal RV, ×130, CB807; (b) external LV, ×110, CB415. Figs. c, d. *Cytheropteron* sp. (c) external RV, ×100, CB145; (d) internal RV, ×90, CB508. Figs. e, f. *Bythocythere* sp. (e) external LV, ×100, CB614; (f) internal RV, ×120, CB613. Figs. g, h. *Baltraella* sp. (g) internal LV, ×80, CB525; (h) external LV, ×80, CB526. Fig. i. *Semicytherura*? sp., external RV, ×130, CB302. Fig. j. *Schlerochilus* sp., internal LV, ×80, CB314.

ACKNOWLEDGEMENTS

I would like to thank Drs. G. C. O. Bischoff, P. De Deckker and K. G. McKenzie and especially my wife, Helen. Without them this study would never have appeared.

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Remarks on the Benthic Ostracoda on the Tunisian Shelf

GIOACCHINO BONADUCE,[1] MARIO MASOLI[2] AND NEVIO PUGLIESE[2]
Statione Zoologica di Napoli[1] *and*
Istituto di Geologie e Paleontologie di Trieste, Italy[2]

ABSTRACT

More recent acquisition of taxonomic and environmental data on Mediterranean benthic ostracod faunas has prompted us to examine in greater detail the material that had already been studied by Bonaduce and Masoli (1968) and Bonaduce, Masoli, Minichelli and Pugliese (1979) from the Tunisian shelf, an extremely interesting area because of its geographical location and geological significance.

The benthic ostracods found belong to thanatocoenoses which have been compared with the thanatocoenoses and biocoenoses of other Mediterranean areas. For autochthonous ostracod species, we have tried to correlate these species with environmental parameters such as depth, sediment composition and grain-size, sea-bottom facies, currents, salinity and temperature. For allochthonous ostracod species, it has been possible to hypothesize the contamination of sediments and reworking due to bottom currents and/or post-Miocene tectonic activity.

INTRODUCTION

In 1975, the Oil Companies operating in the Mediterranean Sea East of Tunisia (C.F.P. and S.N.E.A.P.) proposed a sedimentological, ecological and neotectonic study of the Tunisian shelf. Within this framework, through the courtesy of Dr. H. J. Oertli, one of us (G.B.) was asked to collaborate in defining the ostracod fauna and its ecology in this region. Unfortunately, the related paper (Bonaduce, Masoli, Minichelli and Pugliese, 1979) was published without the table showing the ostracod species distribution. Because of this, Dr. H. J. Oertli has allowed the preparation of the present paper which, we hope, gives a more complete picture of the ostracod faunal distribution on the Tunisian shelf as a function of the facies and type of bottom.

This paper deals with 102 bottom samples from the Tunisian shelf furnished by C.F.P. and S.N.E.A.P. and collected down to a depth of 300 m. To obtain a more complete distributional picture, some near-shore samples collected by Benson and Bonaduce from Cekhira and Gabès have been studied (Bonaduce and Masoli, 1968). Text-figure 1 shows the sample location. For the sample preparation technique we refer to Bonaduce, Masoli, Minichelli and Pugliese (1979).

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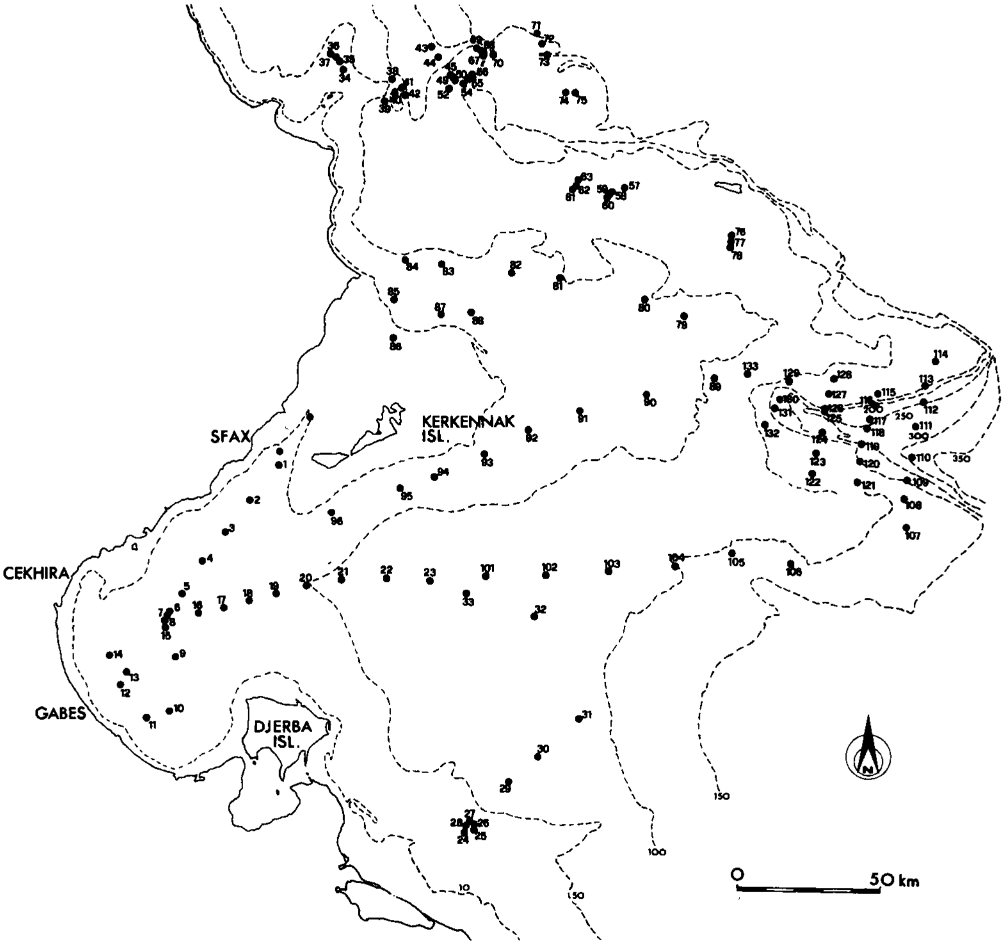


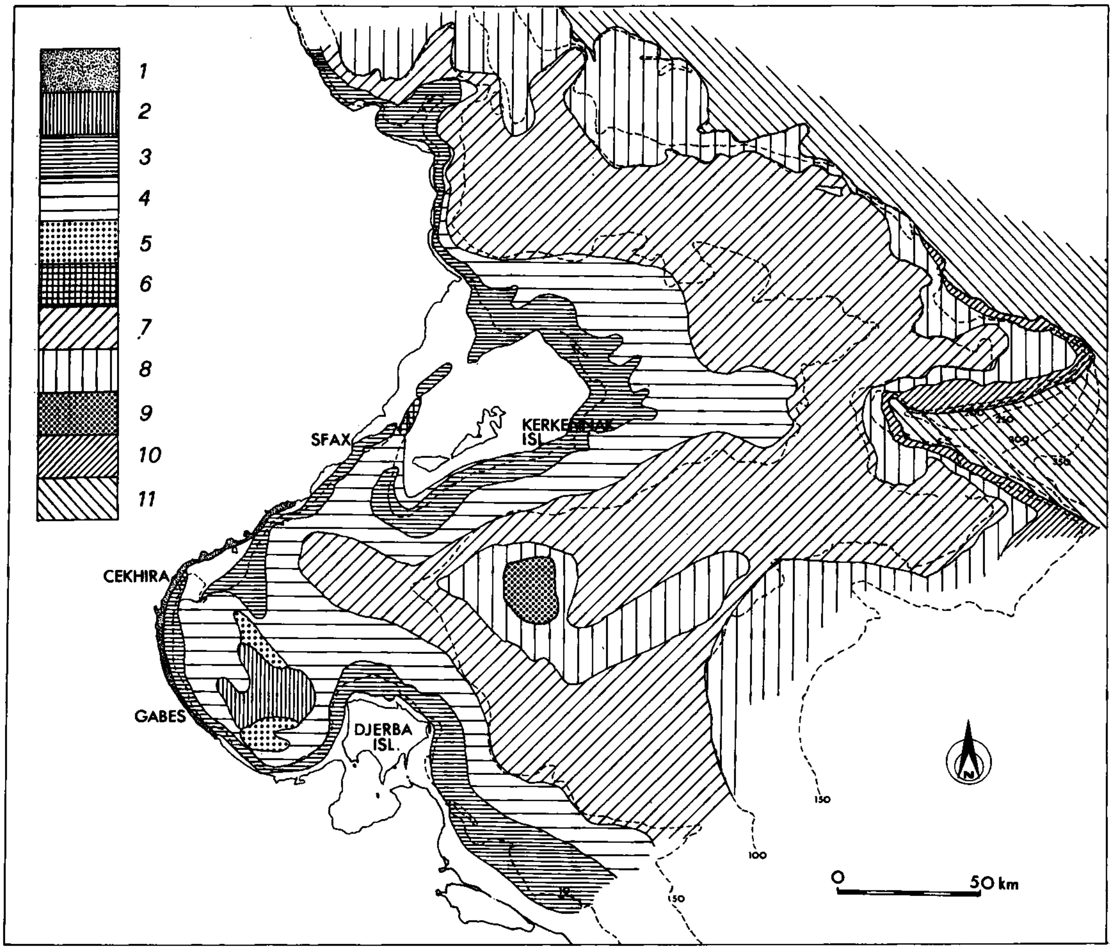
TEXT-FIG. 1—Sample location map.

THE ENVIRONMENT

Clairefond and Cochet (1979) established 12 marine bottom facies in the Gulf of Gabès. Their data have been integrated by those furnished by Blampied, Burollet, Clairefond and Shimi (1979) on recent sediments for the same area.

The purpose of the present paper is to define the correlation between bottom facies, sedimentology and composition of the ostracod assemblages belonging to the thanatocoenosis. In defining the ostracod assemblages we did not take into consideration the fossil and allochthonous specimens, on the basis of the previous literature and our knowledge of the living and recent ostracod distributions in the Mediterranean Sea.

According to Clairefond and Cochet, our samples belong to the following 11 bottom facies (Text-fig. 2):
1) coastal sand; 2) muddy sand; 3) *Posidonia oceanica* meadow; 4) *Caulerpa prolifera* meadow; 5) infralittoral mud; 6) sorted channel sand; 7) circalittoral bioclastic sand; 8) circalittoral muddy bioclastic sand; 9) circalittoral mud; 10) outer shelf sand and gravel; 11) open marine mud.



TEXT-FIG. 2—Bottom facies map (after Clairefond and Cochet, 1979), modified. 1) coastal sand; 2) muddy sand; 3) *Posidonia oceanica* meadow; 4) *Caulerpa prolifera* meadow; 5) infralittoral mud; 6) sorted channel sand; 7) circalittoral bioclastic sand; 8) circalittoral muddy bioclastic sand; 9) circalittoral mud; 10) outer shelf and gravel; 11) open marine mud.

THE OSTRACOD DISTRIBUTION

1—Coastal Sand, with *Posidonia* and Algal Detritus.

Samples: near-shore from Cekhira and Gabès.

Bathymetry: 0–1 m.

The coastal environment from Cekhira and Gabès is mostly sandy, but appears partly rocky in some sampling sites. In both cases, the ostracod assemblage seemed to include the same species. The most frequently recorded were the following, in alphabetical order:

Aurila convexa (Baird, 1850)
Aurila sp. 1
Bairdia reticulata G.W. Müller, 1894
Callistocythere adriatica Masoli, 1968
Callistocythere flavidofusca (Ruggieri, 1950)

Callistocythere littoralis (G.W. Müller, 1894)
Callistocythere lobiancoi (G.W. Müller, 1912)
Caudites sp. 1
Costa batei (Brady, 1866)
Cytheretta subradiosa (Roemer, 1838)
Hiltermannicythere aff. *H. rubra* (G.W. Müller, 1894)
Loculicytheretta pavonia (Brady, 1866)
Loxoconcha bairdi G.W. Müller, 1912
Loxoconcha rubritincta Ruggieri, 1964
Loxoconcha tumida Brady, 1868
Pontocythere turbida (G.W. Müller, 1894)
Procytherideis complicata (Ruggieri, 1953)
Sagmatocythere napoliana (Puri, 1963)
Semicytherura acuticostata (Sars, 1866)
Semicytherura kaloderma Bonaduce and Pugliese, 1976
Semicytherura incongruens (G.W. Müller, 1894)
Semicytherura inversa (Seguenza, 1880)
Semicytherura sulcata (G.W. Müller, 1894)
Triebelina raripila (G.W. Müller, 1894)
Urocythereis neapolitana Athersuch, 1977
Xestoleberis communis G.W. Müller, 1894
Xestoleberis rara G.W. Müller, 1894

Together with mostly typical infralittoral marine species, we found some species which live under a wide range of salinity conditions, such as:

Leptocythere lagunae Hartmann, 1958
Loxoconcha elliptica Brady, 1868
Loxoconcha stellifera G.W. Müller, 1894

These species commonly occur in brackish water environments in the Mediterranean area (Northern Adriatic Sea Lagoon, Orbetello Lagoon). Moreover, we recorded the common presence of *Leptocythere macella* Ruggieri, 1975 and *Neocytherideis fasciata* (Brady and Robertson, 1894) which are characteristic of marine environments that are strongly influenced by continental waters (Gulf of Salerno, Gulf of Policastro, Gulf of Taranto). In the thanatocoenosis, we frequently recorded the presence of scattered valves of *Cyprideis torosa* (Jones, 1857) coming from the nearby brackish environment.

2—Muddy Sand.

Samples: 10, 11, 12.

Bathymetry: 18–28 m.

Type of bottom: varies from sandy pelite to very sandy pelite, mostly with scattered algal vegetation. The muddy-sand area represented by the 3 samples is located West of Dijerba Island. The basic ostracod assemblage included: *Costa edwardsi* (Roemer, 1838); *Cytherois triangularis* Bonaduce, Masoli, Minichelli and Pugliese, 1979; *Leptocythere macella* Ruggieri, 1975; *Loxoconcha tumida* Brady, 1868; *Pseudopsammocythere similis* (G.W. Müller, 1894); *Semicytherura ruggierii* (Pucci, 1955); *Xestoleberis communis* G.W. Müller, 1894.

Of lesser quantitative importance were *Basslerites berchoni* (Brady, 1860); *Cytherois* aff. *C. uffenordei* Ruggieri, 1975; *Microcythere* spp.; *Paradoxostoma simile* G.W.Müller, 1894; *Semicytherura neglecta* (G.W. Müller, 1894).

The cited assemblages and above all *Leptocythere macella, Hemicytherura defiorei, Loxoconcha tumida* and *Semicytherura ruggierii,* appeared fairly abundant in most of the area except for a small region at the boundary of the *Caulerpa* meadow where the number of specimens was very low and the assemblage was dominated by several species of *Semicytherura,* and above all *Semicytherura neglecta.* Moreover, we observed the scattered presence of the brackish *Cyprideis torosa* (Jones, 1857), which we consider a contaminant in the assemblage.

3—*Posidonia oceanica* Meadow.
Samples: 7, 85, 86, 87.
Bathymetry: 17–26 m.
The *Posidonia oceanica* meadow forms a belt around Kerkennak Isle and occurs in a small area in front of Cekhira.
Type of bottom: more or less pelitic fine sands.
The assemblage appeared more diversified and abundant around Kerkennak Isle and included:

Aurila sp. 1
Basslerites berchoni (Brady, 1860)
Callistocythere flavidofusca (Ruggieri, 1950)
Callistocythere littoralis (G.W. Müller, 1894)
Callistocythere mediterranea (G.W. Müller, 1894)
Callistocythere rastrifera Ruggieri, 1953
Caudites sp. 1
Costa batei (Brady, 1866)
Cytheretta adriatica Ruggieri, 1952
Cytherois frequens G.W. Müller, 1894
Cytherois aff. *C. uffenordei* Ruggieri, 1975
Hemicytherura defiorei Ruggieri 1953
Loxocauda decipiens (G.W. Müller, 1894)
Loxoconcha bairdi G.W. Müller, 1912
Loxoconcha rhomboidea (Fischer, 1855)
Loxoconcha tumida Brady, 1868
Microcythere spp.
Polycope reticulata G.W. Müller, 1894
Pseudopsammocythere similis (G.W. Müller, 1894)
Semicytherura acuta (G.W. Müller, 1912)
Semicytherura acuticostata (Sars, 1866)
Semicytherura alifera Ruggieri, 1959
Semicytherura kaloderma Bonaduce and Pugliese, 1976
Semicytherura quadridentata (Hartmann, 1953)
Semicytherura rarecostata Bonaduce, Ciampo and Masoli, 1976
Semicytherura sulcata (G.W. Müller, 1894)
Semicytherura trachina Bonaduce, Ciampo and Masoli, 1975
Tenedocythere prava Baird, 1850
Xestoleberis communis G.W. Müller, 1894

The most common species was *Pseudopsammocythere similis* (sample 86). The assemblage seemed 'contaminated by scattered valves of *Cyprideis torosa* (Jones, 1857).

The area in front of Cekhira showed a very poor assemblage mostly consisting of *Aglaiocypris complanata* (Brady and Robertson, 1869), *Bairdia* gr. *B. mediterranea* G.W. Müller, 1894, *Loxoconcha bairdi* G.W. Müller, 1912. *Loxoconcha gibberosa* Terquem, 1878, *Pseudopsammocythere similis* (G.W. Müller, 1894) and juveniles of *Xestoleberis communis* G.W. Müller, 1894.

4—*Caulerpa prolifera* Meadow.
Samples: 1, 2, 5, 6, 8, 13, 14, 15, 16, 17, 18, 25, 26, 27, 28, 81, 83, 84, 90, 91, 92, 93, 95, 99.
Bathymetry: 15–48 m.

The *Caulerpa* meadow is widely distributed in the area examined. It generally occurred from the *Posidonia* boundary down to circalittoral bioclastic sand bottoms. It was well represented in the area around Kerkennak Isle, in the bay south of Cekhira and east and southeast of Djerba Isle.

The type of bottom appeared different from area to area. In fact around Kerkennak Isle, it varied from more or less pelitic fine sand to sandy pelite.

The ostracod assemblage included:

Aurila convexa (Baird, 1850)
Aurila speyeri (Brady, 1868)
Aurila sp. 1
Bairdia corpulenta G.W. Müller, 1894
Bairdia longevaginata G.W. Müller, 1894
Bairdia reticulata G.W. Müller, 1894
Callistocythere flavidofusca (Ruggieri, 1950)
Callistocythere mediterranea (G.W. Müller, 1894)
Callistocythere praecincta Ciampo, 1976
Costa batei (Brady, 1866)
Cytherella vandenboldi Sissingh, 1971
Cytherois frequens G.W. Müller, 1894
Hemicytherura defiorei Ruggieri, 1953
Loxoconcha bairdi G.W. Müller, 1912
Loxoconcha gibberosa Terquem, 1878
Loxoconcha rhomboidea (Fisher, 1855)
Loxoconcha rubritincta Ruggieri, 1964
Loxoconcha stellifera G.W. Müller, 1894
Loxoconcha tumida Brady, 1868
Microcythere spp.
Paracytheridea depressa G.W. Müller, 1894
Paradoxostoma versicolor G.W. Müller, 1894
Semicytherura aenariensis Bonaduce, Ciampo and Masoli, 1975
Semicytherura alifera Ruggieri, 1959
Semicytherura amorpha Bonaduce, Ciampo and Masoli, 1975
Semicytherura dispar (G.W. Müller, 1894)
Semicytherura heinzei Puri, 1963
Semicytherura incongruens (G.W. Müller, 1894)
Semicytherura inversa (Seguenza, 1880)
Semicytherura rarecostata Bonaduce, Ciampo and Masoli, 1975
Semicytherura robusta Bonaduce, Ciampo and Masoli, 1975
Tenedocythere prava Baird, 1850
Xestoleberis communis G.W. Müller, 1894
Xestoleberis dispar G.W. Müller, 1894
Xestoleberis pellucida G.W. Müller, 1894
Xestoleberis plana G.W. Müller, 1894

Callistocythere flavidofusca, Callistocythere mediterranea, Callistocythere praecincta, Costa batei, Cytherella vandenboldi, Cytherois frequens, Hemicytherura defiorei, Loxoconcha stellifera, Microcythere spp., *Paradoxostoma versicolor* and *Tenedocythere prava* occurred rarely and in scattered samples. From the bathymetric point of view, we noted the first appearance of *Microxestoleberis xenomys* (Barbeito-Gonzalez, 1971) at 48 m (sample 81).

In the bay south of Cekhira, the sediments varied from pelitic medium to very sandy pelite. These sediments encircled a muddy sand-infralittoral mud area. Their depth range was between 17 and 33 m.

The ostracod assemblage was as follows:

Aurila sp. 1
Cytherois triangularis Bonaduce, Masoli, Minichelli and Pugliese, 1979
Hemicytherura defiorei Ruggieri, 1953
Loxoconcha bairdi G.W. Müller, 1912
Loxoconcha gibberosa Terquem, 1878
Loxoconcha rhomboidea (Fisher, 1855)
Loxoconcha tumida Brady, 1868
Paracytheridea depressa G.W. Müller, 1894
Semicytherura acuticostata (Sars, 1866)
Tenedocythere prava Baird, 1850
Xestoleberis communis G.W. Müller, 1894
Xestoleberis dispar G.W. Müller, 1894

We also noted the sporadic occurrence of:

Aglaiocypris rara G.W. Müller, 1894
Callistocythere diffusa (G.W. Müller, 1894)
Callistocythere mediterranea (G.W. Müller, 1894)
Callistocythere praecincta Ciampo, 1976
Cytherois frequens G.W. Müller, 1894
Leptocythere macella Ruggieri, 1975
Pseudopsammocythere similis (G.W. Müller, 1894)
Semicytherura dispar (G.W. Müller, 1894)
Semicytherura ruggierii (Pucci, 1955)

We cite *Aurila* sp. 1 (sample 17) as one of the quantitatively most important species.

The area southeast of Djerba Isle was characterized by a pelitic medium sandy bottom varying from a depth of 16 to 25 m. This area seemed to be influenced by vortex currents (Burollet, 1979). The ostracod assemblage included:

Aurila sp. 1
Bairdia longevaginata G.W. Müller, 1894
Bythocythere minima Bonaduce, Ciampo and Masoli, 1975
Cytherella vandenboldi Sissingh, 1971
Loxoconcha bairdi G.W. Müller, 1912
Loxoconcha tumida Brady, 1868
Loxoconcha turbida G.W. Müller, 1894
Paracytheridea depressa G.W. Müller, 1894
Paracytheridea pachina Barbeito-Gonzalez, 1971
Paracytheridea parallia Barbeito-Gonzalez, 1971
Semicytherura alifera Ruggieri, 1959
Semicytherura inversa (Seguenza, 1880)
Tenedocythere prava Baird, 1850
Xestoleberis communis G.W. Müller, 1894
Xestoleberis dispar G.W. Müller, 1894
Xestoleberis plana G.W. Müller, 1894

Some of the samples (26, 27) were very poor in ostracods.

5—Infralittoral Mud.

Sample: 9.
Bathymetry: 24 m.

This facies, restricted to a small area located southwest of Djerba Isle, was represented by a very sandy pelite bottom. It occurred between muddy sand and the *Caulerpa* meadow facies.

The ostracod assemblage was characterized by the absence of dominant species; the most common species were the following:

Costa edwardsi (Roemer, 1838)
Leptocythere macella Ruggieri, 1975
Loxoconcha rhomboidea (Fisher, 1855)
Semicytherura acuticostata (Sars, 1866)
Xestoleberis communis G.W. Müller, 1894

We also recorded the scattered presence of:

Aurila sp. 1
Cytheridea neapolitana Kollmann, 1960
Cytherois triangularis Bonaduce, Masoli, Minichelli and Pugliese, 1979
Cytherois sp. 1
Loxoconcha tumida Brady, 1868
Paradoxostoma simile G.W. Müller, 1894
Pseudopsammocythere reniformis (G.W. Müller, 1894)
Semicytherura dispar (G.W. Müller, 1894)
Xestoleberis dispar G.W. Müller, 1894

6—Sorted Channel Sand.

Sample: 97.
Bathymetry: 17 m.

This area located west of Kerkennak Island was characterised by a coarse sandy bottom.

The ostracod fauna was very poor in both species and number of specimens and included: *Callistocythere mediterranea* (G.W. Müller, 1894), *Hemicytherura defiorei* Ruggieri, 1953, *Semicytherura* spp., *Xestoleberis dispar* G.W. Müller, 1894.

7—Circalittoral Bioclastic Sand.

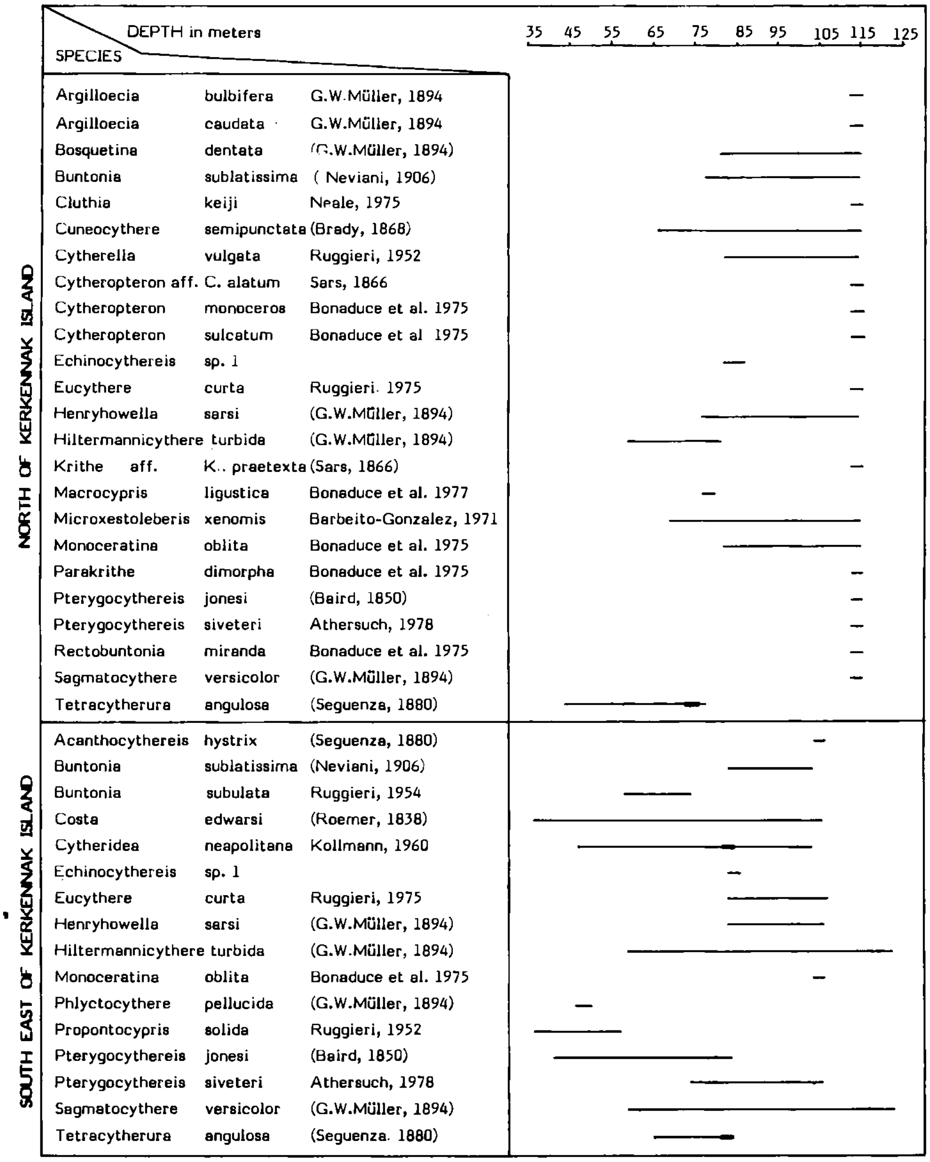
Samples: 3, 4, 8, 18, 19, 20, 29, 31, 35, 37, 39, 40, 45, 47, 48, 49, 50, 52, 54, 55, 56, 58, 59, 60, 61, 63, 67, 68, 69, 76, 77, 79, 89, 101, 102, 105, 106, 121.
Bathymetry: 35–125 m.

Type of bottom: the grain-size of the sediments varied from shallower medium sand to the deeper very sandy pelite.

This facies was generally circumscribed by the shallower *Caulerpa* meadow and the deeper circalittoral muddy bioclastic sandy facies and appeared widely distributed in the area studied. This facies, together with the following ones, showed a very high number of species and specimens. Most of the species were considered allochthonous, deriving mainly from previous shallower facies, several of which (especially the vegetable-dwellers) tended to disappear with increasing depth. Among the contaminants, the following species occurred more commonly:

Aurila convexa (Baird, 1850)
Aurila speyeri (Brady, 1868)
Aurila sp. 1
Bairdia longevaginata G.W. Müller, 1894
Callistocythere adriatica Masoli, 1968
Callistocythere flavidofusca (Ruggieri, 1950)
Callistocythere praecincta Ciampo, 1976
Caudites sp. 1
Cytheretta subradiosa (Roemer, 1838)

Loxoconcha bairdi G.W. Müller, 1912
Loxoconcha gibberosa Terquem, 1878
Loxoconcha rhomboidea (Fisher, 1855)
Loxoconcha tumida Brady, 1868
Paracytheridea depressa G.W. Müller, 1894
Pontocythere turbida (G.W. Müller, 1894)
Semicytherura heinzei Puri, 1963
Semicytherura inversa (Seguenza 1880)
Semicytherura paradoxa (G.W. Müller, 1894)
Semicytherura ruggierii (Pucci, 1955)
Xestoleberis communis G.W. Müller, 1894
Xestoleberis dispar G.W. Müller, 1894



TEXT-FIG. 3—Depth range distribution of the ostracod assemblage of bottom facies 7.

The areal distribution of the species considered autochthonous did not appear uniform within the facies. In fact, the southern area showed a reduced number of species and specimens with respect to the northern one. Moreover, the greatest variety occurred mostly in the deepest part of the facies.

Text-fig. 3 shows the areal and bathymetric distribution of the autochthonous species in both areas.

8—Circalittoral Muddy Bioclastic Sand.

Samples: 21, 22, 32, 33, 41, 42, 43, 44, 66, 73, 103, 104, 107, 114, 122, 129, 131.

Bathymetry: 52–175 m.

Type of bottom: varied from pelitic fine sands to more or less sandy pelites.

In spite of considerable contamination of the ostracod assemblage from the generally shallower, previously treated facies (*Aurila convexa, Bairdia* spp., *Callistocythere* spp., *Cytherois* spp., *Leptocythere* spp., *Loxoconcha bairdi, L. rhomboidea, L. tumida, Paradoxostoma versicolor, Semicytherura* spp., *Tenedocythere prava, Xestoleberis communis, X. dispar,* etc.) we have been able to define two areas, North and South of Kerkennak Island, respectively, which were characterised by different assemblages. Text-figure 4 shows the composition of the assemblages and their changes related to bathymetry.

9—Circalittoral Mud.

Samples; 23, 100.

Bathymetry: 66, 67 m.

Type of bottom: pelite.

This facies was restricted to a small area located in the Ashtart basin surrounded by a circalittoral muddy bioclastic sandy facies. Allochthonous species were frequently present, the most common of which included *Callistocythere adriatica, C. flavidofusca, Cytherella vandenboldi, Cytherois* aff. *C. uffenordei, Leptocythere macella, Loxoconcha tumida, Semicytherura ruggierii,* and *Xestoleberis communis.*

The authochthonous assemblage, represented by few specimens, mainly included:

Argilloecia acuminata G.W. Müller, 1894
Buntonia subulata Ruggieri, 1954
Cytheridea neapolitana Kollmann, 1960
Cytheropteron aff. *C. alatum* Sars, 1866
Phlyctocythere pellucida (G.W. Müller, 1894)
Pterygocythereis jonesi (Baird, 1850)
Sagmatocythere versicolor (G.W. Müller, 1894)

10—Outer Shelf Sand and Gravel.

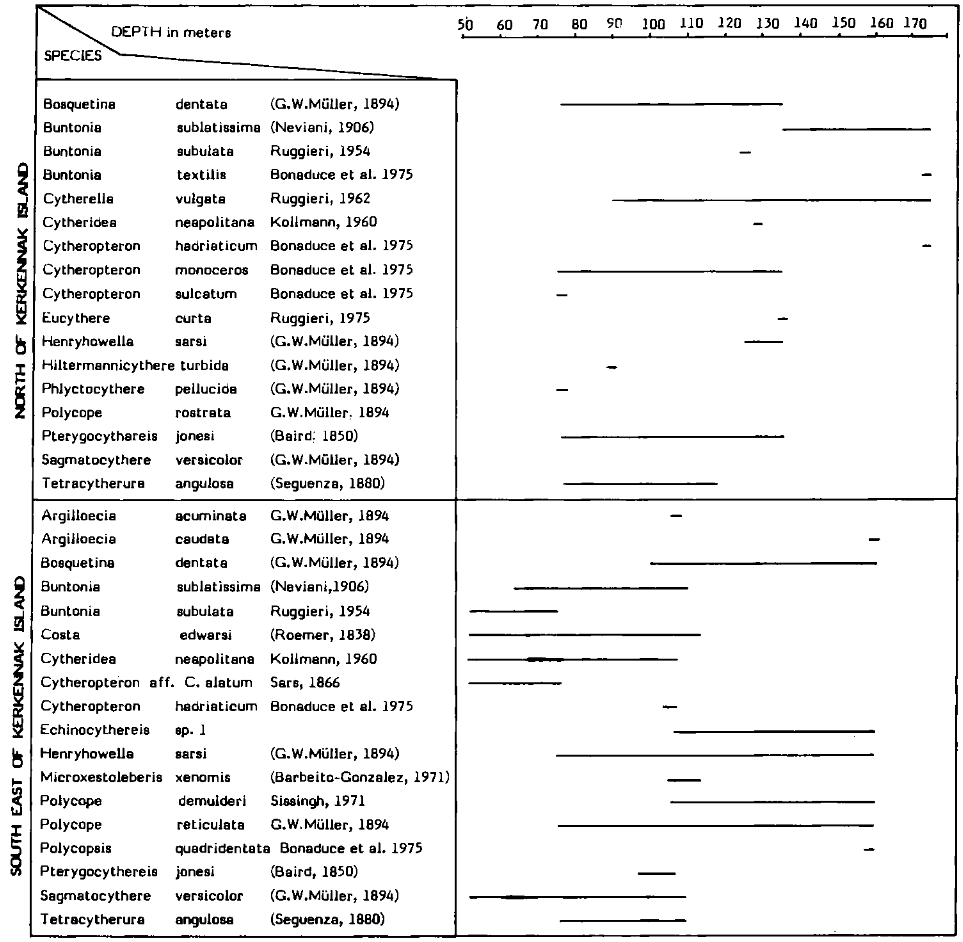
Samples: 109, 120, 128, 130.

Bathymetry: 114–170 m.

Type of bottom: from more or less pelitic medium-fine sand to very sandy pelite.

This type of bottom was restricted to a small area east of Kerkennak Island, characterised by a steep topography which explains the great contamination of the ostracod assemblages from shallower facies (*Aurila* spp., *Callistocythere* spp., *Caudites* sp. 1, *Leptocythere* spp., *Loxoconcha* spp., *Paracytheridea* spp., *Semicytherura* spp., *Xestoleberis* spp., etc.).

The autochthonous assemblage included the following species:



TEXT-FIG. 4—Depth range distribution of the ostracod assemblage of bottom facies 8.

Acanthocythereis hystrix (Ruess, 1850)
Argilloecia bulbifera G.W. Müller, 1894
Argilloecia caudata G.W. Müller, 1894
Argilloecia levis G.W. Müller, 1894
Argilloecia robusta Bonaduce, Ciampo and Masoli, 1975
Buntonia sublatissima (Neviani, 1906)
Cytherella vulgata Ruggieri, 1962
Cytheropteron aff. *C. alatum* Sars, 1866
Cytheropteron monoceros Bonaduce, Ciampo and Masoli, 1975
Echinocythereis sp. 1
Eucythere curta Ruggieri, 1975
Henryhowella sarsi (G.W. Müller, 1894)
Krithe aff. *K. praetexta* (Sars, 1866)
Parakrithe dimorpha Bonaduce, Ciampo and Masoli, 1975
Polycope demulderi Sissingh, 1971
Polycope parareticulata Bonaduce, Ciampo and Masoli, 1975
Polycope reticulata G.W. Müller, 1894
Polycope vasfiensis Sissingh, 1971
Polycopsis quadridentata Bonanduce, Ciampo and Masoli, 1975
Tuberculocythere infelix (Bonaduce, Ciampo and Masoli, 1975)

DEPTH in meters		0-1	19-28	17-26	15-48	24	17	36-123	52-175	66-67	114-170	160-300
BOTTOM FACIES		1	2	3	4	5	6	7	8	9	10	11
SPECIES												
Acanthocythereis	hystrix							—			—	
Aglaiocypris	complanata			—								
Aglaiocypris	rara				—							
Argilloecia	acuminata								—	—		—
Argilloecia	bulbifera							—			—	—
Argilloecia	caudata							—	—		—	—
Argilloecia	levis										—	
Argilloecia	minor											—
Argilloecia	robusta											
Aurila	convexa	—			—							
Aurila	speyeri	—			—							
Aurila	sp. 1	—		—	—	—						
Bairdia	corpulenta				—							
Bairdia	longevaginata	—			—							
Bairdia	mediterranea group			—								
Bairdia	reticulata	—			—							
Basslerites	berchoni		—	—								
Bosquetina	dentata							—	—			—
Buntonia	sublatissima							—	—		—	—
Buntonia	subulata							—	—	—		—
Buntonia	textilis								—			
Bythocythere	minima				—							
Callistocythere	diffusa				—							
Callistocythere	flavidofusca	—		—	—							
Callistocythere	littoralis	—		—								
Callistocythere	lobiancoi	—										
Callistocythere	mediterranea			—	—		—					
Callistocythere	praecincta				—							
Callistocythere	rastrifera			—								
Caudites	sp. 1	—		—								
Cluthia	keiji							—				
Costa	batei	—		—	—							
Costa	edwarsi		—			—		—	—			
Cuneocythere	semipunctata							—				
Cytherella	vandenboldi	—			—							
Cytherella	vulgata								—		—	—
Cytheretta	adriatica	—		—								
Cytheretta	subradiosa	—										
Cytheridea	neapolitana					—		—	—	—		
Cytherois	frequens			—	—							
Cytherois	triangularis		—		—	—						
Cytherois	aff. C. uffenordei		—	—								
Cytherois	sp. 1					—						
Cytheropteron	aff. C. alatum							—	—	—	—	—
Cytheropteron	hadriaticum								—			
Cytheropteron	monoceros							—	—		—	—
Cytheropteron	sulcatum							—	—			—
Cytheropteron	venustum											—
Echinocythereis	sp. 1							—			—	
Eucythere	curta							—			—	—
Hemicytherura	defiorei		—	—	—		—					
Henryhowella	sarsi							—	—		—	—
Hiltermannicythere	aff. H. rubra	—										
Hiltermannicythere	turbida	—						—	—			
Krithe	aff. K. praetexta							—			—	
Leptocythere	lagunae	—										
Leptocythere	macella		—		—	—						
Loculicytheretta	pavonia	—										
Loxocauda	decipiens			—								
Loxoconcha	bairdi	—		—	—							
Loxoconcha	elliptica	—										
Loxoconcha	gibberosa			—	—							
Loxoconcha	rhomboidea			—	—	—						
Loxoconcha	rubritincta	—										
Loxoconcha	stellifera	—			—							
Loxoconcha	tumida	—	—	—	—	—						

Text-fig. 5—Ostracod distribution plotted against bottom facies and depth range. (*Continued*)

DEPTH in meters		0-1	19-28	17-26	15-48	24	17	36-123	52-175	66-67	114-170	160-300
BOTTOM FACIES		1	2	3	4	5	6	7	8	9	10	11
SPECIES												
Loxoconcha	turbida				—							
Macrocypris	ligustica							—				
Microcythere	spp.		—	—	—							
Microxestoleberis	xenomis				—			—				
Monoceratina	oblita							—				
Neocytherideis	fasciata	—										
Paracytheridea	depressa	—			—							
Paracytheridea	pachina				—							
Paracytheridea	parallia				—							
Paradoxostoma	simile		—			—						
Paradoxostoma	versicolor				—							
Parakrithe	dactylomorpha											—
Parakrithe	dimorpha							—			—	—
"Pedicythere"	tessellata											—
Phlyctocythere	pellucida							—		—		
Polycope	demulderi							—	—		—	—
Polycope	frequens											—
Polycope	orbulinaeformis											—
Polycope	ovalis											—
Polycope	parareticulata										—	
Polycope	reticulata			—				—			—	—
Polycope	rostrata								—			
Polycope	striata											—
Polycope	vasfiensis										—	—
Polycopsis	quadridentata								—		—	—
Pontocythere	turbida	—										
Procytherideis	complicata	—										
Procytherideis	subspiralis	—										
Propontocypris	solida							—				
Pseudopsammocythere	reniformis					—						
Pseudopsammocythere	similis		—	—	—							
Pterygocythereis	jonesi							—	—	—		
Pterygocythereis	siveteri							—			—	
Rectobuntonia	miranda							—				
Sagmatocythere	napoliana	—										
Sagmatocythere	versicolor							—	—	—		
Semicytherura	acuta			—								
Semicytherura	acuticostata	—		—	—	—						
Semicytherura	aenariensis				—							
Semicytherura	alifera			—	—							
Semicytherura	amorpha				—							
Semicytherura	dispar				—	—						
Semicytherura	heinzei				—							
Semicytherura	kaloderma	—		—								
Semicytherura	incongruens	—			—							
Semicytherura	inversa	—			—							
Semicytherura	mediterranea	—										
Semicytherura	neglecta		—				—					
Semicytherura	quadridentata			—								
Semicytherura	rara	—										
Semicytherura	rarecostata			—	—							
Semicytherura	robusta				—							
Semicytherura	ruggierii		—		—							
Semicytherura	trachina			—								
Tenedocythere	prava			—	—							
Tetracytherura	angulosa							—	—			
Triebelina	raripila	—										
Tuberculocythere	infelix										—	
Urocythereis	neapolitana	—										
Xestoleberis	communis	—	—	—	—	—						
Xestoleberis	decipiens	—										
Xestoleberis	dispar	—			—	—	—					
Xestoleberis	pellucida				—							
Xestoleberis	plana				—							
Xestoleberis	rara	—										

TEXT-FIG. 5—*Continued*

This assemblage was better represented in terms of number of specimens in the deepest samples.

11—Open Marine Mud.

Samples: 71, 110, 111, 112, 116, 118, 124, 125.

Bathymetry: 160–300 m.

Type of bottom: more or less sandy pelite, rarely pelitic fine sand.

The study of this widely represented facies took into consideration an area east of Kerkennak Island. The bottom topography corresponded to a submarine valley that borders on the shallower outer shelf and gravel facies. Contamination from shallower facies appeared less significant with increasing depth. The contaminants included mainly *Aurila* spp., *Bairdia* spp., *Callistocythere* spp., *Cytheretta subradiosa, Cytheridea neapolitana, Cytheromorpha fuscata, Loxoconcha gibberosa, L. rhomboidea, L. tumida, Paracytheridea depressa, Sagmatocythere napoliana, S. versicolor, Semicytherura* spp., *Xestoleberis communis, X. dispar.*

The autochthonous assemblage consisted of:

Argilloecia acuminata G.W. Müller, 1894
Argilloecia bulbifera G.W. Müller, 1894
Argilloecia caudata G.W. Müller, 1894
Argilloecia minor G.W. Müller, 1894
Argilloecia robusta Bonaduce, Ciampo and Masoli, 1975
Bosquetina dentata (G.W. Müller, 1894)
Buntonia sublatissima (Neviani, 1906)
Buntonia subulata Ruggieri, 1954
Cytherella vulgata Ruggieri, 1962
Cytheropteron aff. *C. alatum* Sars, 1866
Cytheropteron monoceros Bonaduce, Ciampo and Masoli, 1975
Cytheropteron sulcatum Bonaduce, Ciampo and Masoli, 1975
Cytheropteron venustum Bonaduce, Ciampo and Masoli, 1975
Eucythere curta Ruggieri, 1975
Henryhowella sarsi (G.W. Müller, 1894)
Parakrithe dactylomorpha Ruggieri, 1962
Parakrithe dimorpha Bonaduce, Ciampo and Masoli, 1975
Pedicythere tessellata Bonaduce, Ciampo and Masoli, 1975
Polycope demulderi Sissingh, 1971
Polycope frequens G.W. Müller, 1894
Polycope orbulinaeformis Breman, 1976
Polycope ovalis Bonaduce, Ciliberto, Masoli, Minichelli and Pugliese, 1982
Polycope reticulata G.W. Müller, 1894
Polycope striata G.W. Müller, 1894
Polycope vasfiensis Sissingh, 1971
Polycopsis quadridentata Bonaduce, Ciampo and Masoli, 1975

The distribution of the previous species appears more related to the bottom topography than to the depth itself. In fact, the assemblage was reduced in number of species and specimens along the steep flanks of the valley, whereas it appeared better represented over the central plain.

REMARKS ON THE OSTRACOD ASSEMBLAGES

Data for the autochthonous ostracod assemblages related to the different facies are reported in Text-fig. 5. On the basis of these data and those given in the previous literature, some species seemed characteristic of a specific facies and depth range.

In our opinion, the possible facies markers are the following:

A—*Near-shore coastal sand*

Cytheretta subradiosa
Hiltermannicythere aff. *H. rubra*
Leptocythere lagunae
Loculicytheretta pavonia
Loxoconcha elliptica
Loxoconcha rubritincta
Neocytherideis fasciata
Procytherideis complicata
Procytherideis subspiralis
Triebelina raripila
Urocythereis neapolitana

Some of the cited species (*Leptocythere lagunae* and *Loxoconcha elliptica*) are known to be especially common in brackish water environments.

B—*Posidonia and Caulerpa meadows*

Aglaiocypris complanata (1)
Aglaiocypris rara (2)
Bairdia corpulenta (2)
Bairdia gr. *mediterranea*
Callistocythere diffusa (2)
Callistocythere praecincta (2)
Cytherois frequens
Loxocauda decipiens (1)
Loxoconcha gibberosa
Paracytheridea pachina (2)
Paracytheridea parallia (2)
Semicytherura acuta (1)
Semicytherura aenariensis (2)
Semicytherura alifera
Semicytherura amorpha (2)
Semicytherura heinzei (2)
Semicytherura quadridentata (1)
Semicytherura rarecostata
Semicytherura robusta (2)
Semicytherura trachina (1)
Xestoleberis pellucida (2)
Xestoleberis plana (2)

The species marked (1) seemed to occur on *Posidonia* only, whereas those marked (2) were also found on *Caulerpa*.

C—*Infralittoral mud*

Cytherois sp. 1
Pseudopsammocythere reniformis

D—*Circalittoral bioclastic sand*

Cluthia keiji
Cuneocythere semipunctata
Macrocypris ligustica
Monoceratina oblita
Rectobuntonia miranda
Propontocypris solida

E—*Circalittoral muddy bioclastic sand*

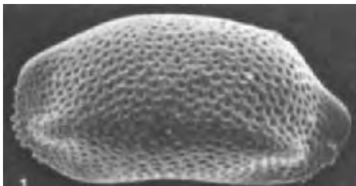
Buntonia textilis
Cytheropteron hadriaticum
Polycope rostrata

F—*Outer shelf sand and gravel*

Argilloecia levis
Polycope parareticulata
Tuberculocythere infelix

G—*Open marine mud*

Argilloecia minor
Cytheropteron venustum
Parakrithe dactylomorpha
Pedicythere tessellata
Polycope frequens
Polycope orbulinaeformis
Polycope ovalis
Polycope striata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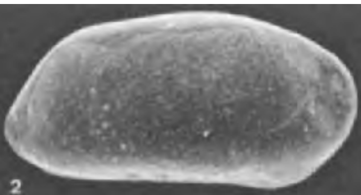
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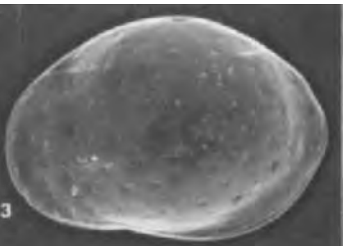
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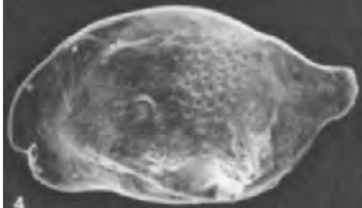
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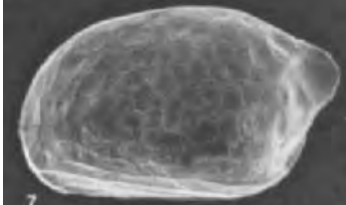
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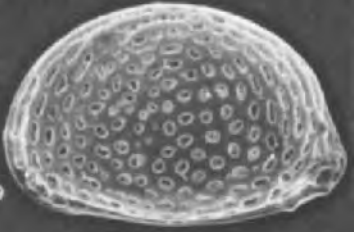
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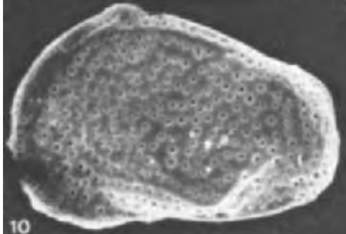
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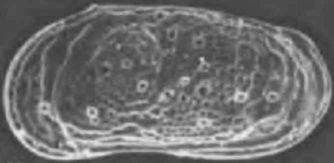
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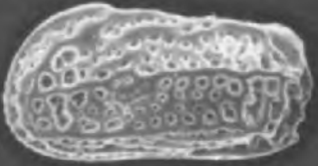
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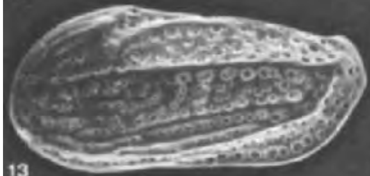
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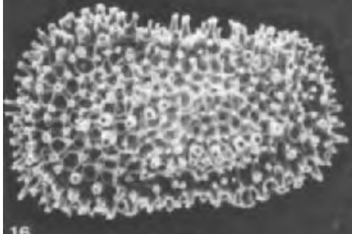
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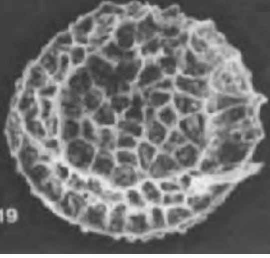
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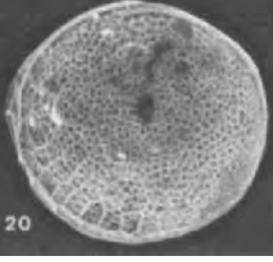
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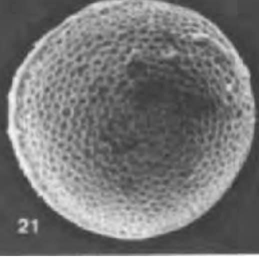
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Plate 1 illustrates some of the species characterizing the previously cited facies, especially in cases where they have been insufficiently represented in the literature.

CONCLUSIONS

The study of the ostracod fauna of the Tunisian shelf has provided the following results: a) Eleven ostracod assemblages have been recognized and related to the different bottom facies. Several species, or groups of species, have been shown to characterize a particular facies or group of facies (see Text-fig. 5). It has also been possible to define several depth range distributions within the same facies and/or group of facies (see Text-figs. 3 and 4). Most of the autochthonous assemblages generally appear contaminated by the contiguous and/or shallower facies and contamination was shown to decrease with increasing depth. Furthermore, 9 bottom facies were characterized by a more or less high number of species; the 2 assemblages related to sorted channel sand and circalittoral mud did not show any characteristic species.

b) At the boundary between two facies, the diversity and abundance of ostracods decreases; this may be related to the instability of the environment.

c) In the bottom facies 2, 3, and 4, the plant-dwellers decrease with increasing pelitic percentage composition in the sediments. In our opinion, a diminution of plants occurs with increasing turbidity resulting in bottom instability.

d) From the zoogeographical point of view, the near-shore ostracod assemblage appears well characterized with respect to different northern areas of the Mediterranean basin whereas it becomes more and more uniform with increasing depth.

e) The presence of post-Miocene fossil forms in the sediments suggests relatively recent erosion and/or tectonic activity which brought to the surface forms that are no older than the Pliocene. These fossil specimens are in fact represented from Pliocene to Recent in the Mediterranean basin. The study of the Ashtart 1 well from the Gulf of Gabès (Bonaduce *et al.*, in preparation) seems to confirm the absence of these forms in pre-Pliocene sediments.

In general, we have been able to point out the differences between the ostracod assemblages belonging to different facies and sedimentology; moreover a more precise depth range distribution of the species and assemblages has been defined.

In our opinion these results allow a different approach to a more detailed definition of Recent and ancient environments.

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PLATE 1—1. *Triebelina raripila*, LV (×67). 2. *Bairdia reticulata*, RV (×67). 3. *Loxoconcha stellifera*, LV (×58). 4. *Cytheropteron venustum*, LV (×122). 5. *Cytheropteron monoceros*, LV (×103). 6. *Cytheropteron* aff. *C. alatum*, RV (×94). 7. *Semicytherura kaloderma*, LV (×90). 8. *Caudites* sp. 1, LV (×70). 9. *Aurila* sp. 1, LV (×58). 10. *Cluthia keiji*, LV (×158). 11. *Leptocythere lagunae*, LV (×75). 12. *Hiltermannicythere* aff. *H. rubra*, LV (×53). 13. *Loculicytheretta pavoniamale*, LV (×75). 14. *Buntonia sublatissima*, LV (×90). 15. *Argilloecia acuminata*, RV (×90). 16. *Henryhowella sarsi*, LV (×61). 17. *Tuberculocythere infelix*, LV (×206). 18. *Monoceratina oblita*, RV (×72). 19. *Polycope demulderi*, LV (×107). 20. *Polycope parareticulata*, LV (×98). 21. *Polycope orbulinaeformis*, LV (× 122).

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DISCUSSION

Hartmann: It surprises me that you found *Leptocythere lagunae* and *Cyprideis* in an open gulf. Is there any brackish water influence and from where does it come?

Bonaduce: The presence of many species of living *Leptocythere* in the Ionian Sea (down to a depth of over 60 m) in the Gulfs of Salerno and Policastro (Tyrrhenian Sea) is in our opinion due to the influence of fresh water of land origin in areas where there are inlet rivers which filter through the sediment beds and reduce the salinity level.

Relationships Between Ecological Models Based on Ostracods and Foraminifers from Sepetiba Bay (Rio de Janeiro-Brazil)

DIMAS DIAS-BRITO[1], JOEL A. MOURA[1] AND NORMA WÜRDIG[2]
Petrobràs Research Center, Rio de Janeiro[1] *and*
Universidade Federal do Rio Grande do Sul, Porto Alegre[2], *Brasil*

ABSTRACT

Ecological models based on the distribution of recent ostracods and foraminifers from Sepetiba Bay, Rio de Janeiro, Brazil, are presented, compared and discussed. It may be verified that there is a very good agreement between them. The study area was divided into three environmental realms, subdivided into ten ostracod biofacies and seven foraminiferal biofacies. The relationships between the biotic and abiotic components are discussed. Distribution maps of some associated organic groups are also presented.

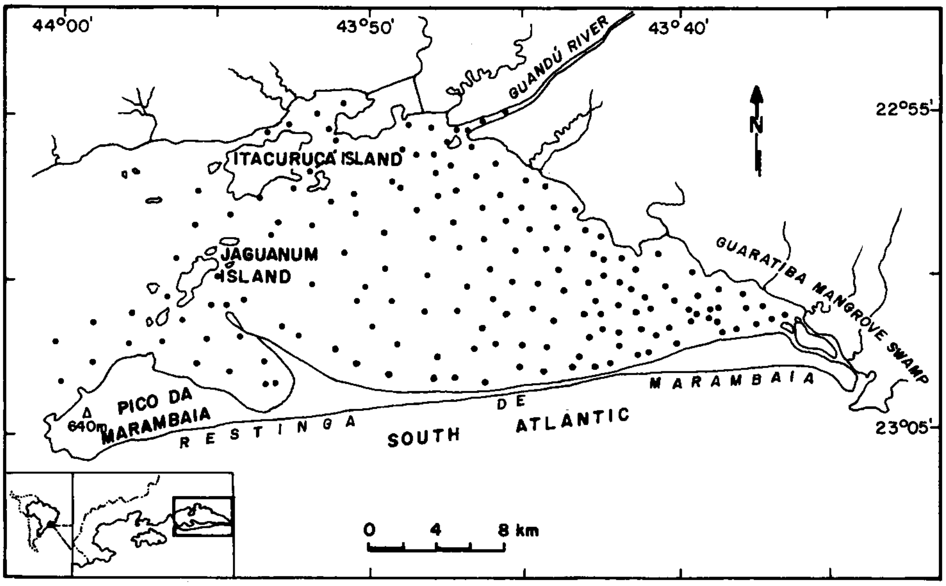
INTRODUCTION

The knowledge of recent biofacies models is of the utmost importance for palaeoecological research. Through these models the earth scientist perceives and understands the dynamics of spatial variations of biotic and abiotic parameters in the environment, and may, when working with old sediments, use this perception to reconstitute the geohistorical evolution of a given sedimentary basin. Taking into account this concept, Brazil's petroleum company, PETROBRÁS, which has been widely employing palaeoecological research to analyze basins in Brazil's Atlantic margin, conducted a program of ecological studies at the Sepetiba Bay and Guaratiba tidal flat coastal complex. This program was the origin of several papers, particularly relating to Foraminifera, which have been published in the last ten years (Zaninetti *et al.*, 1976, 1977; Bronnimann and Beurlen, 1977a, b, c; Bronnimann, 1978, 1979; Bronnimann *et al.*, 1979; Dias-Brito and Zaninetti, 1979; Bronnimann, 1980, 1981; Bronnimann *et al.*, 1981a, b; Bronnimann and Dias-Brito, 1982; Dias-Brito *et al.*, 1982, Moura *et al.*, 1982; Bronnimann, 1984).

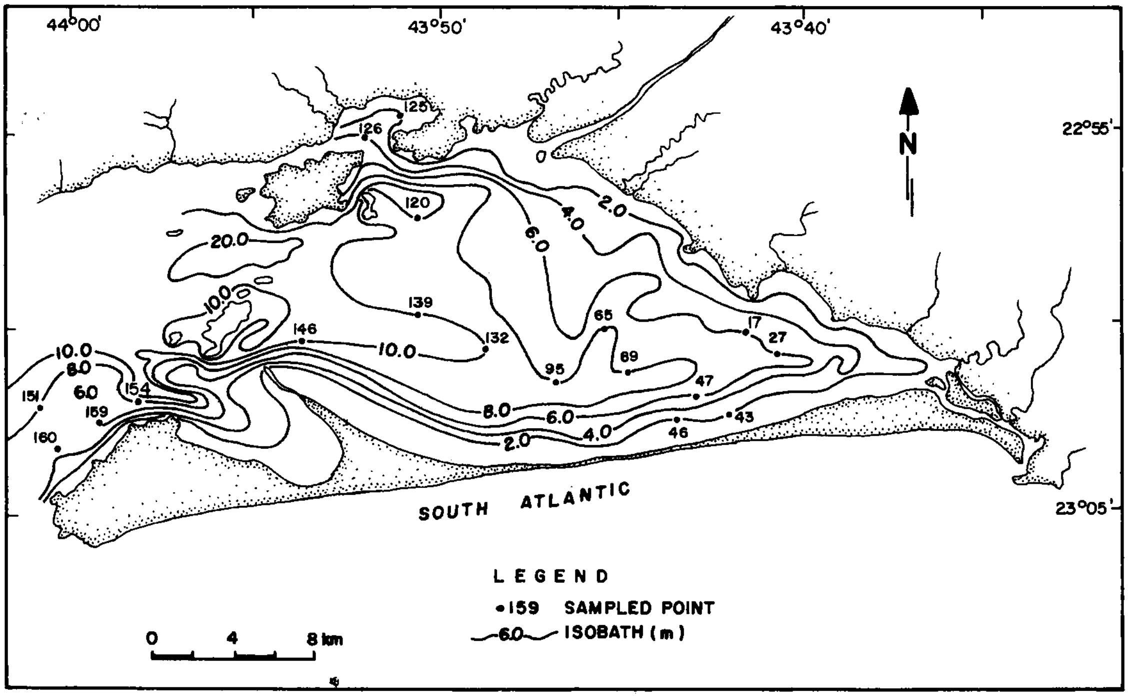
This paper presents, compares and discusses the distributions of Ostracoda and Foraminifera in Sepetiba Bay. It shows the relationships prevailing between the ecological models of these two groups and represents the first study relating to ostracoda in this area. It has been conducted at PETROBRÁS' Research and Development Center—CENPES and at the Institute of Biological Sciences of the Federal University of Rio Grande do Sul.

THE SEPETIBA-GUARATIBA COASTAL COMPLEX

Approximately 500 km, this coastal complex is part of a large bay located on the South coast of the State of Rio de Janeiro (Text-fig. 1). It is a classical complex involving a sandy barrier



Text-fig. 1—Study area and sampled points in Sepetiba Bay.



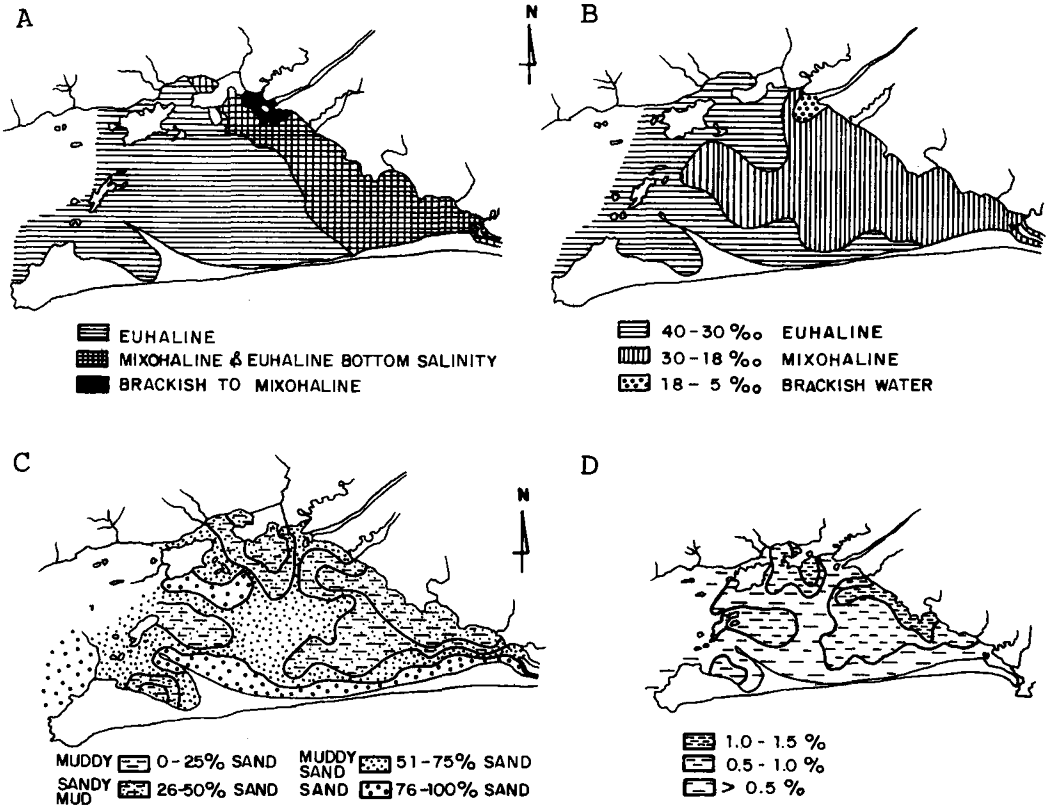
Text-fig. 2—Bathymetry in Sepetiba Bay (after Carvalho *et al.*, 1979).

island (Restinga de Marambaia), a lagoon (Sepetiba Bay), a small delta dominated by fluvial processes (delta of the Guandu River) and a tidal flat, partially covered with mangroves (Guaratiba area). The system has its present configuration tied to events which occurred after the Würm glacial interval; more accurately, it is a post-Flandrian transgression. It fits exactly the microtidal estuary of Hayes (1976). The climate of this area is the tropical type, hot and humid, rainy in the summer and dry in the winter, belonging to group A of Koppen's classification. Quaternary coastal plains and pre-Cambrian rocks of the Serra do Mar constitute the neighbourhood of the complex.

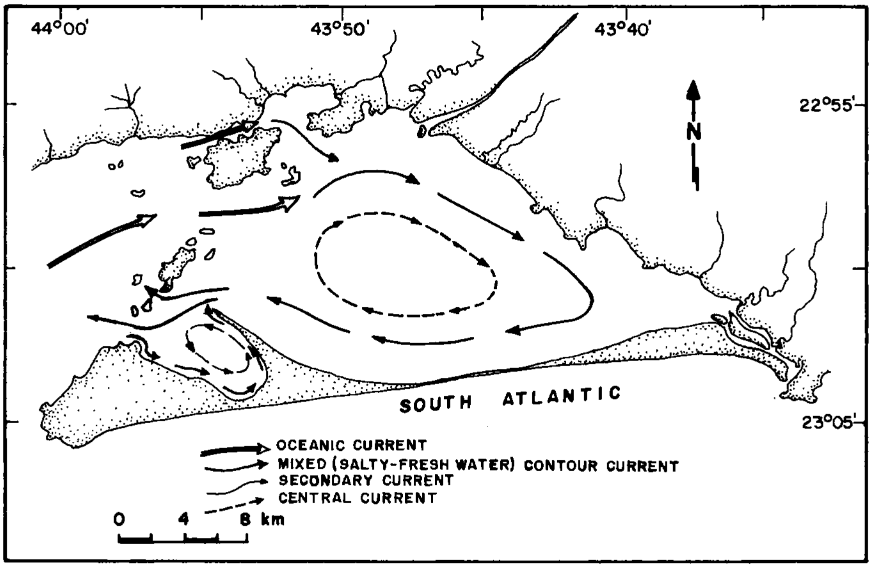
Sepetiba Bay: Abiotic Components

This lagoon, with an area of nearly 305 km^2, is semi-isolated from the Atlantic Ocean by an approximately 40 km-long sand bar, which links the metamorphic Pico da Marambaia in the West to the mangrove area of Guaratiba in the East. A string of metamorphic islands, of which the largest are Jaguanum in the South and Itacurçá in the North, contributes to the isolation of the bay.

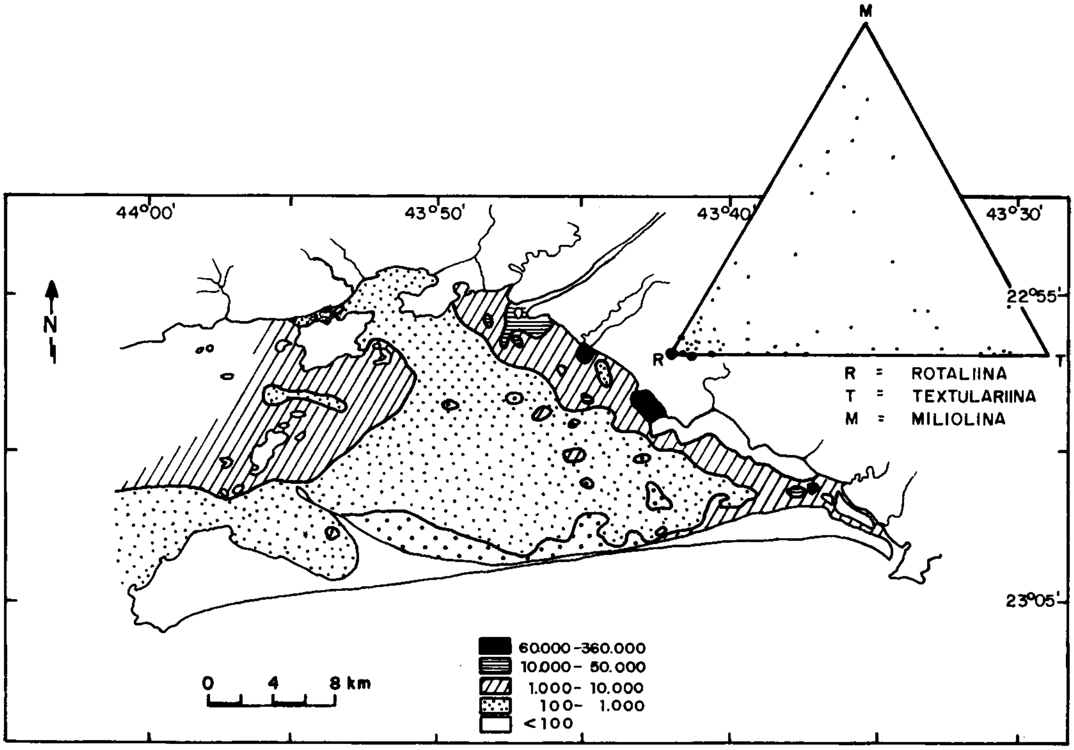
The bathymetry is shown on the map (Text-fig. 2). The depth increases gradually from east to west and is 8–10 m in the central portion; there are deep channels between the Jaguanum and Itacuruçá islands reaching down to 27 m. The water temperature ranges from 19.7° to 25.1° C; the pH values range from 7.6 to 8.3. Concerning salinity, adopting Boltovskoy's classification



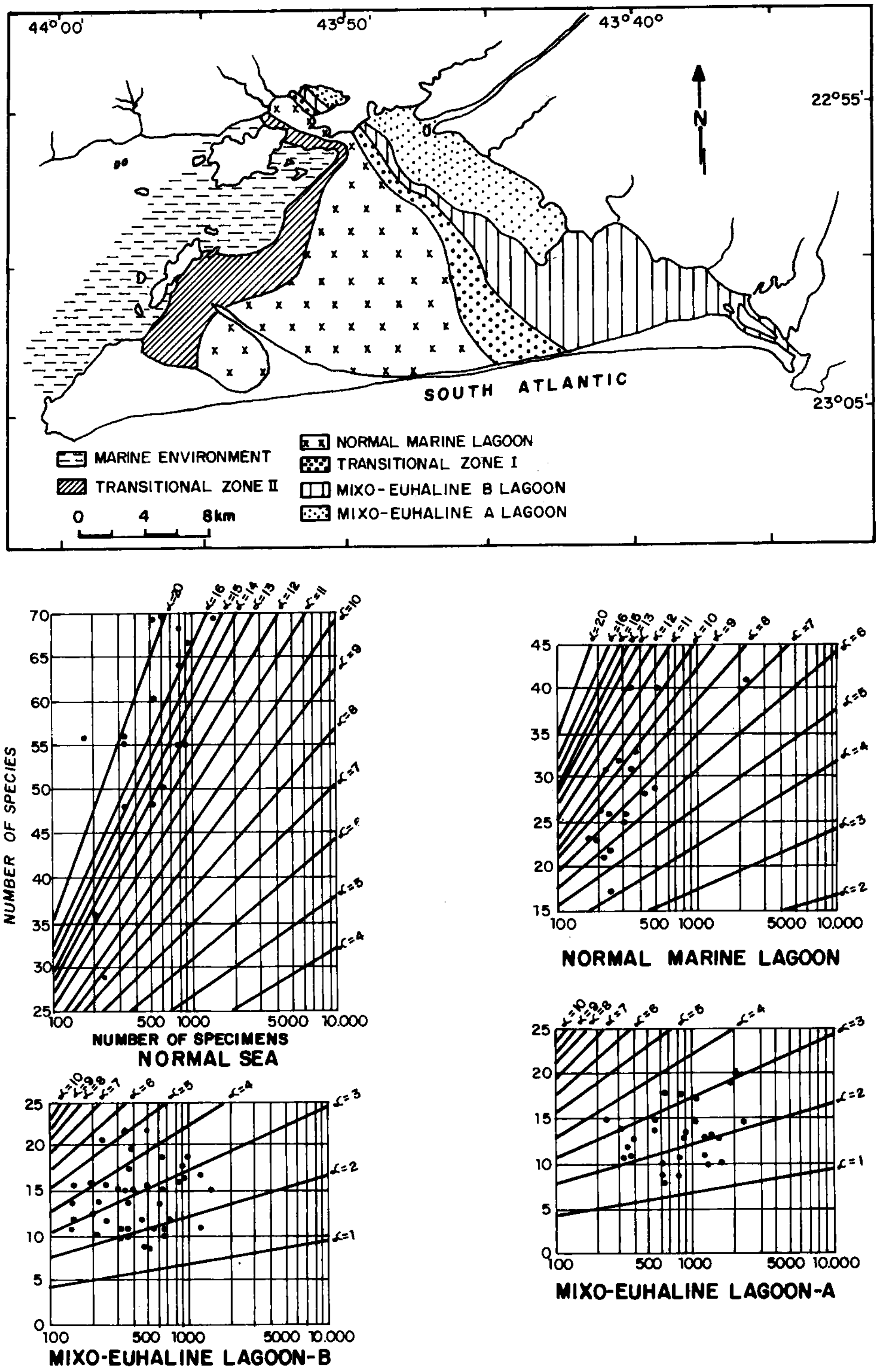
TEXT-FIG. 3—A. Bottom salinity (mod. from Carvalho *et al.*, 1979). B. Surface salinity (mod. from Carvalho *et al.*, 1979). C. Sediment distribution in Sepetiba Bay. D. Organic matter content.



TEXT-FIG. 4—System of currents in Sepetiba Bay based on the distribution of benthic and planktonic micro-organisms.



TEXT-FIG. 5—Absolute frequency of foraminifers (*per* 3000 cm^3 of wet sediment).

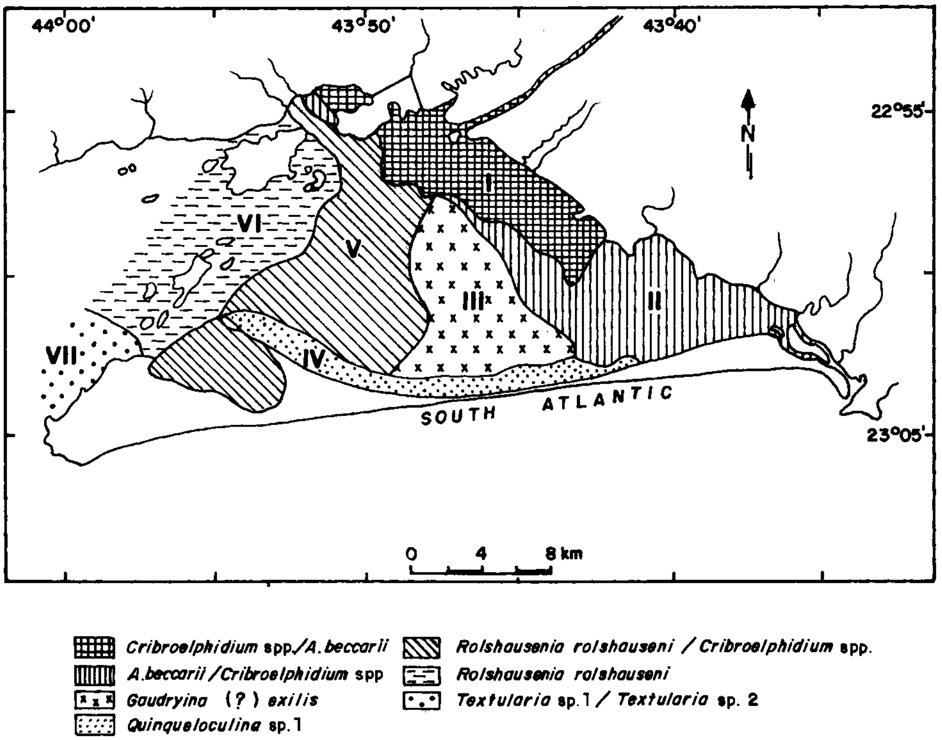


TEXT-FIG. 6—Environmental compartments based on specific diversity of foraminifers and specific diversity in the environmental compartments (Fisher's α index).

(1976, p. 139), the waters at the bottom are brackish near the mouth of the Guandu River, mixohaline to euhaline in the north-east part as a consequence of the interaction of microtidals (less than 2 m) and a variable influx of fluvial waters, and euhaline in the main part of the bay. The surface waters are predominantly mixohaline (Text-figs. 3A, B). A salt wedge estuary of Pritchard (1967) may, thus, be recognized in this area.

The sediments deposited in the lagoon are predominantly fine siliciclastics, with the exception of the area adjacent to the barrier island and the mouth of the Guandu River, where coarse sediments occur (Text-fig. 3C). The highest content of organic matter, 0.5 to 1.5 %, occurs associated with the most argillaceous sediments (Text-fig. 3D). The $CaCO_3$ content in the sediments ranges from 5 to 25 %, the highest levels being found in the most argillaceous sediments. The granulometry increases from east to west as a consequence of the progressive, parallel energy increment of the waters in this direction.

Sepetiba Bay is a relatively calm environment. An ocean stream, however, penetrates the inner portion of the lagoon, passing between the Jaguanum and Itacuruçá Islands and heading north; near the mouth of the Guandu River, the stream suffers a deflection towards the east and proceeds around the bay. Its action causes severe erosion effects in the central portion of the barrier island. The central area of the bay is calm and, as a consequence of the main stream, a slow moving ellipsoidal stream probably exists there (Text-fig. 4).



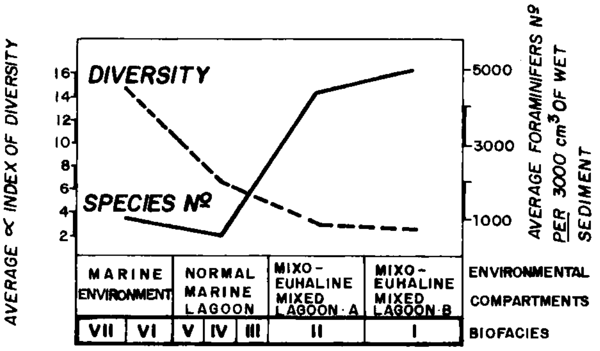
TEXT-FIG. 7—Biofacies of foraminifers.

Sepetiba Bay: Biotic Components

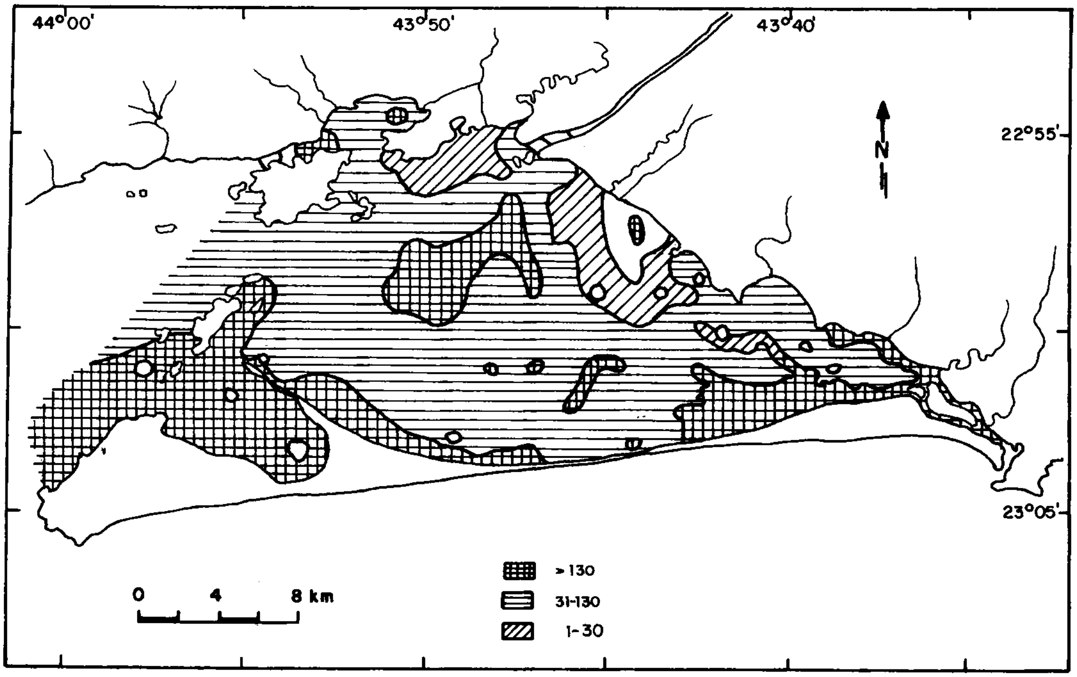
The major microbiological elements present in the Sepetiba Bay include, in addition to Foraminifera and Ostracoda, micromollusca, diatoms, Radiolaria (not common), Archeomonadidae and sponge spicules (not common). Maps showing their distribution were presented by Moura *et al.* (1982). The biotic data, as well as the abiotic, were obtained from 176 sample stations. The field work was carried out between May and August, 1978.

FORAMINIFERA

Essentially benthic Foraminifera occurred in the area researched. The contents include euryhaline and stenohaline species, distributed in specific areas: mixed Lagoon (mixohaline to euhaline



TEXT-FIG. 8—Foraminiferal frequency/diversity in the 4 environmental divisions (including the biofacies).

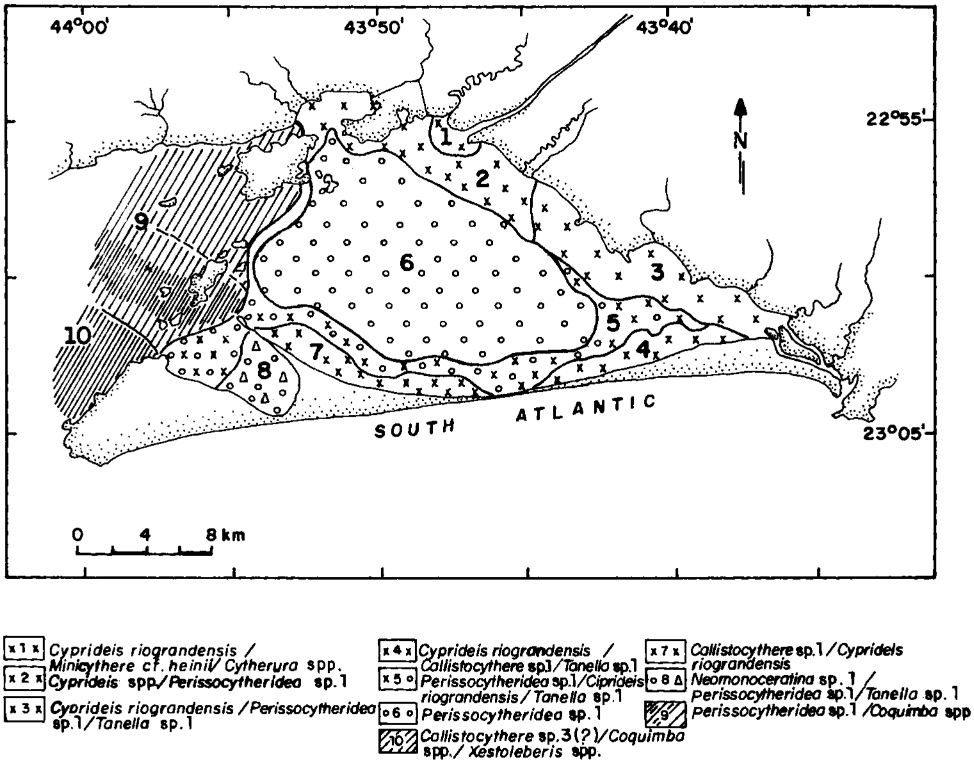


TEXT-FIG. 9—Absolute frequency of ostracods (*per* 3000 cm³ of wet sediment).

waters), marine Lagoon (euhaline waters) and marine environment (euhaline waters with good circulation). No distinction between live and dead specimens was made at the time of collection. Thus, the work was based on total populations existing in the surface sediments collected. Considering that the sedimentation rate in this area is significant and utilizing the results obtained by Walton (1955), it may be assumed that the maps represent primarily the distribution of live foraminifera.

Frequency

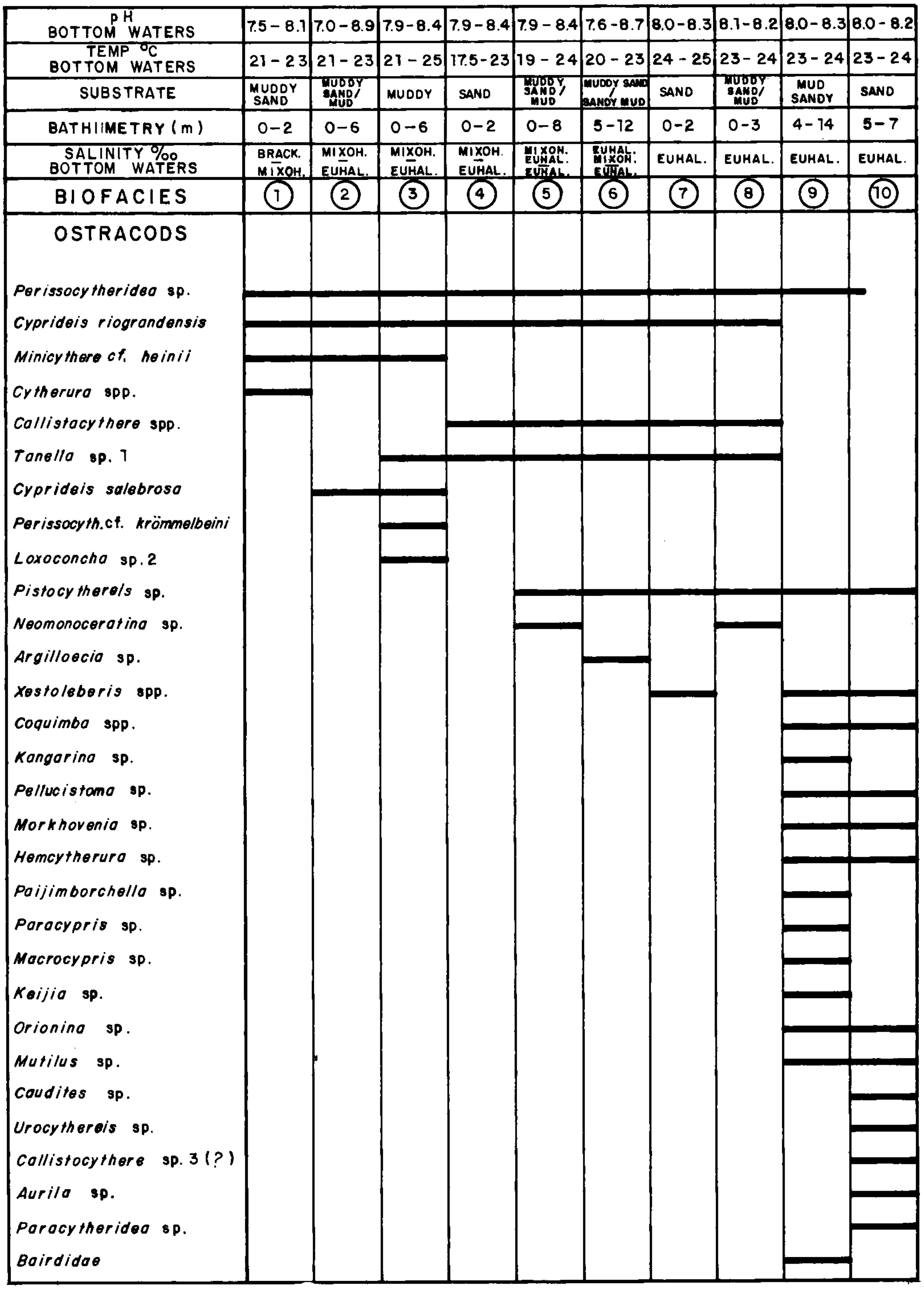
The foraminifers are distributed throughout the lagoon. The highest frequencies occur in the most unstable environments, where stresses are high and there is a large availability of nutrients. Rotalids largely predominate and miliolids are rare (Text-fig. 5). Maps showing the distribution of the three suborders have been published by Bronnimann, Moura and Dias-Brito (1981b).



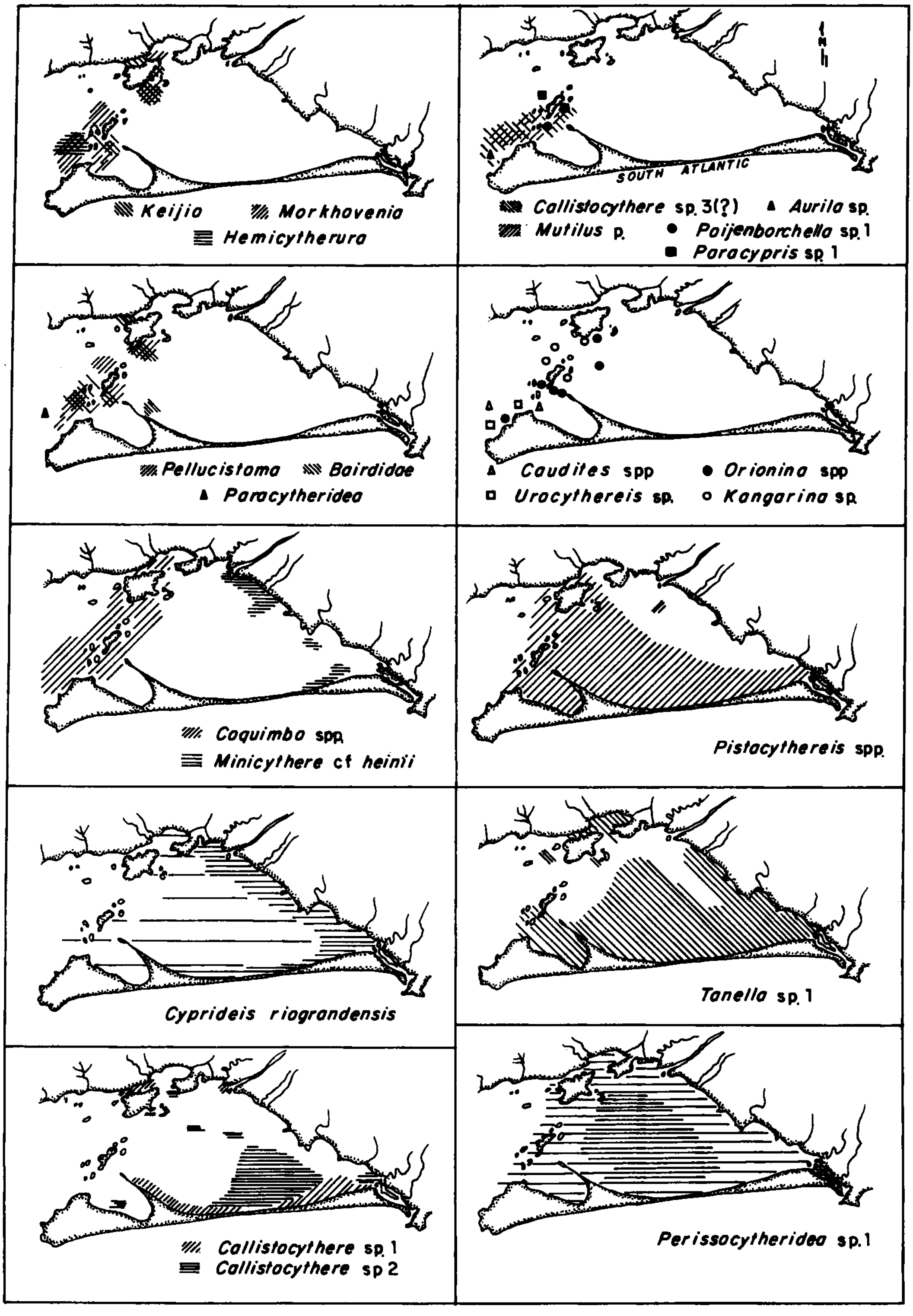
TEXT-FIG. 10—Biofacies of ostracods in Sepetiba Bay.

TEXT-FIG. 11—Ostracod biofacies: specific distribution. Remarks concerning the biofacies 9 and 10. In Biofacies 9, several species that occur in the north, as well as in the south, are not present in the deeper central part (27 m). This is characteristic of *Kangarina* sp., *Orionina* sp., *Keijia* sp., *Morkhovenia* sp., *Xestoleberis* sp. and Bairdidae (Text-fig. 13). This phenomenon should be related to the presence of the marine current that enters the bay this way. This is in agreement with the interpretations of Bronnimann, Moura and Dias-Brito (1981). However, *Perissocytheridea* sp. 1, *Coquimba* spp. and *Pistocythereis* spp. occur in this central area. On the other hand, *Mutilus* spp., *Callistocythere* sp. 3(?), *Paracypris* sp., *Hemicytherura* sp. and *Paijenborchella* sp. only occur in the south of Biofacies 9. This assemblage characterizes a sub-facies under the influence of a more marine water mass, here called the *Mutilus**spp. subfacies after the most common genus in the area. The remarkable difference between Biofacies 9 and 10 is the insignificant occurrence of *Perissocytheridea* sp. 1 in Biofacies 10.

BIO FACIES	MAIN SPECIES	RELAT. FREQ. (%)	SPATIAL OCCURRENCE	ASSOCIATED SPECIES	RELAT. FREQ. (%)	SPATIAL OCCURRENCE
①	*Cyprideis riograndensis*	7-90	*Widespread*	*Perissocytheridea* sp. 1	53	*Very rare*
	Minicythere cf. heinii	4-30	*Widespread*			
	Cytherura spp.	4-15	*Widespread*			
②	*Cyprideis* spp.	21-100	*Widespread*	*Minicythere cf. heinii*	16-23	*Two stations*
	Perissocytheridea sp.1	5-60	*Widespread*			
③	*Cyprideis riograndensis*	21-100	*East part*	*Cyprideis salebrosa*	1-25	*Eastern part*
		6-10	*West part*		<5	*Eastern part*
	Perissocytheridea sp. 1	5-60	*West part (most important)*	*P. cf. krammelbeini*	1-35	*West part*
				Minicythere cf. heinii	1-03	*Three stations*
	Tanella sp. 1	4-07	*Widespread*	*Loxoconcha* sp. 2	8-12	*Four stations*
④	*Cyprideis riograndensis*	51-100	*Widespread*	*Perissocytheridea* sp. 1	4-13 < 21	*Widespread* *Eastern part*
	Callistocythere sp. 1	<10	*Widespread*			
	Tanella sp.1	<10	*Widespread*			
⑤	*Perissocytheridea* sp.1	7-80	*Widespread*	*Pistocythereis* sp.	1-05	*Very rare*
	Cyprideis riograndensis	6-90	*Widespread*	*Neomonoceratina* sp.	1-05	*Very rare*
	Tanella sp. 1	0.5-19	*Widespread*	*Callistocythere* sp. 2	1-22	*Very rare*
⑥	*Perissocytheridea* sp. 1	81-100	*Widespread*	*Pistocythereis* sp. *Tanella* sp. *Callistocythere* sp. 2 *Argillaecia* sp. *Cyprideis riograndensis*	1-05 0.1-10 0.1-10 <5	*South part* *South part* *Southeast part* *Scarce stations* *Northeast part*
⑦	*Callistocythere* sp. 1	6-07	*East part*	*Perissocytheridea* sp. 1	0.1-20	*Widespread*
		25-70	*West part*	*Pistocythereis* sp.	11-20	*Sporadic*
	Cyprideis riograndensis	38-50	*East part*	*Tanella* sp. 1	< 10	*Rare*
		7-25	*West part*	*Xestoleberis* spp.	<10	*Widespread*
⑧	*Neomonoceratina* sp.	21-55	*Widespread*	*Cyprideis riograndensis*	< 5	*Dispersed*
	Perissocytheridea sp. 1	25-50	*Widespred*	*Pistocythereis* sp.		
	Tanella sp. 1	10-50	*Widespred*	*Callistocythere* sp. 1		
⑨	*Perissocytheridea* sp. 1	21-80	*Widespread*	*Kangarina* sp. *Pistacythereis* sp. *Xestoleberis* spp. *Callistocythere* spp. *Callistocythere* sp. 1	1.5-08 1-10 1-08 0.5-09 2,5-06	*Dispersed* *Widespread* *Dispersed* *Rare* *Three stations*
	Coquimba spp.	0.5-28	*Widespread*	*Bairdidae* *Cyprideis riograndensis* *Pellucistoma* sp. *Markhovenia* sp. *Hemicytherura* sp. *Paimjenborchella* sp. *Parocypris* sp. *Macrocypris* sp. *Keijia* sp. *Orionina* sp. *Mutilus* sp. *Caudites* sp.	< 5	*Dispersed*
⑩	*Callistocythere* sp. 3 (?)	25-80	*Widespread*	*Perissocytheridea* sp. 1 *Urocythereis* sp. *Mutilus* spp.	7-32 1-12 0.1-11	*Two stations* *Two stations* *Dispersed*
	Coquimba spp.	5-25	*Widespread*	*Markhovenia* sp. *Hemicytherura* sp. *Orionina* sp. *Pellucistoma* sp. *Porocytheridea* sp. *Caudites* sp. , *Aurila* sp.	< 5	*Dispersed*
	Xestoleberis spp.	1-12	*Widespread*			



TEXT-FIG. 12—Ostracod biofacies: specific distribution.



TEXT-FIG. 13—Distribution of ostracod species in Sepetiba Bay.

Specific Diversity

A high dispersion in the specific diversity (Fisher's α index) was recorded in Sepetiba Bay. Once this fact was verified, four station groups were recognized where the index varied, respectively, from 1 to 3, 2 to 5, 5 to 10, and > 10. It was then possible to define four environmental divisions, with two transitional zones: MIXED LAGOON A, MIXED LAGOON B, MARINE LAGOON and MARINE ENVIRONMENT (Text-fig. 6). Stations with less than 300 specimens were not taken into account in the calculations of the index.

Biofacies

In addition to having been divided into four environmental divisions, the lagoon was subdivided into seven biofacies, the names of which originated from the predominant taxon or taxa (Text-fig. 7).

Text-fig. 8 summarizes the frequency and diversity patterns recognized for Sepetiba Bay. This is the synthetic, fundamental graph for the distribution of foraminifers in the area studied. The distribution of the species in the biofacies as well as the parameters controlling such distribution are shown by Bronnimann, Moura and Dias-Brito (1981b, Text-figs. 4 and 5, p. 1866). The distribution of the major species, among the 180 found in the bay, is also discussed in this paper.

OSTRACODA

The study of Ostracoda includes a preliminary taxonomic study, which will form the basis of a more detailed one in the future. Specific differentiation was usually informal, the various species being given numbers. Such a classification, however, provided good support for the research into the ecological model of Ostracoda in Sepetiba Bay.

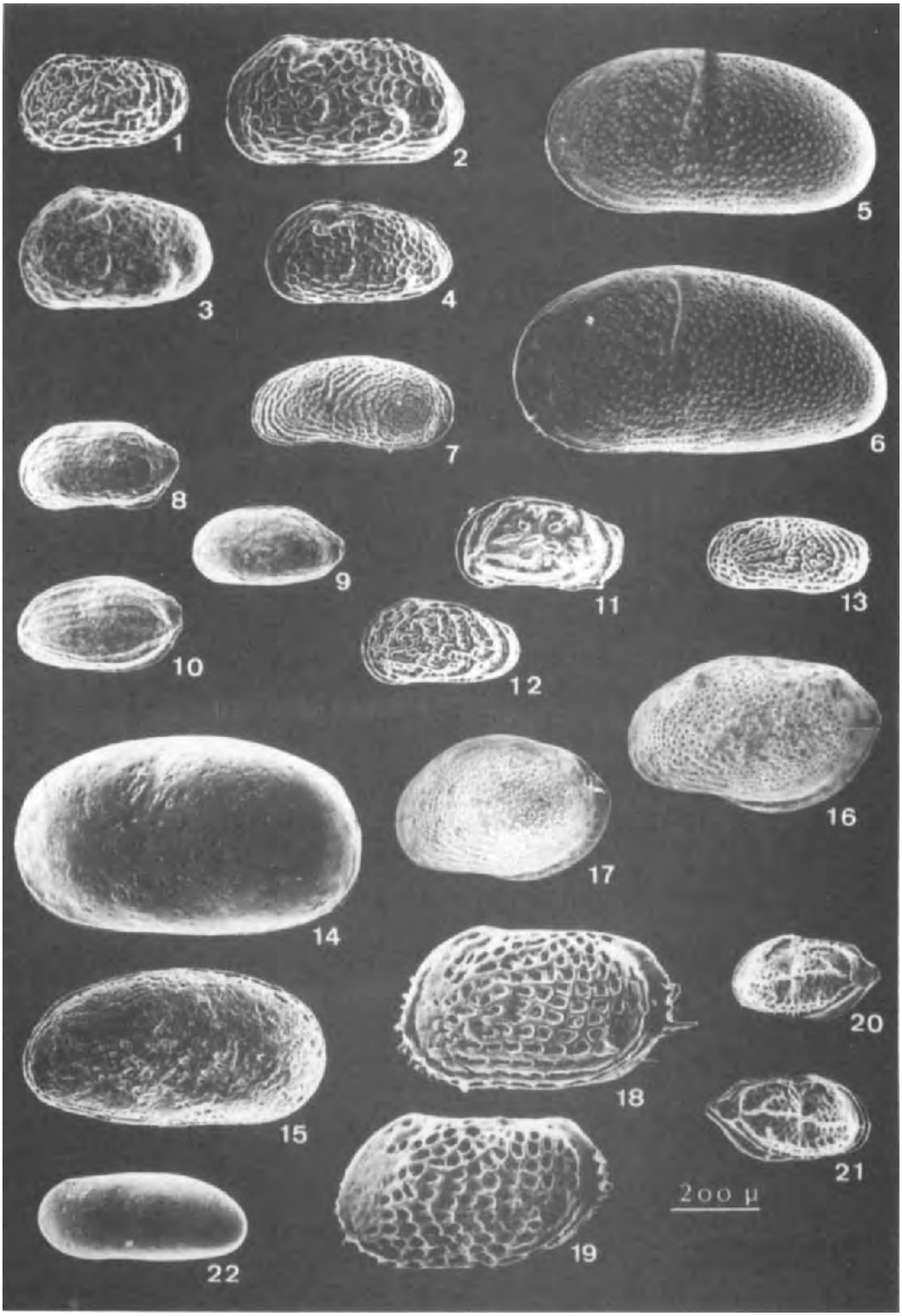
Frequency

The Ostracoda are distributed throughout the area researched. The largest area of the lagoon contains between 30 and 130 ostracods per 3,000 cm^3 of wet sediment collected from the lagoon floor. Some areas are almost destitute of ostracods; there are areas, however, with richer faunal contents (Text-fig. 9).

Specific Diversity

No diversity index was calculated for Ostracoda in the bay. Nevertheless, the number of species which occurs in each defined biofacies was recognized based on Ostracoda.

PLATE 1— 1. *Perissocytheridea* sp.1, station BS 4, Biofacies 4. 2. *Perissocytheridea* sp. 2, station BS 1, Biofacies 3. 3. *Perissocytheridea* sp. 3(?), station BS 175, Biofaces 9. 4. *Perissocytheridea* cf. *P. Kroemmelbein* Pinto and Ornellas. station BS 22, Biofacies 5. 5. *Cyprideis riograndensis* Pinto and Ornellas (♀), station BS 37, Biofacies 4. 6. *Cyprideis riograndensis* (♂), station BS 37, Biofacies 4. 7. *Minicythere* cf. *M. heinii* Ornellas, station BS 5, Biofacies 4. 8. *Cytherura* sp. 1, station BS 1, Biofacies 3. 9. *Cytherura* sp. 2 (?), station BS 37, Biofacies 4. 10. *Cytherura* sp. 3(?), station BS 155, Biofacies 5. 11. *Callistocythere* sp. 1, station BS 1, Biofacies 3. 12. *Callistocythere* sp. 2, Biofacies 8 (slide 153). 13. *Tanella* sp. 1, station BS 5, Biofacies 4. 14. *Cyprideis salebrosa* Van den Bold (♀), station BS 8, Biofacies 3. 15. *Cyprideis salebrosa* Van den Bold (♂), station BS 8, Biofacies 3. 16. *Loxoconcha* sp. 1, station BS 147, Biofacies 9. 17. *Loxoconcha* sp. 2, station BS 1, Biofacies 3. 18. *Pistocythereis* sp. 1, station BS 164, Biofacies 9. 19. *Pistocythereis* sp. 2, station BS 138, Biofacies 6. 20. *Neomonoceratina* sp. 1, station BS 150, Biofacies 8. 21. *Neomonoceratina* sp., station BS 149, Biofacies 8. 22. *Argilloecia* sp. 1, station BS 157, Biofacies 5.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Biofacies

Combining taxonomic and quantitative data (relative frequency as percentage of each species per sample), it was possible to identify station groups with similar associaions of ostracods. Such groups were recognised individualy as ten biofacies (Text-fig. 10), the biotic characteristics of which are shown in Text-fig. 11. Based on this, the lagoonal biofacies proved to contain between 3 and 7 species, whereas the marine biofacies (numbers 9 and 10) contained between 15 and 18 species. The overall distribution of the species in the biofacies is shown on Text-fig. 12. Some of these species have their distribution shown in the maps of Text-fig. 13. Scanning microphotos are also provided in Plates 1 and 2, for the main ostracod species found.

OSTRACODA DISTRIBUTION—DISCUSSION

Based on the data obtained, it was found that the lagoonal system was best represented by the following species:

a. *Perissocytheridea* sp. 1 is the most cosmopolitan species present in the area studied. It is an euryhaline species, the most favorable habitat of which is the centre of the bay (Biofacies 6) where the waters are calm and always euhaline. It is almost absent from Biofacies 10 where the conditions are strongly marine. It is thus a typically lagoonal species in the area researched.

b. *Cyprideis riograndensis* in its lagoonal distribution is somewhat controlled by bathymetry. It occurs very often in the periphery of the lagoon, particularly in sandy facies, between 0 and 6 m. It is notably present between 2 and 6 m, but of insignificant occurrence in the centre of the lagoon and in part of the marine Biofacies 9. Its behaviour is, thus, that of an euryhaline species that prefers the shallow periphery of the lagoon.

c. *Minicythere* cf. *M. heinii* occurs at present in the unstable lagoonal segment (Biofacies 1, 2 and 3), where the influx of fresh water provided from the land is significant. There, salinity varies daily from mixohaline to euhaline, according to the tidal fluctuation. *Cytherura* sp. occurs only at the mouth of the Guandu River (Biofacies 1).

d. *Callistocythere* sp. 1 occurs only along the sandy barrier island. It has, therefore, an euryhaline character, preferring very shallow waters (0–2 m), and depends on the sandy substrate. *Callistocythere* sp. 2 occurs in a transitional area composed of the eastern part of the central lagoon and part of a segment of its unstable periphery.

e. *Tanella* sp. occurs almost throughout the lagoonal area but is very scarce in Biofacies 1 and 2 which are the areas of highest stress in the bay. It is these biofacies that show the highest physi-

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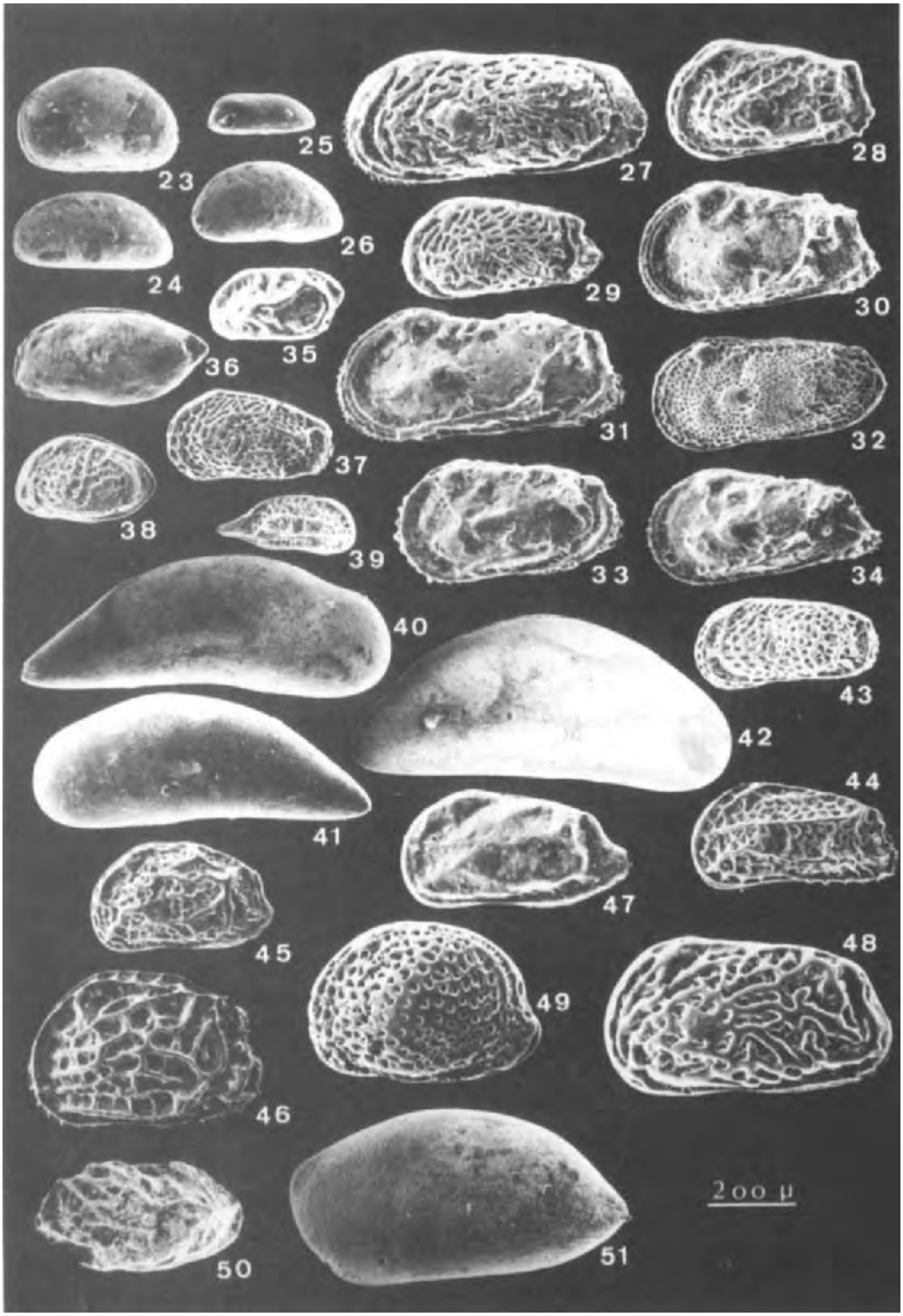
PLATE 2—23. *Xestoleberis* sp. 1, station BS 164, Biofacies 9. 24. *Xestoleberis* sp. 2, station BS 155, Biofacies 5. 25. *Xestoleberis* sp. 4, station BS 176, Biofacies 9. 26. *Xestoleberis* sp. 3, station BS 39, Biofacies 4. 27. *Coquimba* cf. *C. labyrinthica*, station BS 147, Biofacies 9. 28. *Coquimba* sp. 1, station BS 158, Biofacies 10; 29. *Coquimba* sp. 2, station BS 159, Biofacies 10. 30. *Coquimba* sp. 3, station BS 148, Biofacies 9. 31. *Coquimba* sp. 4, station BS 148, Biofacies 9. 32. *Coquimba* sp. 5, station BS 3, Biofacies 3. 33. *Coquimba* sp. 6, station BS 164, Biofacies 9. 34. *Coquimba* sp. 7, station BS 164, Biofacies 9. 35. *Kangarina* sp. 1, station BS 105, Biofacies 7. 36. *Pellucistoma* sp., station BS 156, Biofacies 9. 37. *Morkhovenia* sp. 1, station BS 164, Biofacies 9. 38. *Hemicytherura* sp., station BS 164, Biofacies 9. 39. *Paijenborchella* sp. 1, station BS 156, Biofacies 9; 40. *Paracypris* sp. 1, station BS 165, Biofacies 9. 41. *Paracypris* sp., station BS 165, Biofacies 9. 42. *Macrocypris* sp., station BS 171, Biofacies 9. 43. *Keijia* sp., station BS 148, Biofacies 9. 44. *Orionina bradyi* Van den Bold, station BS 164, Biofacies 9. 45. *Mutilus* sp. 1, station BS 159, Biofacies 10. 46. *Mutilus* sp. 2, station BS 148, Biofacies 9. 47. *Caudites* sp. 1, station BS 155, Biofacies 5. 48. *Urocythereis* sp., station BS 160, Biofacies 10. 49. *Aurila* sp., station BS 160, Biofacies 10. 50. *Paracythereidea* cf. *P. tschoppi* Van den Bold, station BS 161, Biofacies 10. 51. Bairdidae sp. 2, station BS 176, Biofacies 9.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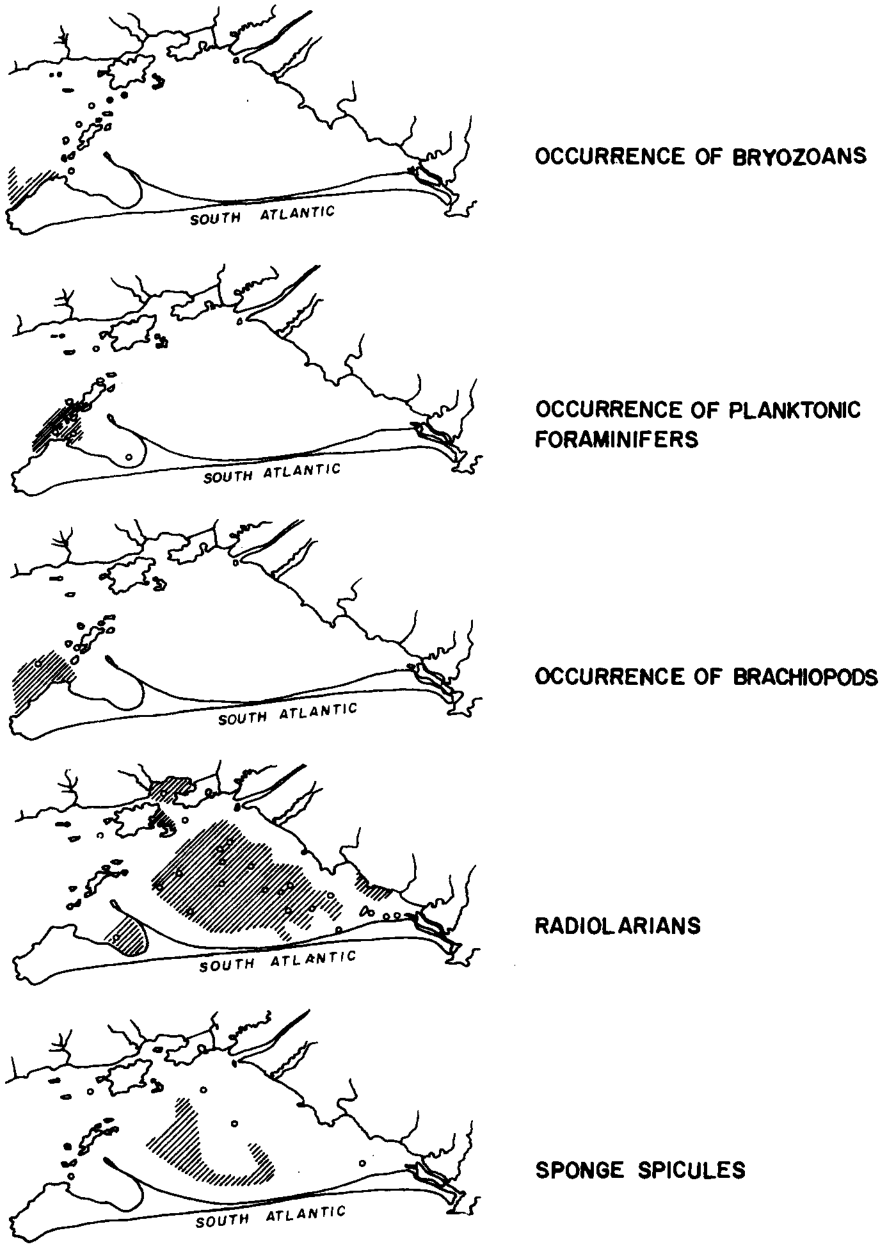
co-chemical fluctuations in the Sepetiba Bay ecosystem. This species is also absent from the westen area of Biofacies 6 that is under the influence of the marine water mass.

f. *Pistocythereis* spp. prefers the stable areas of the lagoon, where great variations of salinity do not exist. It has, therefore, a stenohaline character. It is not present in Biofacies 10, *i.e.* the more open marine biofacies. The ostracods found in Biofacies 9 and 10 are practically restricted to this part of the studied area.



TEXT-FIG. 14—Occurrences of bryozoans, planktonic foraminifers, brachiopods, radiolarians and sponge spicules in Sepetiba Bay.

ENVIRONMENT, FORMAINIFERA AND OSTRACODA: RELATIONSHIPS BETWEEN THE ECOLOGICAL MODELS—DISCUSSION AND CONCLUSIONS

Comparing the ecological models for Foraminifera and Ostracoda obtained for Sepetiba Bay, it is clear that there is very good agreement between them. The indications supplied by the model of Bronnimann, Moura and Dias-Brito (1981b) were confirmed by the model now recognized for the Ostracoda. Nevertheless, large differences concerning frequency may be observed when the maps of Figs. 8 and 9 are compared. The qualitative data on the Ostracoda was better than the quantitative data (no minimum number of specimens per sample was established, whereas this was done when studying the foraminifera when a minimum number of 300 was examined). This does not seem to have vitiated the research, since the results were very consistent.

The maps of the environmental divisions and biofacies established based on foraminifers are closely comparable with those of the ostracod biofacies. The "marine environment" division and Biofacies VII and VI are equivalent to Biofacies 10 and 9 of the Ostracoda. The normal marine lagoon and Biofacies III and V are equivalent to ostracod Biofacies 6. Mixo-euhaline lagoons A and B and Biofacies I and II based on Foraminifera correspond roughly to ostracod Biofacies 1, 2 and 3. The foraminiferal Biofacies IV corresponds to ostracod Biofacies 7. There is, thus, a remarkable correspondence of both biofacies models. From the investigation of the ostracod and foraminiferal ecological models, it can be concluded that the area studied has basically three different realms:

a. A marine area which in its south part has a more open marine character where bryozoans, brachiopods and planktonic foraminifers occur (Text-fig. 14). The general environment is physico-chemically stable, having euhaline and alkaline waters, availability of nutrients, good oxygenation and illumination. There are here the optimum conditions for benthonic life with the ostracods and foraminifers occurring with high specific diversity.

b. A central lagoonal area where more restrictive conditions prevail for a high biological development. The waters are euhaline and alkaline, the sediments are relatively poor in nutrients and the circulation is somewhat deficient. The relatively calm water in this area allows the deposition of sponge spicules and radiolarians that penetrate the bay (Text-fig. 14). The benthic fauna of foraminifers and ostracods is not rich and the specific diversity is a little low.

c. A peripheral lagoonal area, of which its north to east segment characterizes the most unstable part of the whole ecosystem. There occur strong variations in salinity and pH, high availability of nutrients, relatively poor inter-sedimentary grain oxygenation and reasonable illumination. The foraminifers in this area reach the highest frequency values and the lowest diversity values; the ostracods, in general, are not well developed in this area of high stress. The south segment, along the sandy barrier island, has sediments poor in nutrients, particularly in the western part. The foraminifers are scarce, but the ostracods reach their highest frequency values in relation to other parts of the lagoon.

ACKNOWLEDGEMENTS

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We also would like to thank the Management of PETROBRÁS for their permission to publish this work.

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In Search of *Cypris* and *Cythere*— A Report of the Evolutionary Ecological Project on Limnic Ostracoda from the Mondsee (Austria)*

DAN L. DANIELOPOL,[1] WALTER GEIGER,[1] MARTINE TÖLDERER-FARMER,[2]
CARMEN P. ORELLANA[1] AND MARIE-NOËLLE TERRAT[3]
Limnologisches Institut der Österreichischen Akademie der Wissenschaften, Abt. Mondsee, Austria,[1] *Université Bordeaux, Talence,*[2] *and Université Metz, France*[3]

ABSTRACT

After a brief review of the limnological situation of the Mondsee and an overview of the distribution of the ostracod fauna of this lake, we discuss several ecological and biogeographical aspects of *Cytherissa lacustris*. We present data on three topics we have studied since 1982.

1. The macro-and micro-scale distribution of *Cytherissa lacustris* in the Mondsee;
2. The morphology of the carapace of this species and its relationship to the lacustrine environment of the Mondsee;
3. The origin and the phylogenetical affinities of *C. lacustris*. This latter aspect is of potential importance to the achievement of a better understanding of some of the ecological characteristics of *C. lacustris* (such as its rather wide temperature tolerance) and its bio-and palaeobiogeographical distribution.

INTRODUCTION

Ostracods are good tools for studies dealing with evolutionary ecology. This branch of ecology is a modern field of research which studies, *inter-alia*, how organisms developed biological specialization in order to cooperate with an environment which remains far from equilibrium. Evolutionary ecology also explains the ecological characteristics (and sometimes the geographical distribution) of organisms in terms of historical causes (Lack, 1972). In the case of the Ostracoda from the Mondsee, we are interested in a better understanding of the mechanisms which lead to selective decline down to local extinction of some of the ostracod taxa, *e.g. Cytherissa lacustris, Leucocythere mirabilis* etc. The importance of selective extinction as an ecological factor has been recently emphasised by Fowler and MacMahon (1982). Studying problems of selective extinction implies an understanding of how some of the morphological and biological characteristics of a species are not always necessarily beneficial in maintaining the organism in an environment which changes rapidly and in a catastrophic manner. We believe that the study of the ecology of some of the Mondsee ostracod species can help to advance our knowledge in this domain.

THE MONDSEE, LIMNOLOGICAL DATA

The Mondsee is located in the Salzkammergut (Upper Austria), on the northern side of the

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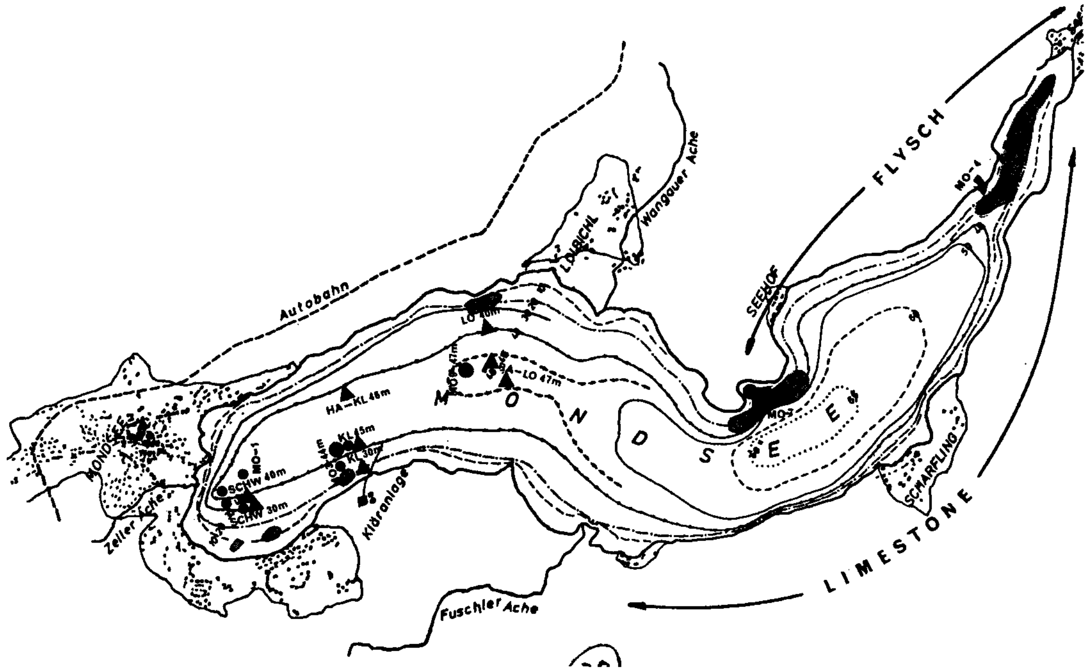
* This contribution is dedicated to Professor Dr. Heinz Löffler on the occasion of his 60th birthday.



TEXT–FIG. 1—Lake Mondsee with sampling sites for subfossil ostracods. Short cores where 20 cm³ (circles) and 120 cm³ (triangles) have been analysed for each sediment depth; stippled areas show where *Cytherissa lacustris* still lives.

TABLE 1—MORPHOMETRIC AND HYDROLOGICAL PARAMETERS OF THE MONDSEE.

Altitude	431 m a.s.l.
Surface area	14.21 km²
Depth max.	68.3 m
mean	36.0 m
Volume	510,000,000 m³
Theor. retention time	1.7 years
Mean discharge	9.2 m³/sec.
Drainage basin	247 km²

Alps. It is surrounded to the south and west by limestone mountains and by morainic sediments; the south-eastern side is situated in a flysch area (Text-fig. 1). The present lake originated about 17,000 years ago, after the melting of the Traun glacier which occupied the landscape during the Würm period. Table 1 shows the most important morphometric and hydrological parameters of the lake.

The lake was for a long time an oligo-mestorophic one (Liepolt, 1935), well oxygenated and sustaining, even in the deeper areas, a rich and diversified fauna. In the last 20–30 years, tourist activity around the Mondsee has increased alarmingly with the inevitable consequence that the water quality of the lake has deteriorated, especially in the north-western part of the lake in the so-called Mondsee bay. Until 1968 the oxygen penetrated, even during the time of summer stagnation down to 60 m depth (Jagsch and Megay, 1982). After 1970, practically every year, there is in the deeper parts of the lake a period of strong oxygen depletion (Müller, 1982). A slight eutrophication of the Mondsee has been recorded for the first time by Findenegg (1969). Since 1968 large algal blooms, mainly of *Oscillatoria rubescens* and of various diatoms, have been recorded (Jagsch and Megay, 1982).

These facts have been documented recently by our interdisciplinary working group on the Mondsee sediments, *i.e.* an increase in: the diatom abundances (Schmidt *et al.*, 1985), the carotenoid paleopigments (Schultze, 1985), the total phosphorus and organic carbon (Helbig *et al.*, 1985), the abundances of some of the benthic macrofauna like Oligochaeta (Herzig, 1985), a decrease in the species diversity of Oligochaeta (Newrkla, 1985b), the disappearance of some of the ecologically sensitive ostracod species (Löffler, 1972; Danielopol *et al.*, 1985). Irlweck and Danielopol (1985) showed that the mean annual sediment accumulation rate is higher in the deeper zone of the northwestern part of the lake (5–6 mm/yr) as compared with that of the shallower areas of the Mondsee bay or even with the deeper zone of the southern part of the lake (2–3 mm/yr).

THE LIVING OSTRACODA

Kaufmann (1896, 1897) mentioned for the first time the presence in the Mondsee of *Cytherissa lacustris*, *Leucocythere mirabilis* and *Limnocythere sanctipatricii*, and Liepolt (1935) and Graf (1938) also quoted, besides these species, *Candona neglecta*. During our three year investigation we analysed more than 500 samples* which covered the entire lake.

TABLE 2—OSTRACODA OF THE MONDSEE.

Super-fam. Cypridacea
Fam. Cyprididae
- *Candona candida* (O.F. Müller)†[2]
- *Candona neglecta* Sars†[2]
- *Fabaeformiscandona caudata* (Kaufmann)†[2]
- *Fabaeformiscandona protzi* (Hartwig)†[2]
- *Pseudocandona* sp. (cf. *marchica* ?)
- *Cypria lacustris* Sars†[2]
- *Cyclocypris ovum* (Jurine)
- *Herpetocypris reptans* (Baird)
- *Isocypris beauchampi* Paris
- *Prionocypris zenkeri* (Chyser)†[1]
- *Cypridopsis vidua* (O.F. Müller)
- *Potamocypris similis* Müller
- *Potamocypris villosa* (Jurine)
- *Ilyocypris* sp.

Super-fam. Cytheracea
Fam. Limnocytheridae
- *Limnocythere sancti-patricii* Br. and Rob.†[2]
- *Limnocythere inopinata* (Baird)
- *Leucocythere mirabilis* Kaufmann†[2]
- *Metacypris cordata* Br. and Rob.†[1]
- *Cytherissa lacustris* (Sars)†[2]

Super-fam. Darwinulacea
Fam. Darwinulidae
- *Darwinula stevensoni* Br. and Rob.

†[1] only carapaces have been found; †[2] ostracod species which occur in the deeper zone of the lake.

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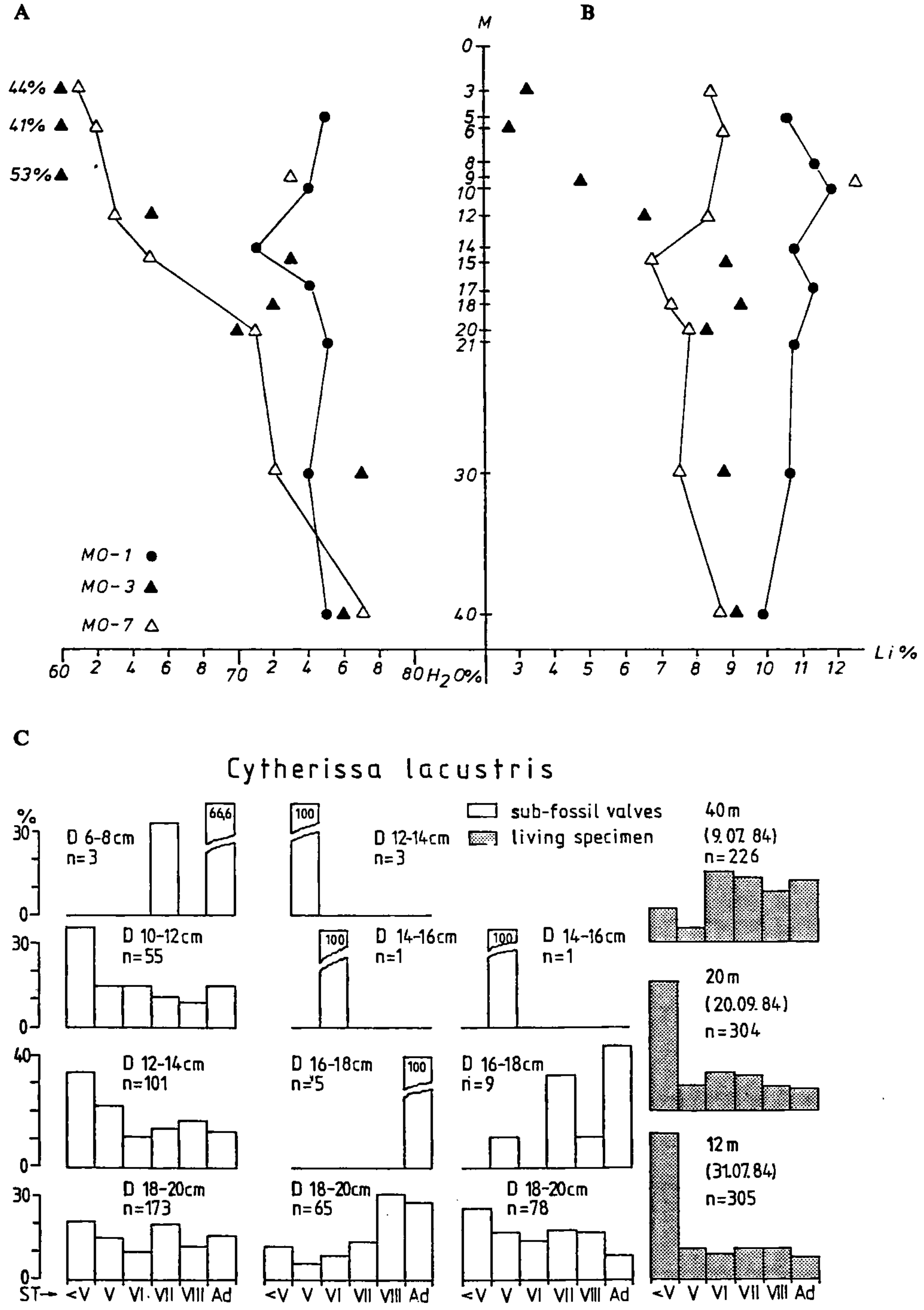
* We sampled with a modified Kajak-corer with an inner diameter of 5 cm devised by R. Niederreiter (Mondsee); for qualitative sampling we took 1–3 samples and for quantitative we took 6–8 replicate samples at each site.



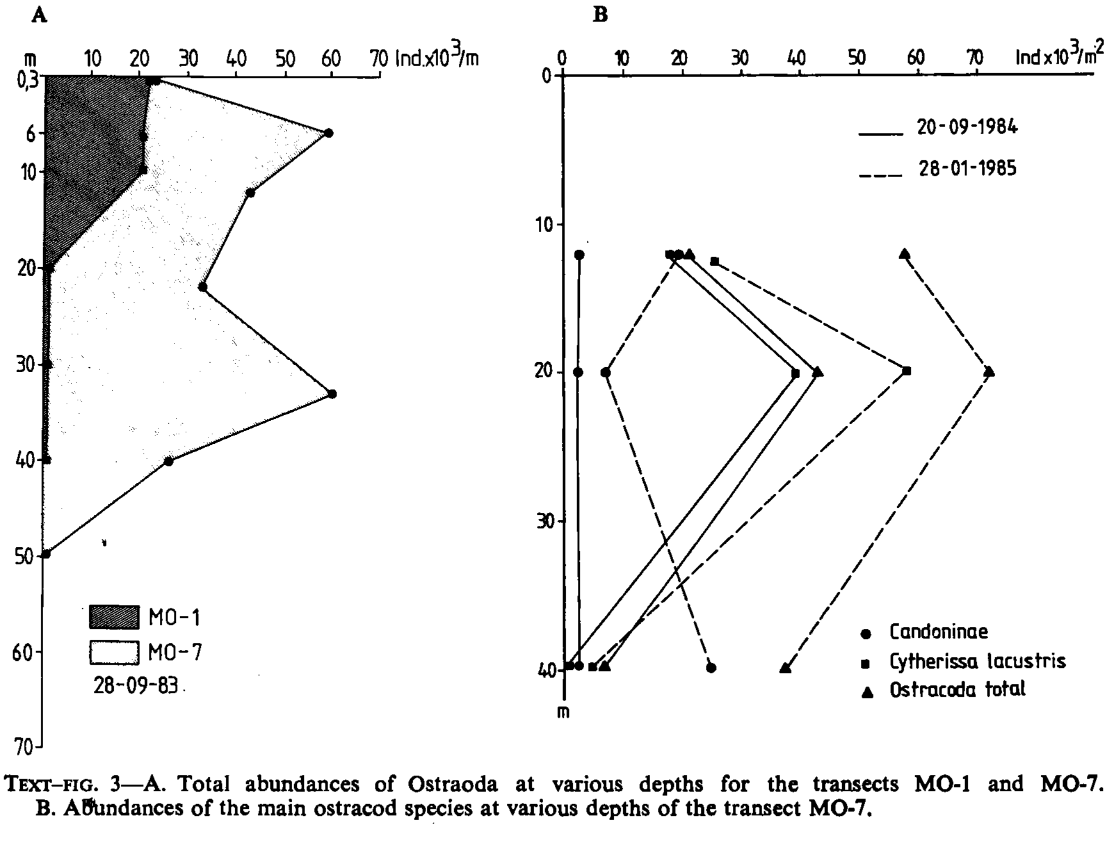
TEXT-FIG. 2—A. Water content in the upper 2 cm of sediment from various sites and depths in the Mondsee. B. Weight loss on ignition values from the samples used in A. C. Evolution of the age structure of the palaeopopulations of *Cytherissa lacustris* from sites MO-3 and MO-9 as compared with those of living *Cytherissa* from site MO-7 (V-VIII-instars).

The ostracod fauna of the Mondsee (Table 2) is very similar to that of other pre-alpine lakes (see data in Absolon, 1973; Löffler, 1972, 1975, 1978).

A first survey during the summer of 1982 allowed us (C.O.P., D.L.D. and M.-N.T.) to compare the ostracod fauna from sites differing in sediment quality. The Mondsee bay has sediments with a higher organic content (as expressed by the weight loss on ignition 550° C/2 h), and also a higher percentage in water (we investigated the upper two centimetres of sediment) than the central or southern parts of the lake. We compared the transect MO-1 from the Mondsee bay with two other sites located off the bay, *i.e.* MO-3 and MO-7 (Text-figs. 1 and 2A, B). Our data show that the total ostracod abundance and also species diversity are higher at site MO-7 when compared with those of MO-1 (Text-fig. 3A). The figures for MO-3 are intermediate between the other two.

Several ostracod species which occur abundantly as subfossils in the deeper sediments of the lake (*i.e. Cytherissa lacustris, Limnocythere santi-patricii, Leucocythere mirabilis* and *Fabaeformiscandona caudata*) are rare in the lake and always in areas where the organic content is low; oxygen situation during the summer stagnation does not become critical and the yearly sediment accumulation rate is reduced (Danielopol *et al.*, 1985). The deeper zone of the lake, which constitutes the largest area (Text-fig. 1), is sparsely inhabited by ostracods (with the exception of site MO-7/40 m). It seems that no permanent ostracod population lives at depths greater than 40 m.

The most common ostracod species in the whole lake are *Candona neglecta, Fabaeformiscandona protzi* and *Cypria lacustris. Cytherissa lacustris* at site MO-7 at intermediate depths (10–20 m) occurs very abundantly when compared with other sites an ddepths (Text-fig. 3B). *Limnocythere*



Text-fig. 3—A. Total abundances of Ostraoda at various depths for the transects MO-1 and MO-7. B. Abundances of the main ostracod species at various depths of the transect MO-7.

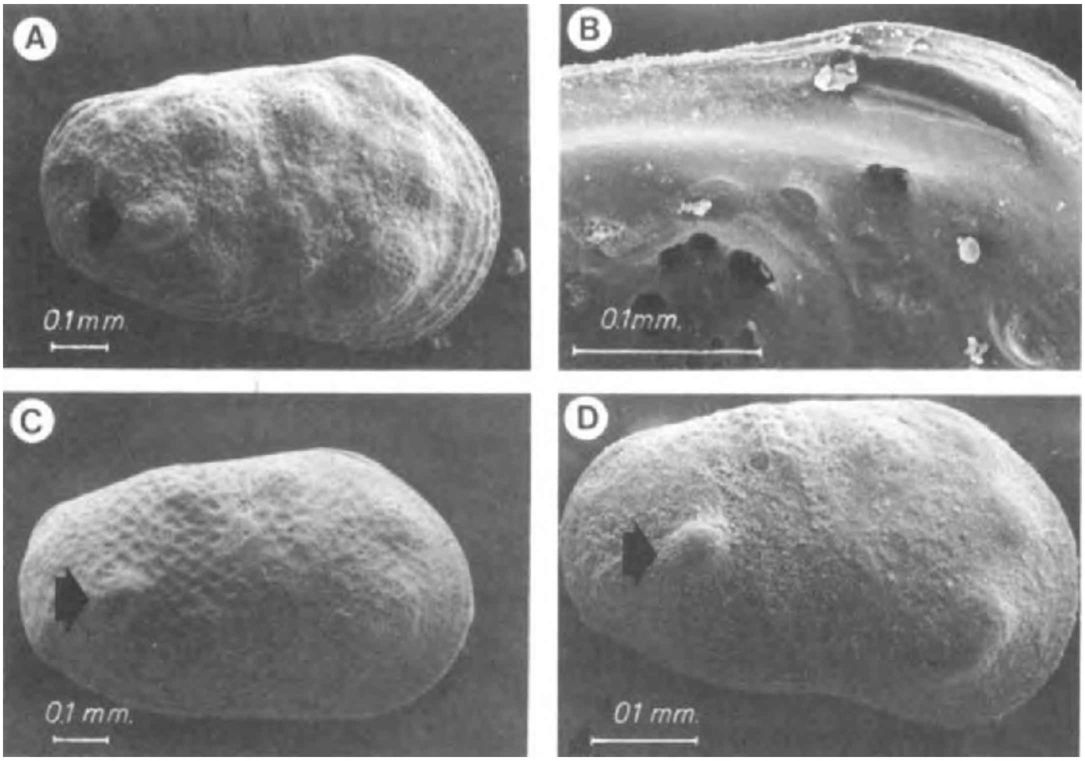
sanctipatricii and *Leucocythere mirabilis* occur mainly in the southern part of the lake. *Fabaeformiscandona cuadata* reproduces parthenogenetically in most European and North American lakes. In the Mondsee this species is amphigonic and, as a consequence, we are able to describe in detail the morphology of the male.

The first general survey allowed us to select those species worthy of more detailed study.

Cytherissa lacustris, THE *Drosophila* OF PALAEOLIMNOLOGY

It is to the credit of Prof. H. Löffler that he demonstrated the importance of *Cytherissa lacustris* as a potential palaeoecological indicator which can be used in the reconstruction of the oligotrophic phase in pre-alpine lakes (Löffler, 1972, 1975, 1978, 1983). It has become a tradition at the Limnological Institute of the Austrian Academy of Sciences to study the causes which result in the disappearance of *Cytherissa lacustris* in pre-alpine lakes. Before us Jäger (1974), Powell (1976) and Newrkla (1985a) have investigated aspects of this problem. We still do not know why this species started to decline in abundance before the massive deterioration of the lake environment, e.g. the occurrence of strong anoxic conditions, development of highly organogenic sediments (Löffler 1972, 1975; Danielopol *et al.*, 1985). We also admit that, despite being able to make some interesting observations on this species, we still know little of its autecology.

In this paper we present our preliminary observations on the macro- and micro-scale distribu-



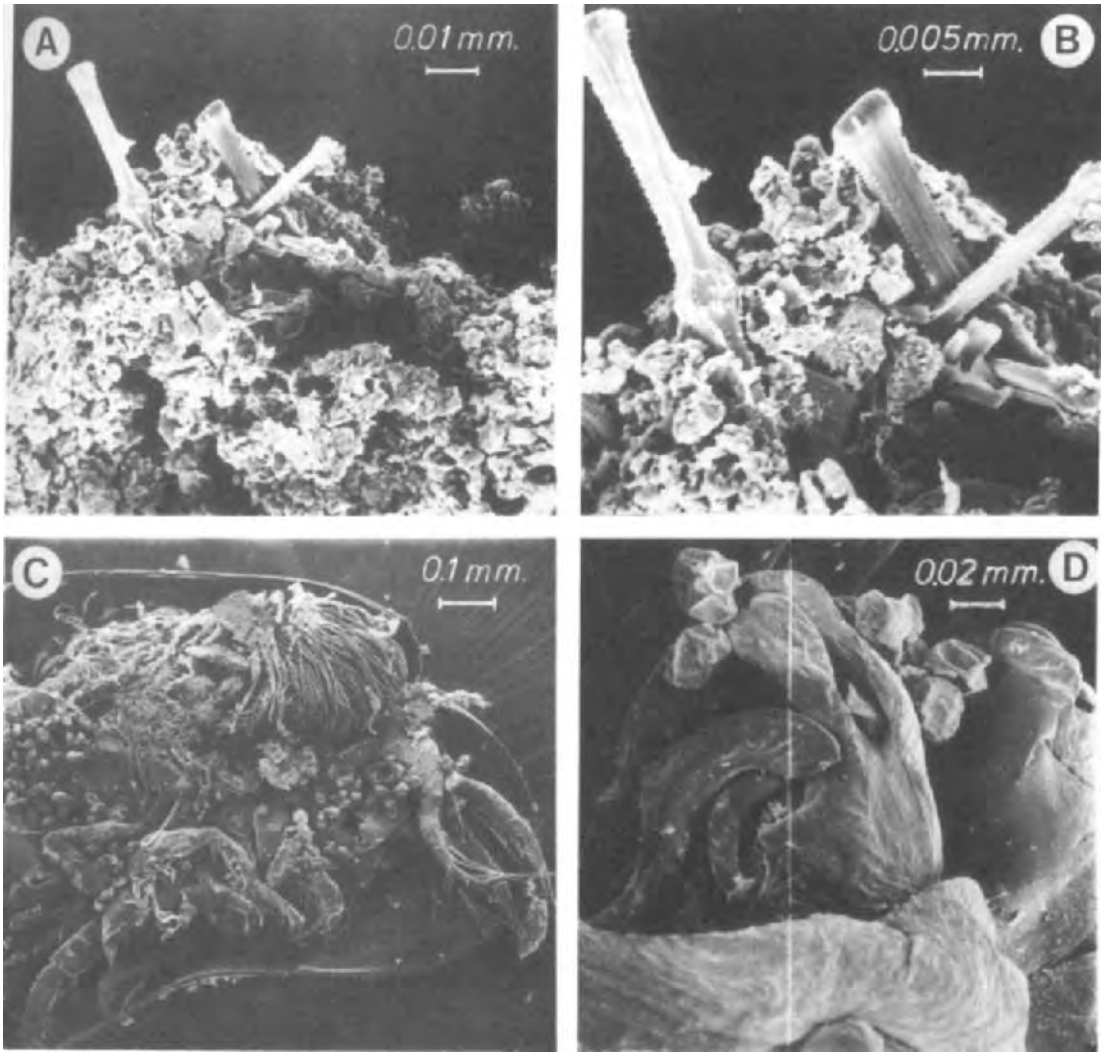
TEXT-FIG. 4—A-D. *Cytherissa lacustris*. A. 7th juvenile instar; B-D. adults, female; B. inner valve anterior hinge groove; C, D. right valve, external side (arrow: the posterior node).

tion of *Cytherissa lacustris* under field and laboratory-conditions. We expect to obtain from these data a better idea of the local extinction of this species in the Mondsee.

The Macro- and Micro-scale Distribution of *Cytherissa lacustris*

We first investigated the distribution of this species in the Mondsee on a macro-scale (metre scale). We found that *C. lacustris* lives in sublittoral and deeper habitats from 3 m to 40 m depth (Text-figs. 1 and 3B).

Large populations have been found in those areas where the sediment accumulation rate is low (2-3 mm/yr) and the sediment is represented by fine sand (more than 20%) and silt-clay (60–80%). The sediments in the deeper zone of the northern and central part of the lake at depths greater than 30–40 m are very fine grained (silt-clay fraction more than 90%).



TEXT-FIG. 5—A, B. organogenic sediment from site MO-1/40 m; C, D. *Candona neglecta*, female, covered with peritrichous Protozoa.

Text-figures 5A and B show that these sediments are highly organogenic. Abundant bacterial populations develop on the sediment type (Dokulil, pers. comm.).

We investigated the extent of the area from which *C. lacustris* disappeared in the last 30 to 50 years, examining short cores from sites MO-1/30 m and 40 m, MO-3/43/44/45 m, MO-7/50–65 m, MO-9/47 m*[1], MO-1 (SCHW/30–40 m), MO-3 (KL/30–46 m), MO-9 (BA-LO/40–47m)*[2] (Text-fig. 1). In these samples we investigated the age structure of the palaeo-population*[3].

Text-figure 2C shows that in the deeper layer *C. lacustris* is represented by all the post-embryonic stages starting with the 4th instar, which one can find in the living population from site MO-7 (Text-fig. 1). In the upper layers, an abrupt reduction in the number of valves occurs which suggests that the population structure is disturbed down to its disappearance in the next layers. We conclude from these data that *Cytherissa lacustris* disappeared from the deeper part of the lake (deeper than 40 m) at least in the Mondsee bay, or in other words became locally extinct.

We approached the study of the spatial distribution of *Cytherissa lacustris* also at a micro-scale level (mm and cm scale), as it is at this level that the ostracods most probably interact directly with their environment. Traditionally it was believed that *Cytherissa lacustris* lives on the sediment and penetrates into the superficial layers for only short periods of time. Powell (1976) showed that this ostracod species normally lives in fine sediments, preferring those with a granulometry between 10 and 100 μm.

Löffler (1975, 1978) suggested that in the eutrophic lakes the deeper zone will become too fluffy and the sedimentation rate will be too high to allow *Cytherissa* to live on the sediment; therefore, it will slowly disappear from these types of habitats.

Our first interest therefore, was to check the validity of these hypotheses. We found that *Cytherissa lacustris* at site MO-7/20 m and 40 m depth lives mainly in the sediment down to 1–2 cm depth (*e.g.* Text-fig. 6D). Powell (1976) showed that the sandy sediments above 200 μm are inimical to the "burrowing" ability of *Cytherissa.*

Our experiments showed that *Cytherissa,* which digs into the substrate, needs light grains in order to penetrate inside the sediments. It is not the grain size which is decisive, but the quality of the substrate and its texture. Cullen (1973) mentioned that ostracods can effectively bioturbate marine sediments. We checked the validity of this process by culturing *Cytherissa* on different substrate types. Especially in fine glacial silty-clay sediments, one can see how *Cytherissa lacustris* digs small tubes which remain open for several days. So a high density of *Cytherissa* can effectively bioturbate the sediment. The first centimetre, especially, will be inhabited by about 90% of the ostracod population (Text-fig. 6, MO-7/40 m, MO-1/40 m). The depth of penetration depends on the compactness of the sediments. One should notice that in our experiments the sediments of site MO-7/40 m were more mineralogenic and less compact which allowed the ostracods to penetrate down to 18 mm depth (Text-figs. 6 A–C).*[4] The older instars (8th stage and the adult) penetrate deeper than younger ones. Compared with site MO-7, the sediments of site MO-1/40 m (which we used in our experiments) are very rich in diatom remains and agglutinate readily (Text-fig. 5A, B). As Seki (1982) showed, this situation occurs commonly in eutrophic environments where microorganisms develop abundantly and exudate. The densest populations of *Cytherissa lacustris* at site MO-7/12–20 m have a small number of specimens covered with sticky sediment (Text-figs. 4A, C, D). The opposite is the rule in the case of *Cytherissa lacustris* from MO-7/40 m depth. Here three

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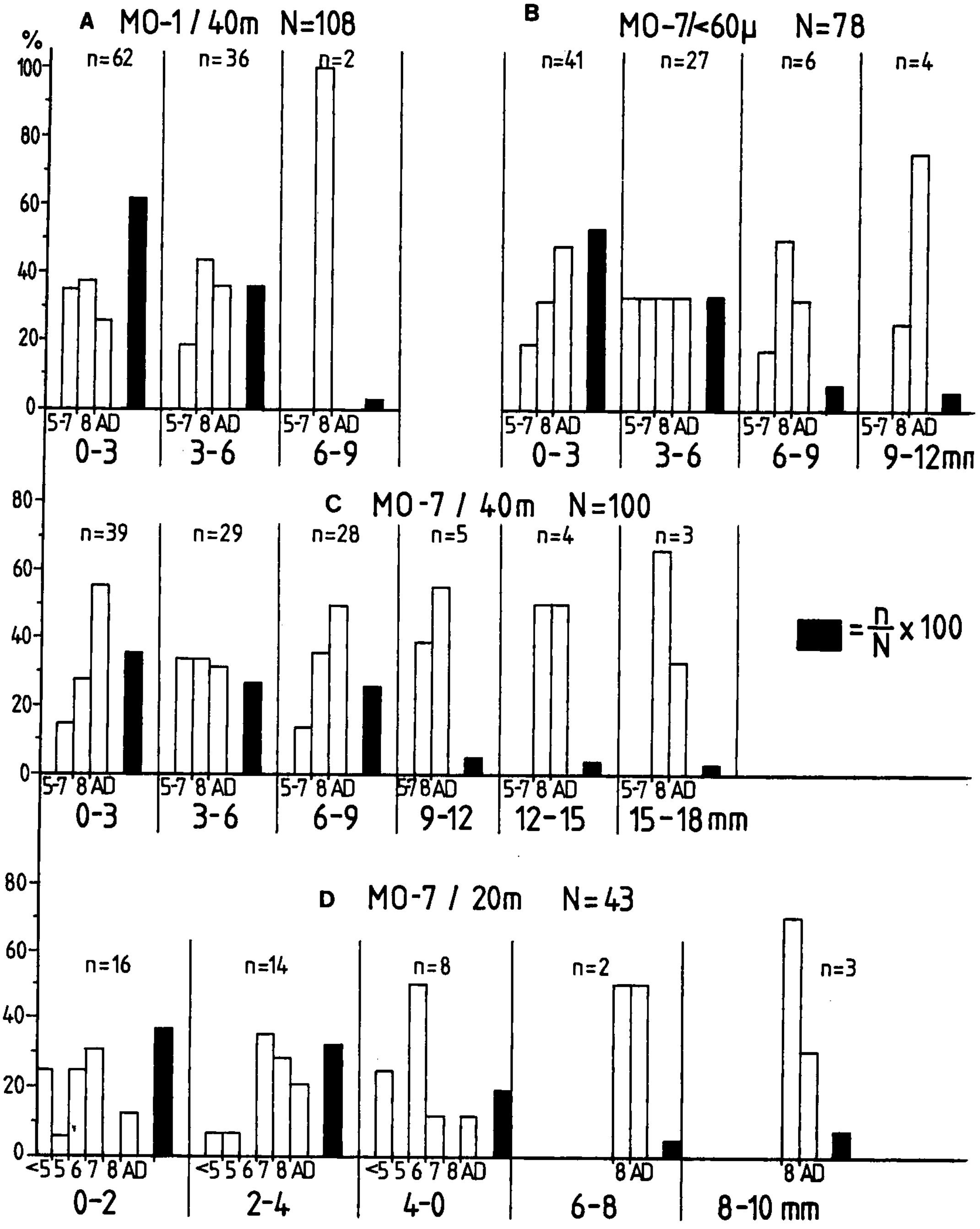
*[1] 10–20 cm^3 sediment have been examined for 1–2 cm depth.

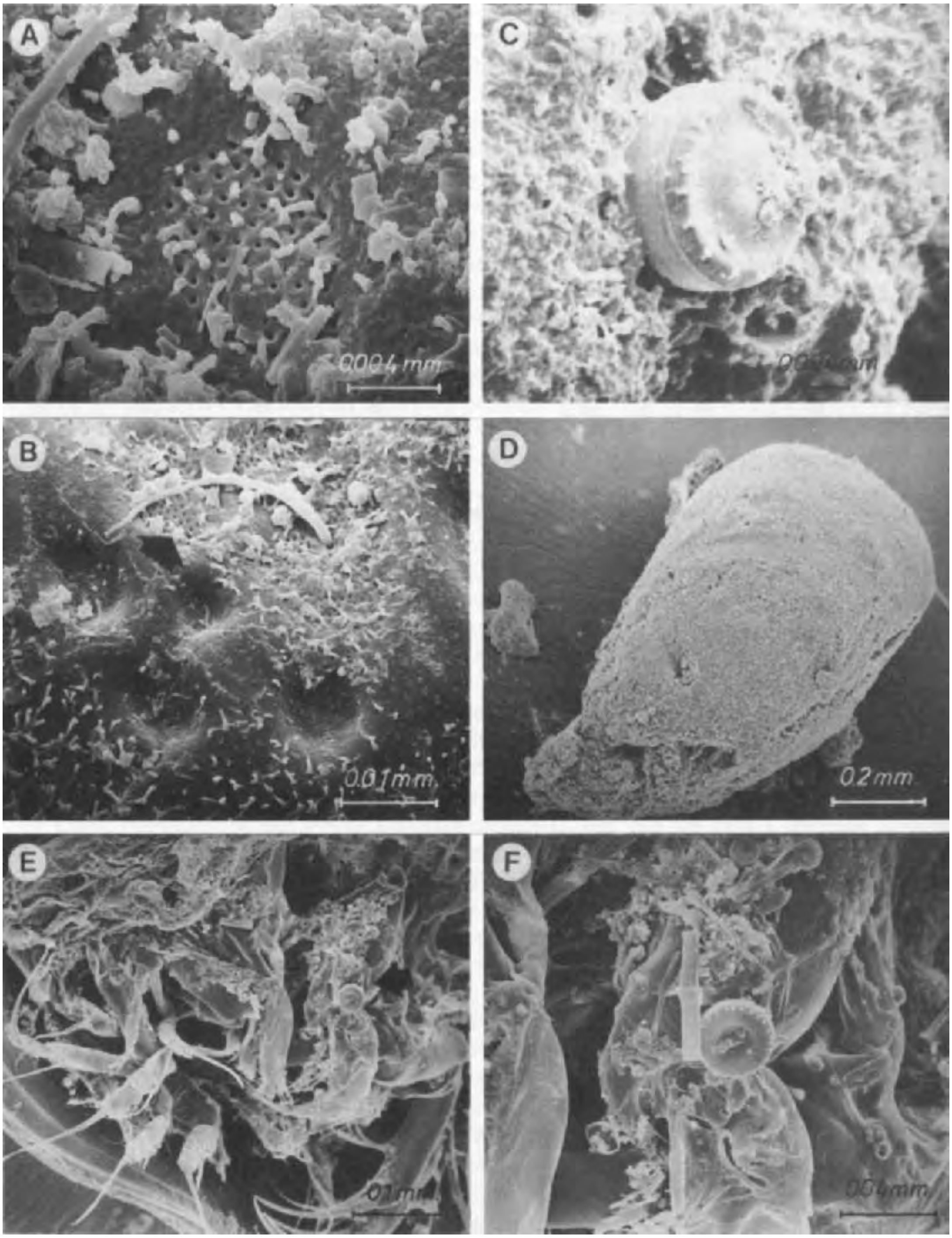
*[2] 120 cm^3 sediment for every 2 cm depth.

*[3] We sieved the sample with a 100 μm sieve and we normally recovered the valves from the 4th stage up to the adult.

*[4] For the study of the microvertical distribution we used the method of Joint *et al.*, (1982), *i.e.* a syringe of 0.5 cm diameter; we sliced the sediment every 3 mm.



TEXT–FIG. 6—Vertical distribution of Cytherissa lacustris in various sediment types (see explanation in text).


A
0.004 mm
C
B
0.01mm
D
0.2mm
E
0.1mm
F
0.04mm

times more specimens than in the former case are covered by fine mineralogenic and organogenic particles (Pl. 1A–D).

We cultured *Cytherissa lacustris* on organogenic sediments from site MO-1/40 m and on natural sediment from MO-7/12–20 m mixed with Cerophil (a laboratory food for microorganisms like Protozoa). Plate 2A–D, shows that after several weeks, ostracods which have been on this latter substrate are covered with fine sediments and/or with a dense bacterial film. Obviously these specimens will die, because they will be stuck to the sediment. In another experiment we placed specimens on fine sulphidic and organogenic sediment from site MO-1/40 m and found that after 4–7 days, some of the specimens moved slowly and could not close their carapaces. After 1–4 more days they died with the carapace open. Several dissected specimens had fine particles of sediment stuck between the limbs and on the inner side of the valve, especially diatom remains (Pls. 1E, F and 2E, F).

We made a similar observation with *Candona neglecta, i.e.* after one week some of our specimens were densely covered with peritrichous Protozoa blocking their normal movement (Text-fig. 5C, D).

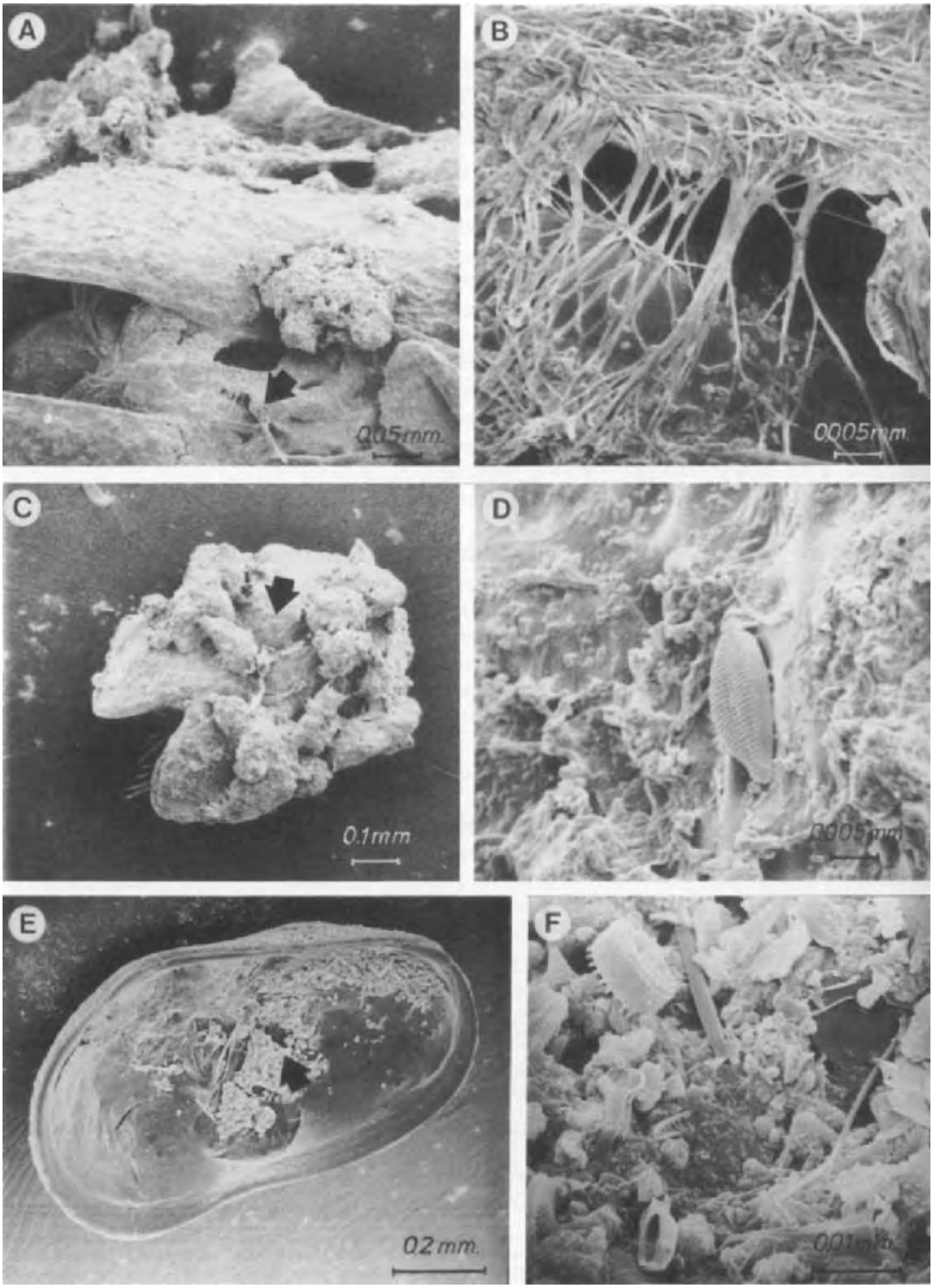
These observations suggest that the negative effect which can exterminate ostracod individuals from a population is the structure and the composition of the fine sediment. However, we believe that this is not the major constraining factor. Possibly the combination of low oxygen content at the sediment-water interface as well as the sediment structure and composition together play the major role in the decline, leading to the local extinction of *Cytherissa lacustris* in the deeper zones of the Mondsee. This is the hypothesis that will be tested next by one of us (W.G.).

The Carapace Morphology and its Relationship to the Lacustrine Environment

The morphology of an organism (both in shape and in structure) is determined in most cases by genetic and environmental factors (Ho, 1984). One of the directions for research in evolutionary ecology is to understand how the environment induces various ecophenotypes. For the palaeoecologist this field of research is extremely interesting as one can use the ecophenotypes of an organism for the recognition of different ecological parameters in past environments. As the morphology of an organism is induced by both genetic and epigenic (development) processes, it is interesting to know if the resultant shape and structure have an adaptive value in the sense that they represent a useful solution for the organism in order to facilitate its better integration into the environment.

We investigated three aspects pertaining to these problems, *i.e.* the structure of the carapace ornamentation, especially the production of nodes (mainly studied by M.T.F.), the variation of the carapace size (investigated by W.G.) and the paedomorphic aspect of carapace shape (observations made by D.L.D.). Triebel (1951) noted that *Cytherissa lacustris* shows strong polymorphism of the carapace. One can find carapaces with nodes and carapaces without nodes. *C. lacustris* can develop up to seven nodes with different degrees of strength, from weakly to strongly developed (Text-fig. 4A, C, D). Juveniles are particularly subject to torosity (Tölderer-Farmer, 1985). One of the most persistent nodes is the one located on the ventro-posterior side. We demonstrate elsewhere (Tölderer-Farmer, 1985; Danielopol *et al.*, 1985) that the percentages of noded *Cytherissa lacustris* are higher at those sites where the lacustrine environment is rich in silica. We noted (Danielopol *et al.*, 1985) that at site MO-4/10–15 m, the percentage of valves with a moderate and/or strong posterior node represent 44% of the sample, whereas in deeper layers of the site (MO-4/25–33 m) we found only 4%. The sediments of the sublittoral and the deeper habitat of transect MO-4 differ conspicuously in their quartz content. The former had twice the amount of quartz than does the latter one, most probably due to the allochthonous impact of sediments

Plate 1—*Cytherissa lacustris*. A–D. Details of the carapace surface. A, B. Sieve pores moderately covered with fine sediment and diatom remains. C, D. Carapace strongly covered with sediment. E, F. Living specimen exposed on organogenic sediment from the site MO-1/40 m.


A
0.05 mm.
B
0.005 mm.
C
0.1 mm
D
0.005 mm
E
0.2 mm.
F
0.01 mm

from the nearby flysch zone (Text-fig. 1). Therefore, we suspect that the production of nodes in the case of *Cytherissa lacustris* is induced by external factors such as high concentrations of silica and possibly also allochthonous organic matter (Tölderer-Farmer, 1985). We are trying now to stimulate in the laboratory these conditions in order to produce noded ecophenotypes. If this hypothesis can be confirmed then one can better interpret the palaeoenvironment of some Pleistocene lakes where *Cytherissa* has been found. For instance, Triebel (1941) in the "*Paludina* deposits" of northern Germany found mainly noded *Cytherissa,* and Devoto (1965) in the lacustrine desposits from the Liri Valley encountered specimens without nodes. These differences could be due to varied chemical environments.

The postembryonic development of the podocopid Ostracoda involves the successive development of limbs starting from the anterior part to the posterior. Consequently, the body volume and the carapace will increase after each moult, especially with respect to the posterior. For instance, in those ostracods where the adults have a more or less rectangular carapace shape (as seen in lateral view) one finds more or less triangular shapes in the juveniles, especially in the younger stages. In the case of many podocopid ostracods a blockage or a slow-down in the normal development of the carapace occurs at some stage in ontogeny. In such cases the carapace shape of the adult will resemble those of the juveniles (a paedomorphic aspect).

This is the case, for instance, with the female of *Leucocythere mirabilis* in comparison with the male, and it is also the case with *Cytherissa lacustris* (Text-fig. 4A). Gould (1977) showed that paedomorphic development could be related to a shortening of the developmental lifetime and, consequently, could represent an advantage for those animals which live in unpredictable environments. In the case of *Cytherissa lacustris* we did not notice a reduction of the number of instars (there are 8 stages as in the case of most of the cytherids and cypridids) and postembryonic development takes probably one year (the investigation of the phenology of this species is done by W.G.). The paedomorphic character of the carapace shape of *Cytherissa,* therefore, does not fit the model proposed by Gould (1977).

Maybe a strong development of the anterior part of the animal as compared with the more pointed posterior, could be an advantage for digging like a "bulldozer" in fine sediments. In another ostracod group, *Mixtacandona* gr. *ljovuschkini,* Danielopol (1980) showed that the carapaces with elongated and pointed posteriors are most probably related to a low fecundity. Seilacher (1984), discussing the constructional morphology of bivalves, noted that in this latter case the best mechanical type to dig in sediments is the tubular (elongated) one. Considering *Cytherissa lacustris* it would be interesting to know, if the paedomorphic shape of the carapace has been developed as an adaptive character in order to dig better in the unconsolidated sediments or if it represents a non-adaptive structure due to a developmental change which originally occurred by chance, but which has now been fixed genetically.

The Origin and Phylogenetical Affinities of *Cytherissa lacustris*

Some of the biological characteristics of *Cytherissa lacustris* could be easier understood, if we could clarify the origin and the phylogenetical affinities of this species. For instance, this species lives nowadays in northern and central Europe as well as in northern America in those areas which experienced, or still have, cold water conditions (Löffler and Danielopol, 1978; Delorme, 1971). It is more or less accepted (*e.g.* Zschokke, 1911) that *Cytherissa lacustris* is a cold stenothermal species which originated in a marine environment during the Quaternary.

PLATE 2—*Cytherissa lacustris* exposed on fine sediment and Cerophil. A–D. Carapace and limbs covered with sediment and microorganisms. A. Ventral side, general view. B. Detail from A (arrow). C. Dorsal side, general view. D. Detail from C (arrow). E, F. Valve, inner side covered with fine organogenic sediment (same specimen as in Plate 1E). F. Detail from E (arrow).

However, *Cytherissa lacustris* as compared to other psychrostenothermal species (*e.g. Limnocythere sancti-particii*) has been found in habitats (*e.g.* in Carinthian lakes) which during the summer reach 16–18° C (Löffler, in Carbonel *et al.*, 1985), and Newrkla (1985a) cultured this species at 20° C and kept them alive at 25° C.

If *Cytherissa lacustris* originated from a marine (Quaternary) cold stenothermal form, it means that it has scarcely changed its ecological requirements in order to live in the inland water bodies in northern and central Europe. In this case the high temperature tolerance found by Newrkla (1985a) is surprising. One should consider also the alternative hypothesis that this species belongs to a pre-Quaternary ostracod group which already lived in inland waters. In this latter case *Cytherissa* changed its thermal requirements from more or less warm waters to cooler ones.

A potential close relative of *Cytherissa lacustris,* considering its general carapace shape and ecological distribution, is *Roundstonia globulifera* (Brady). This Quaternary cold stenothermic species is distributed following Neale (1973), in the marine habitats of the arctic seas as well as in the North Sea and Irish Channel, in Alaska, in northern Canada and the northern Soviet Union. This species displays on the carapace conspicuous nodes which have a similar position to those of *Cytherissa lacustris.* However, considering the differences of the carapace hinge of these two cytherids we believe that they are not directly related. *Roundstonia,* as noted also by Neale (1973), has a gongylodont hinge and *Cytherissa* species a lophodont and/or slightly hemimerodont one (Text-fig. 4B). Our preliminary investigations suggest a pre-Quaternary origin for the *Cytherissa* group. *Cytherissa lacustris* displays a hinge type, general carapace shape and sieve-pores similar to at least one Pliocene species, *Cytherissa bogatschovi* Livental, from the Eastern Paratethys and also like two living *Cytherissa* species from Lake Baikal, *i.e. C. tuberculata* and *Cytherissa* sp. aff. *C. sernovi* Bronstein (1947). *Cytherissa lacustris* has been quoted several times in Pliocene deposits of the Eastern Paratethys (*e.g.* Hanganu and Papaianopol, 1977). It is very likely that most of these identifications refer to species related to *C. bogatschovi* (Olteanu, pers. comm.). A very interesting discovery which should be re-examined is that of Lüttig (1968) who mentions *Cytherissa lacustris* in the Megalopolis basin (Greece) in the Upper Pliocene—Lower Pleistocene. Other Pleistocene records of *C. lacustris* in more southern parts of Europe are those from southern Italy in the Liri Valley (Devoto, 1965) and from the Pannonian basin near Zagreb in Yugoslavia (Sokac, 1978).

If our hypothesis is correct, that *Cytherissa* represents a branch of the family Cyprideidae which diversified in inland waters during a mild climate period before the Quaternary (at least three phylogenetical lineages could be recognized, *i.e.* those of the present day *Cytherissa lacustris,* those of Lake Baikal and those of the Paratethys), then the higher tolerance of such temperatures as mentioned by Löffler in Carbonel (1985) and Newrkla (1985a) become understandable. The presence of *Cytherissa lacustris* (Devoto, 1965) in southern Italy (about 100 km south of Rome) during the Pleistocene in a shallow lake habitat will also be explicable.

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Living Ostracods from the Nature Reserve "Hördter Rheinaue" (Germany)

BURKHARD W. SCHARF
Kettelerstr. 15, D-6500 Mainz 21, F.R. Germany

SUMMARY

The nature reserve "Hördter Rheinaue" is situated in the meander-belt of the Upper Rhine Valley. Forty-one ostracod species have been found there. This is a very large number in relation to the size of the area, about 8 km². The large number of species is explained by the great diversity of biotopes and by the favourable situation in the meander-belt and on a bird migration route. Within a row of loam-pits the number of ostracod species increases with the age of the loam-pit. Data on the phenology (population structure) and the density of ostracod populations are included.

INTRODUCTION

Early man did not colonize meander-belts. This has changed since man acquired more knowledge and more technology. Today many people have lost respect for nature and are ready to commercialize its last reserves.

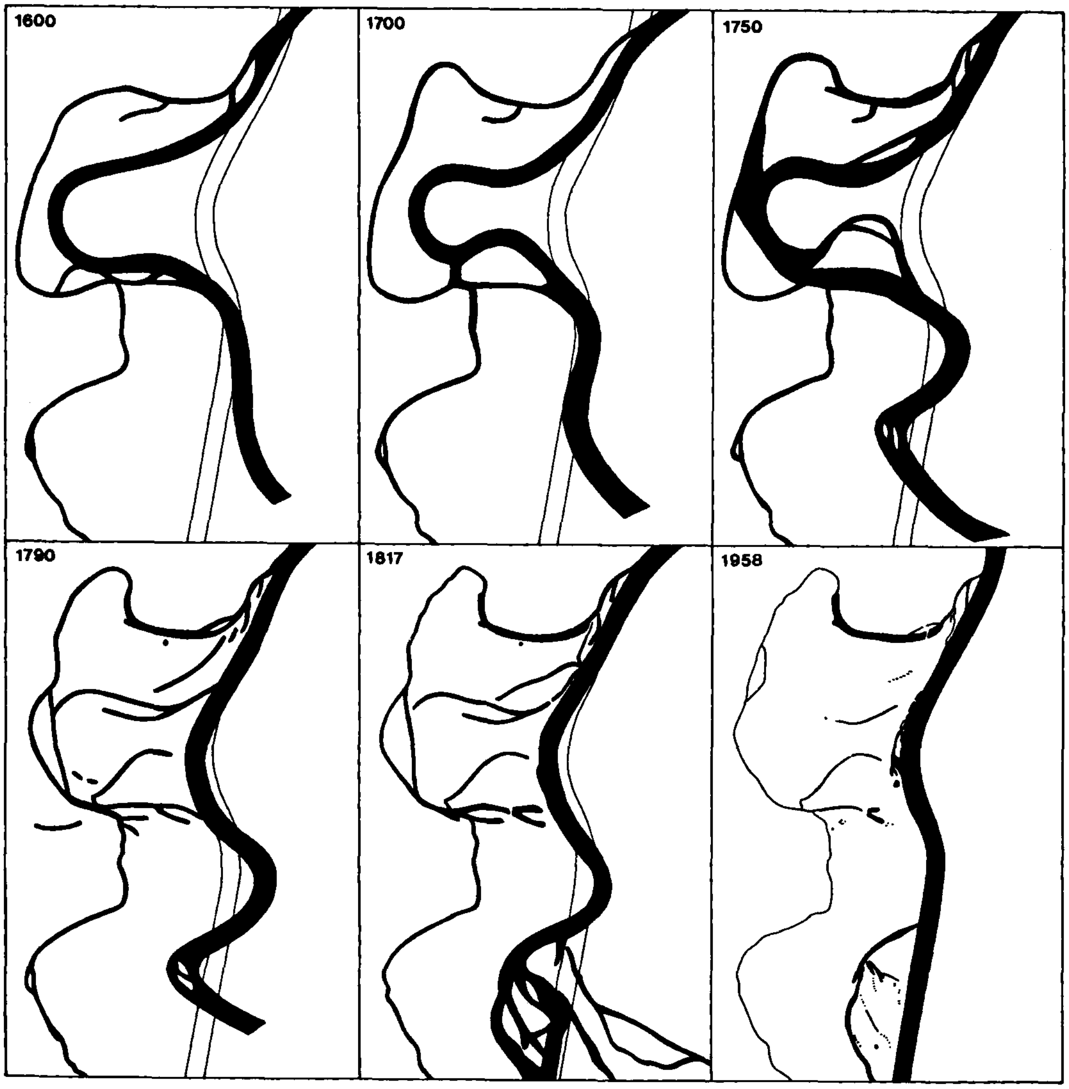
With this background Kinzelbach organized an extensive ecological investigation of the nature reserve "Hördter Rheinaue" situated in the meander-belt of the Upper Rhine Valley. It serves to document the currently available information and to make proposals for the conservation and further development of the area into an ecologically balanced region.

The papers of Kinzelbach and co-workers appeared in volume 64 and 65 of "Mitteilungen der Pollichia" published in 1976 and 1977 respectively. A preliminary report on the living ostracods of the "Hördter Rheinaue" based on an investigation in April 1976 was given by Scharf (1976).

In 1976 and in the first quarter of 1977, ostracods were collected monthly in the "Hördter Rheinaue". Some years later further investigations were carried out to complete the study.

THE AREA

The "Hördter Rheinaue" is one of the few big nature reserves in the Upper Rhine Valley. It is situated 110 km south of Frankfurt and 20 km north of Karlsruhe on the left bank of the Rhine. It has an area of about 8 km², lies in the meander-belt and is bounded by the cliff of the lower terrace. The former meander-belt is now divided by a dike into a wet flood-plain inundated each year and a dry flood-plain. The dike was built in 1800 (Text-fig. 1). Since 1800 the dry meander-belt has only once been flooded, in the year 1882/83 by catastrophic high-water. There are only ox-



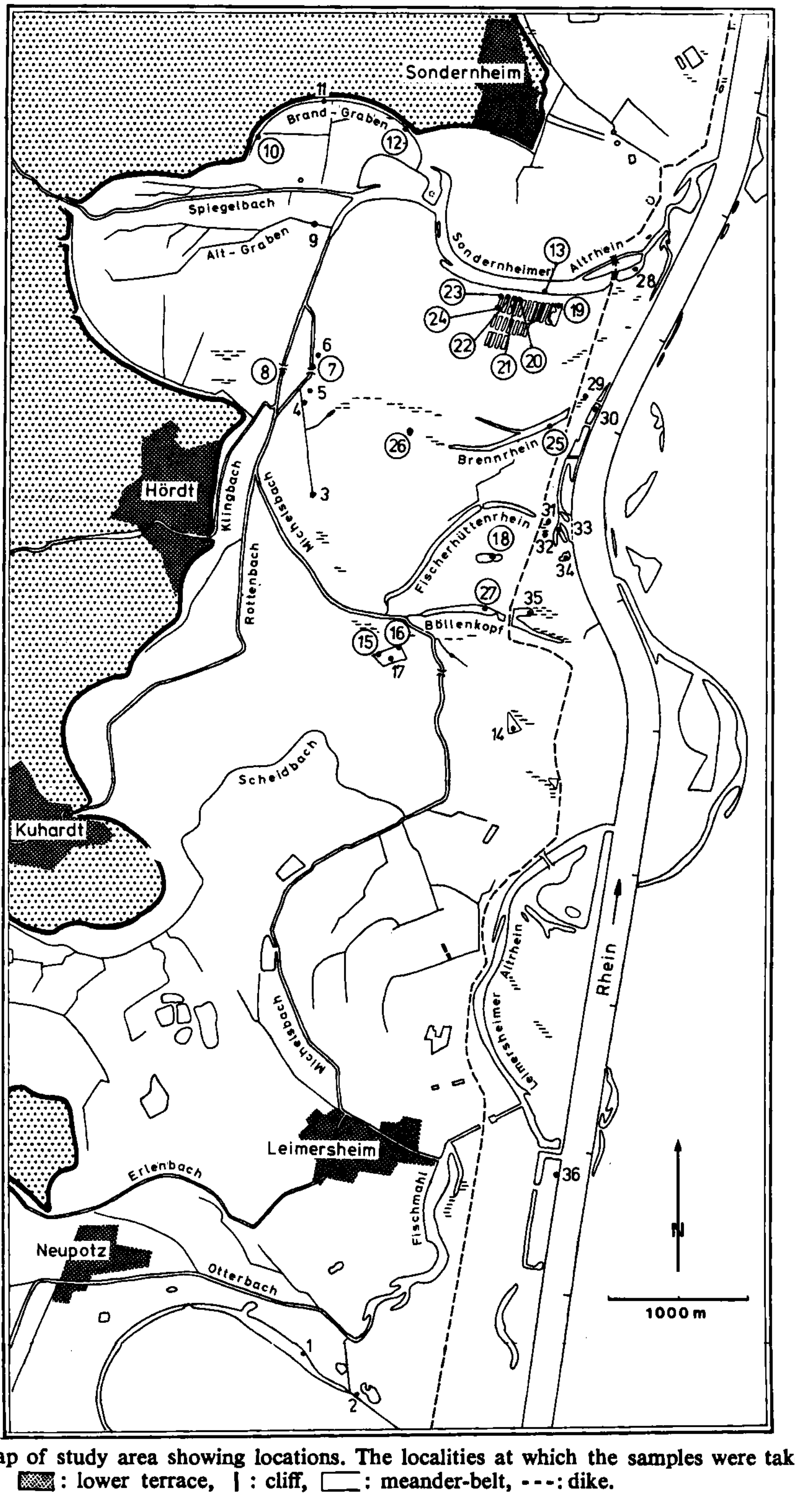
TEXT-FIG. 1—Nature reserve "Hördter Rheinaue". Dynamics of the meander and drying up of the meander-belt (from Kinzelbach, 1976).

bow-lakes in the wet meander-belt while in the dry meander-belt we find running water, gravel-pits, loam-pits and oxbow-lakes (Text-fig. 2 and Table 1).

A detailed description of the nature reserve "Hördter Rheinaue" and its waters is given in Kinzelbach (1976) and Scharf and Kinzelbach (1976). For the vegetation in the individual localities see Dannapfel (1977), for the habitat of the localities studied see Scharf (1976).

Nearly all the waters are formed by the meandering Rhine river. Today some exist as separate oxbow-lakes and others are part of the Michelsbach creek (see Text-figs. 1 and 2). Most of the waters are surrounded by forest. Only the oxbow-lake "im alten Dorf" (No. 1 in Text-fig. 2) and the "Altgraben" creek (No. 9) are situated between meadows and cultivated fields.

All the waters studied are shallow, *i.e.* less than 2 metres deep. Only the gravel-pits have a depth of up to about 10 metres.



TEXT-FIG. 2—Map of study area showing locations. The localities at which the samples were taken monthly are encircled. ▨ : lower terrace, | : cliff, ▭ : meander-belt, - - - : dike.

TABLE 1—LIST OF THE OSTRACOD SPECIES FOUND IN THE "HÖRDTER RHEINAUE".

	dry meander-belt, on the land-side of the dike																											wet meander-belt								
	running water													stagnant water																						
														gravel-pits						loam-pits					oxbow-lakes											
	"im alten Dorf"	drainage ditch	Schlute	Schlute	wet alder wood	flood-plain of Michelsbach	Michelsbach	Michelsbach	Alt-Graben	Brand-Graben, spring	Brand-Graben, middle	Brand-Graben, mouth	Sondernheimer Altrhein	triangular gravel-pit	Mehlfurt, clay-margin	Mehlfurt, gravel-margin	Mehlfurt, in the deep	Herrengrund	Bananensee	made about 1968	made about 1940	made about 1971	made 1975, north	made 1975, south	Brennrhein	Suhle	Bollenkopf	Sondernheimer Altrhein	Brennrhein	Altrhein	Fischerhüttenrhein	Fischerhüttenrhein	Altrhein	Altrhein	Böllenkopf	puddle
number of locality	1	2	3	4	5	6	⑦	⑧	9	⑩	11	⑫	⑬	14	⑮	⑯	17	⑱	⑲	⑳	㉑	㉒	㉓	㉔	㉕	㉖	㉗	28	29	30	31	32	33	34	35	36
Limnocythere inopinata		○						○			○		○		○			●	●	○	○	●						○		○						
L. sp.															○																					
Metacypris cordata	●																																			
Darwinula stevensoni		○		●			●																					○								
Ilyocypris bradyi		●						○							●	○	○																			
I. gibba															●	○	●			○	○															
I. tuberculata							●						●						●									○					○			
I. sp.												○										○								○						
Candona candida	●	●		●	●	●	○	●	●	●	●	●	○	●		○		●	●	●	●	○			●	●	●	○	●				●	○	●	
C. neglecta	●	○		●	○	○	●		○				○						●		●							○					●		●	
C. weltneri v. *obtusa*	●						○						○						●								●	○								
Candona hartwigi	●												●	●					●	●							●	○					●		○	
C. marchica													●	●																						
C. sarsi																														●	●	●				
Candona albicans		○			●		●	●		●	○	●			●	●						○										●	●			
C. pratensis				○	●		○						○																			●				
C. sucki																																●				
Candona fabaeformis			○	●			○						●																							
C. wegelini																																●				

TABLE 1—*Continued*

number of locality	1	2	3	4	5	6	⑦	⑧	9	⑩	11	⑫	⑬	14	⑮	⑯	17	⑱	⑲	⑳	㉑	㉒	㉓	㉔	㉕	㉖	㉗	28	29	30	31	32	33	34	35	36
Candona caudata		○											○															○								
C. hyalina	○						○					○	○								●				○		●	○					●			
C. protzi	●												○														●						●			
Candonopsis kingsleii	●		●	●			○			●	○			●					●	●	●	●					●			●			●			
Cyclocypris laevis				●	●		●		●	●	●	●	○																							
C. ovum s. Klie				●	●		○					●		○													●									
C. ovum s. Petk.	●	●		●	●																						●	○								
C. serena									●																											
Cypria exsculpta	●														○																					
C. lacustris							○						●														●						●			
C. ophtalmica	●	●	●	●	●	●	●	●	●	●	●	●	●					○	●			●			●	○	●	○	●	●	●	●	●		●	
Physocypria kraepelini	●						●						●		●	○		●	●	●	●	●					●	○	●				●	●	●	
Notodromas monacha				○			○							○											○							○				
N. persica				●						●	○	○																								
Heterocypris incongruens																																				●
Eucypris pigra		○																												●						
E. zenkeri							○	●	●																											
E. sp.							○						●																							
Cypricercus affinis		●		●		●								●																						
Isocypris beauchampi							●													●																
Herpetocypris reptans	●	●		○			●	●	●			●	○	●				●												○			●			
Dolerocypris fasciata																				●	●						○									
Cypris pubera																																●			○	
Cypridopsis vidua	●	●		●			●	○					●	●	●	●		●	●	●	●	●	●	●	○		●	○	○	●			●		○	
Potamocypris variegata															●	○				●	●	●														
living (●)	13	7	2	12	7	3	10	5	6	6	3	6	9	7	6	2	1	5	10	8	8	6	1	1	2	1	12	—	3	5	2	7	12	1	4	1
subfossil/fossil (○)	1	6	1	3	1	1	11	3	1	0	4	3	10	2	3	5	1	1	0	2	2	3	0	0	3	1	1	13	1	3	0	1	1	1	3	0

These symbols distinguish between living (●) and subfossil/fossil (○) occurrences. The localities which were collected monthly are encircled.

The puddle (No. 36) dries up in each warm weather period. The Schlute (No. 3), the wet alder wood (No. 5), probably the flood-plain of Michelsbach (No. 6), the Brennrhein (No. 29) and the Altrhein (No. 34) dry up each summer. The Brennrhein (No. 25) was without water in the warm summer of 1969. Normally a small amount of water remains in the oxbow-lake Brennrhein (No. 25) during summer.

METHODS

The methods of catching ostracods, of separating them from the substrate and preparing the animals are described by Scharf (1976 and 1980).

In the period from April 1976 to March 1977 half of the localities were collected monthly (see Table 1 and Text-fig. 2). Later on the other ones were visited. Between April and May 1985 samples were taken from localities 1–3, 14 and 28–35.

Dr. K.H. Dannapfel was kind enough to provide the sample from locality 28. This was a dry mud sample so it was not possible to distinguish between living and subfossil animals.

RESULTS AND DISCUSSION

List of the Ostracods Found

The list of the species which were found in the different localities of the "Hördter Rheinaue" is given in Table 1. It distinguishes between living and subfossil/fossil occurrences. Under "living" are placed all living animals or those that have just died, *i.e.* the muscles have not yet decayed. The term "subfossil" is applied to all those animals whose remains are only a few years old, "fossil" to those that are older. Often it is not possible to distinguish between subfossils and fossils.

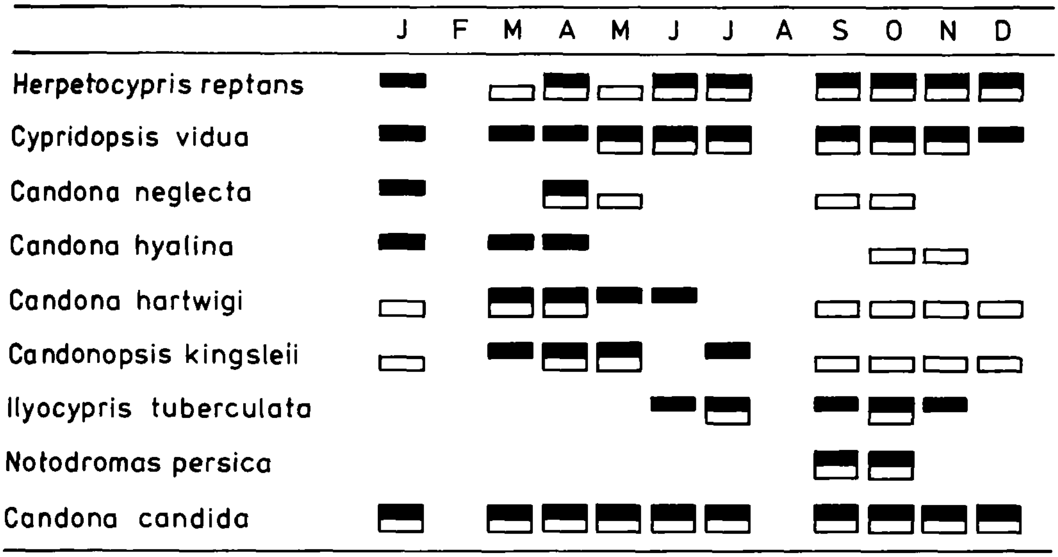
Subfossil valves are examined to see if there are further species that have not been caught before because of it being the wrong season. Sometimes the relation between living and subfossil animals can be an indication of a specific biotope as will be seen later.

In the "Hördter Rheinaue" living specimens of 39 ostracod species were found and will be figured in Scharf (in prep.). Among these species are some that are rarely found in Germany, for example: *Ilyocypris tuberculata, Candona weltneri* var. *obtusa, C. hartwigi, C. sarsi, C. wegelini, C. caudata* (only subfossil found in the "Hördter Rheinaue"), *C. hyalina, Cypria lacustris, Notodromas persica* and *Isocypris beauchampi.* In the "Hördter Rheinaue" no new species nor any species new to Germany were found.

The most frequently found species are given in Table 2. They are all common species.

TABLE 2—THE MOST FREQUENTLY FOUND OSTRACODS

	number of localities occurrences	
	living	subfossil
Cypria ophtalmica	23	3
Candona candida	21	6
Cypridopsis vidua	18	5
Physocypria kraepelini	14	2
Candonopsis kingsleii	12	2
Herpetocypris reptans	9	3
Candona albicans	9	3



TEXT-FIG. 3—Population distribution characteristics of some ostracods from the "Hördter Rheinaue". ■: adults, □: instars. The gaps in February and August are due to the fact that there were no collections.

Phenology (Population Structure)

About 190 samples from different localities in various months were taken in the "Hördter Rheinaue". It is not possible to give the population structure characteristics of many species. Some of the reasons for this are:

—Often only a few specimens were found so that it is not possible to make a reliable statement because of the small numbers.

—The sediment was washed on a 250 μm mesh so that often many instars were not caught.

—In some localities adults and juveniles were found whereas in other localities only adults were caught. For example: In the small running water Brand-Graben (Nos. 10–12) *Cypria ophtalmica* was present not only as adults but also as instars. However, only adults of the same species were found in the oxbow-lakes Brennrhein (No. 25) and Böllenkopf (No. 27). It may be that the instars are in the deeper parts of the bigger lakes. Mallwitz (1984) observed the same feature with other species in some lakes in North-Germany.

In spite of these difficulties it is possible to give the population distribution characteristics of some species (Text-fig. 3). Adults and juveniles of *Herpetocypris reptans* are present practically throughout the year. Adults of *Cypridopsis vidua* were found all the year round, but instars only in the summer time. This species is very frequent in the warm season while the adults are rare in winter. The adults were caught much more frequently than the juveniles. Therefore it is possible that there are instars in winter time (compare Mallwitz, 1984).

Candona neglecta, C. hyalina, C. hartwigi and *Notodromas persica* have only one generation a year in the "Hördter Rheinaue". The adults appear in different months (Text-fig. 3). The population structure of *Candonopsis kingsleii* is similar than that of *Candona hartwigi* but it seems that *C. kingsleii* has a further one or more generations in the early summer time. *Ilyocypris tuberculata* appears only during the warm period and it is not possible the give the number of generations a year.

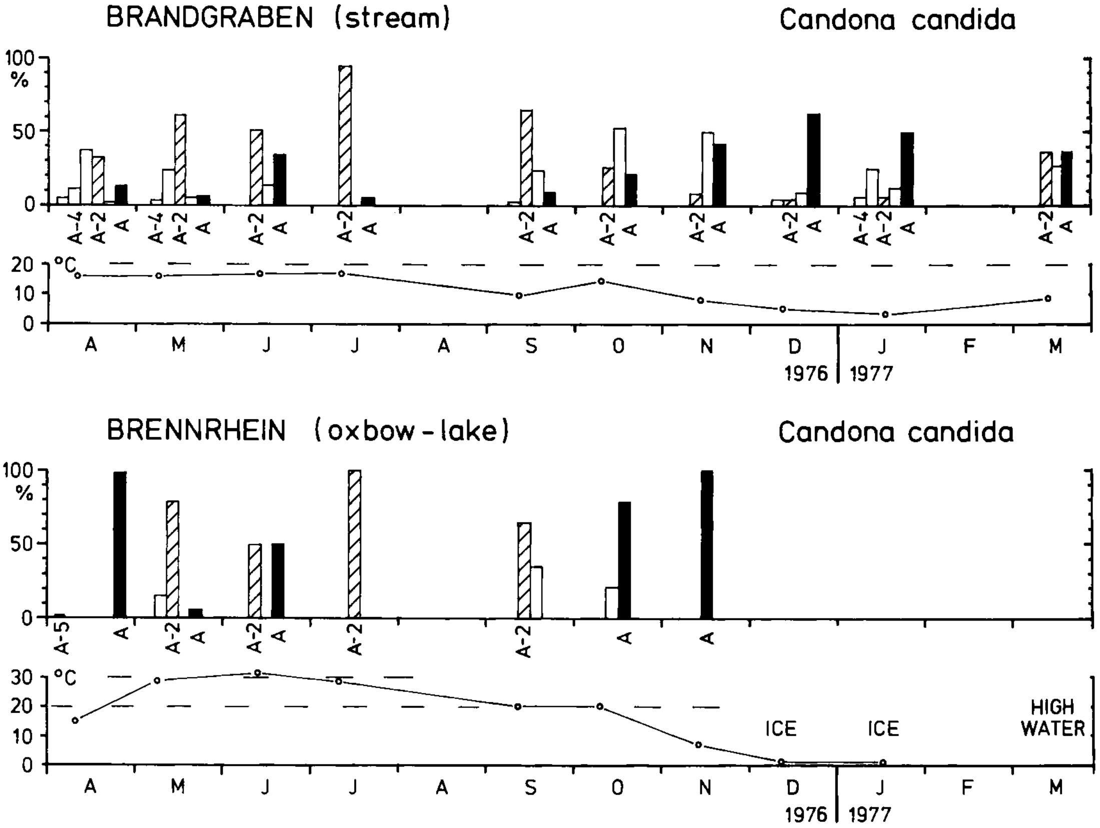
Candona candida seems to be a species with several generations in the year. However, this is not correct as Text-fig. 4 shows. In this figure the development of the *Candona candida*-population

TABLE 3—POPULATION DENSITY OF OSTRACODA. AN ATTEMPT AT A REVIEW TOGETHER WITH THE DATA OF THE "HÖRDTER RHEINAUE"

lake	species	pop. density specimens/m²	remarks	reference
oligotrophic Gerat Lake, Canada		57		Tressler (1957), cit. in Thaler (1977)
Balaton, Hungary	*Darwinula stevensoni*		up to 7.7% of benthic	Ponyi (1966)
	Candona balatonica		up to 0.8% Crustacea	
	Ilyocypris gibba		up to 1.5%	
Lake Constance, Germany	*Cypria ophtalmica*	up to 1,500,000		Löffler (1969)
	Cytherissa lacustris	up to 100,000		
mesotrophic Gull-Lake, Michigan, USA	*Darwinula stevensoni*	up to about 8,000		McGregor (1969)
Balaton, partim in the area of a sewage-inflow, Hungary	*Cypridopsis vidua*	up to 16,800	up to 39% ostracods in relation to total benthic Crustacea	Ponyi *et al.* (1971)
	Limnocythere inopinata	up to 6,600		
	Cyclocypris ovum	up to 3,900		
	Ilyocypris bradyi	up to 2,300		
	Cypridopsis newtoni	up to 2,100		
	Candona spec.	up to 2,000		
	Darwinula stevensoni	up to 800		
	Isocypris arnoldi	up to 400		
vordere Finstertaler See, high mountain region of Austria	*Cypria ophtalmica*	about 7,000	mean biomass: 44 mg/m²	Bretschko (1972), cit. in Thaler (1977)
Laguna de Magalhaes, lagoon in the tropical savanna of North-Brasil	Ostracoda, not specified	45	relative abundance: 2.4%	Reiss (1973)
Loch Leven, U.K.	Ostracoda		mean annual biomass: 100 mg/m²	Maitland and Hutspith (1974), cit. in Thaler (1977)
outflow region	Ostracoda	up to 13,390	up to 348 mg/m² dry weight up to 14.78 % of total dry wt.	Junk (1975)
central region		up to 9,015	up to 235 mg/m² dry weight up to 0.072% of total dry wt.	
littoral region of water reservoir Bung Borapet, Thailand		up to 26,246	up to 68 mg/m² dry weight up to 0.27% of total dry wt.	

TABLE 3—*Continued*

lake	species	pop. density specimens/m²	remarks	reference
7 different lakes in central Amazonian region (black water, blended waters and white water) Brasil	Ostracoda		mean annual abundance: 0.3–63 weight % (average: 21%)	Reiss (1976)
eutrophic Piburger See, Austria	*Cypria ophtalmica*	max.: 250,000 mean annual pop. density: 130,000	max. biomass: 2,800 mg/m² mean annual biomass: 1,500 mg/m²	Thaler (1977)
	Candona candida	max.: 3,600 mean annual pop. density: 3,000	max. biomass: 190 mg/m² mean annual biomass: 50 mg/m²	
	Cypridopsis vidua	max.: 1,900 mean annual pop. density: 500	max. biomass: 42 mg/m² mean annual biomass: 15 mg/m²	
eutrophic lakes	Ostracoda	> 50.000		Wetzel (1984)
Schmalsee, mud, North Germany	Ostracoda	max.: 140,500 mean annual density: 44,000	(in this paper the percentage of each species at the three localities is given)	Mallwitz (1984)
Schmalsee, sand, North Germany	Ostracoda	max.: 43,700 mean annual desnity: 8,000		
Lüttauer See, rhizoms of reed with detritus North Germany	Ostracoda	max.: 4,670 mean annual density: 3,000		
Hördter Rheinaue gravel-pit Mehlfurt, clay-margin (15)	*Cypridopsis vidua*	up to 3,440		Scharf (this paper)
	Potamocypris variegata	up to 800		
Brand -Graben, spring (10)	*Candona candida*	up to 2,800		
	Cyclocypris laevis	up to 820		
	Cypria ophtalmica	up to 530		
Sondernheimer Altrhein (13)	*Physocypria kraepelini*	up to 1,400		
gravel-pit Herrengrund (18)	*Cypridopsis vidua*	up to 940		
loam-pit (21)	*Cypridopsis vidua*	up to 940		
Brand-Graben, mouth (12)	*Cyclocypris ovum*	up to 910		
	Cypria ophtalmica	up to 660		
Brennrhein (25)	*Candona candida*	up to 900		



TEXT-FIG. 4—Population distribution of *Candona candida* and temperature in two localities of the "Hördter Rheinaue". A = adults, A-1 = ultimate larval stage, A-2 = penultimate larval stage and so on.

in Brennrhein (No. 25) is compared with that of the Brand-Graben (No. 12). The water of the shallow oxbow lake is warm in summer and cold in winter while the water of the Brand-Graben stream is, in relation to the temperature, more equable. One can see that the percentage of the penultimate larval stage A-2 increases until July and after that decreases. With the decrease of A-2 in the autumn the percentage of the last larval stage and of the adults increases. The comparison shows that the development is more synchronized in the oxbow lake than in the stream, probably because of the temperature. In the stream there are more development-stages at one time and each single stage is to be found over a longer period than in the oxbow lake. *Candona candida* has only one generation per year in the "Hördter Rheinaue".

Density of Population

There is little data on the density of ostracod populations in the literature. An attempt has been made to compile the available data and this is given in Table 3. Wetzel (1984) in summary states that the individual density ranges from an average of 57 m^{-2} in the oligotrophic Great Slave Lake to about 10,000 m^{-2} in a mestrophic lake and finally to > 50,000 m^{-2} in an eutrophic lake.

The ostracods form a great part of the biomass in some lakes. For example 64% of the total dry weight of biomass in the depths of Lago Tupé in the central Amazonian region are ostracods (Reiss, 1976). Chaoboridae, Hydracarina and Ostracoda can be considered as the common stock

TABLE 4—INDIVIDUAL DENSITY OF OSTRACODS IN "HÖRDTER RHEINAUE" LOCALITIES COLLECTED MONTHLY.

	Michelsbach	Michelsbach	Brand-Graben, spring	Brand-Graben, mouth	Sondernheimer Altrhein	gravel-pit Mehlfurt claymargin	gravel-pit Mehlfurt gravel-margin	gravel-pit Herrengrund	Bananensee	loam-pit, 1968	loam-pit, 1940	loam-pit, 1971	loam-pit, 1975	loam-pit, 1975	Brennrhein	Böllenkopf
number of locality	7	8	10	12	13	15	16	18	19	20	21	22	23	24	25	27
Limnocythere inopinata								sr	sr			15				
Darwinula stevensoni	sr															
Ilyocypris bradyi						sd										
I. gibba						r										
I. tuberculata	d				d				sr							
Candona candida		13	47	45				26	26	r	sr				95	sd
C. neglecta	d								r		sr					
C. weltneri var. *obtusa*									sr							r
Candona hartwigi					sr				d	r						38
C. marchica					sr											
Candona albicans	sr	r	sr	sr		d	55									
Candona fabaeformis					sr											
Candona hyalina											sr					d
C. protzi																d
Candonopsis kingsleii			r						sr	r	sr	sr				sr
Cyclocypris laevis	r		28	sr												
C. ovum s. Klie				17												sd
C. ovum s. Petkovski																sr
Cypria lacustris					sd											18
C. ophtalmica	r	81	22	34	25				sr			sr			d	20
Physocypria kraepelini	64				62	sr		sr	sd	16	22	26				sr
Notodromas persica			sd													
Eucypris zenkeri		r														
Isocypris beauchampi	r									sr						
Herpetocypris reptans	11	sd		sd				sr								
Dolerocypris fasciata										13	sr					
Cypridopsis vidua	sd				sd	80	45	73	59	66	75	56	100	100		r
Potamocypris variegata						d				r	r	sd				
mean annual density (n/m^2)	90	15	1207	1140	438	1427	30	400	139	189	219	148	8	28	438	370

The percentage of the eudominant (> 10%) species is given in each case. d = dominant (10–5%), sd = subdominant (5–2%), r = recedent (2–1%), sr = subrecedent (< 1%).

of the macrobenthic fauna of central Amazonian lakes (Junk, 1973; Fittkau *et al.*, 1975). The large population density suggests that their role could sometimes be considerable in the metabolism of lakes.

Such great numbers of ostracods as those given in the literature were not found in the waters of the "Hördter Rheinaue" The biggest mean annual density was found in the Brand-Graben (Nos. 10 and 12) and in the clay margin of the gravel-pit Mehlfurt (No. 15). In the Brand-Graben *Candona candida, Cypria ophtalmica* and *Cyclocypris laevis* or else *C. ovum* were the most abundant individuals. Leaves of alder and beech were predominant as organic material while in the gravel-pit reed mace and its mud serve as a basis for the food of *Cypridopsis vidua.*

Certainly the absence of fish is a large factor in the relatively large number of ostracods in the Brand-Graben. The population of *Candona candida* is reduced drastically by fish in the Piburger (Thaler, 1977).

The lowest mean annual density of ostracods was found in Michelsbach (No. 8), at the gravel-margin of the gravel-pit Mehlfurt (No. 16) and in the youngest loam-pits (Nos. 23 nad 24) (Table 4). In each of these localities the content of organic material in the sediment is much smaller than at the other localities.

Cypria ophtalmica, Physocypria kraepelini and *Cypridopsis vidua* are small and good swimmers. Table 4 shows that they are not evenly distributed. One of the three species is always much more numerous than the other two species. *C. vidua* seems to occupy the waters with submerged water plants more successfully than *P. kraepelini* or *C. ophtalmica.* For comparison, in the volcanic lakes of the Eifel-region *C. vidua* lives in the belt of submerged water plants, *C. ophtalmica* prefers the depths of the lakes and *P. kraepelini* is absent in these volcanic lakes (Scharf, 1980; Kempf and Scharf, 1980).

Species Frequency in Relation to the Drying up of the Waters

In the "Hördter Rheinaue" there are only a few waters with many ostracod species. These are the localities numbered 1, 4, 27, 33, 7, 19 and 13 in Table 1. With the exception of the gravel-pit Bananensee (No. 19) all the waters mentioned are oxbow lakes and they have never dried up hitherto. All of these are deep enough to ensure that the ice in winter does not reach the bottom.

There are only very few species in the ephemeral waters or waters which rarely dry up such as the localities numbered 36, 23, 24, 26, 34, 17, 31, 3 and 25 in Table 1. The Brennrhein (No. 25) dried up at least once in the warm and dry summer of 1969. It is possible that some very tolerant species have survived the drying up. It is also possible that there was re-colonisation and that the ice in winter has diminished the species diversity.

Species frequency in relation to the age of the water

It was in the old oxbow lakes that most ostracod species within the "Hördter Rheinaue" were found. In the youngest waters there were only a few species. The loam-pits are a good example of this. Table 5 shows the occurrence of ostracod species in loam-pits of different ages. The investigations were made in the years 1975 and 1976, *i.e.* the youngest loam-pit had just been built. One can see that the number of species increases with the age of the loam-pit.

I have called the species in the youngest loam-pits pioneer-species. There are some features that are characteristic of them (Table 6). The characteristic of being small is good for transport from one body of water to another, especially if insects are the transporting agents. If an ostracod can swim, the probability of it meeting an insect is large. Also, if an ostracod reproduces parthenogenetically, only one specimen is enough to build a population. Nevertheless, it is also important that the species occurs in neighbouring waters.

Cypridopsis vidua meets all these conditions. This may be the reason why *C. vidua* is the most

TABLE 5—THE COLONISATION OF LOAM-PITS OF DIFFERENT AGES BY OSTRACODS (The loam-pits were investigated in the years 1975 and 1976).

biotope	loam-pits			
made in the years	1940	1968	1971	1975
Limnocythere inopinata	●			
Candona candida	●	●		
C. neglecta	●			
C. hyalina	●			
Candonopsis kingsleii	●	●	●	
Cypria ophtalmica			●	
Physocypria kraepelini	●	●	●	
Isocypris beauchampi		●		
Dolerocypris fasciata	●	●		
Cypridopsis vidua	●	●	●	●
Potamocypris variegata	●	●	●	
total	9	7	5	1

TABLE 6—SOME CHARACTERISTICS OF OSTRACOD PIONEER-SPECIES

	length < 0.7 mm	good swimmer	reproduction	
			parthenogenetic	bisexual
Candona candida			+	
Candonopsis kingsleii				+
Cypria ophtalmica	+	+		+
Physocypria kraepelini	+	+		+
Isocypris beauchampi		+	+	
Dolerocypris fasciata		+	+	
Cypridopsis vidua	+	+	+	
Potamocypris variegata	+	+	+	
total	4	6	5	3

successful pioneer-species in the loam-pits. The reason why species of the genus *Cyclocypris* are absent in the loam-pits is a problem. They have most of the characteristics mentioned and as yet there is no satisfactory explanation.

Comparison of the Dry and Wet Meander-Belts

The sample from the Sondernheimer Altrhein (No. 28) has to be excluded from the comparison since the animals found can be transported from the dry to the wet meander-belt by the running water.

The species that occur either only in the dry or in the wet meander-belt are given in Table 7. The 14 species that are common to both parts of the meander-belt are not given in Table 7. Table 7 shows that there are more species in the dry part than in the wet one. The difference would possibly be smaller if more samples were investigated in the wet part, especially in other seasons. However, it is certain that a difference would remain because the substrate in the wet part is very uniform due to the annual cover with river-clay at high-water. Furthermore there are more different types of waters in the dry part than in the wet one.

Distribution factors

Until now, 105 freshwater ostracod species have been found in the Federal Republic of Germany (Mertiny, in press) and 41 of them occur in the nature reserve "Hördter Rheinaue", an area of

Table 7—Comparison of the Ostracods from the Dry with the Wet Meander-belt of the "Hördter Rheinaue" (The 14 species that are distributed in both parts of the meander-belt are not in this table).

	dry meander-belt	wet meander-belt without locality No. 28
Limnocythere inopinata	●	O
Metacypris cordata	●	—
Darwinula stevensoni	●	—
Ilyocypris bradyi	●	—
I. gibba	●	—
I. tuberculata	●	O
Candona weltneri var. *obtusa*	●	—
C. marchica	●	—
C. sarsi	—	●
C. sucki	—	●
C. fabaeformis	●	—
C. wegelini	—	●
Cyclocypris laevis	●	—
C. obum sp. Klie	●	—
C. ovum sp. Petk.	●	—
C. serena	●	—
Cypria exsculpta	●	—
Notodromas persica	●	—
Heterocypris incongruens	—	●
Eucypris pigra	O	●
E. zenkeri	●	—
Cypricercus affinis	●	—
Isocypris beauchampi	●	—
Dolerocypris fasciata	●	—
Cypris pubera	—	●
Potamocypris variegata	●	—
living (●)	20	6
subfossil/fossil (O)	1	2
absent (—)	5	18

less than 10 km². This very high percentage appears to be caused by two factors: firstly, the great diversity of biotopes and secondly, the geographical location of the "Hördter Rheinaue".

Sywula (1977) provided that most freshwater ostracods prefer a specific habitat. The chance of a species discovering an adequate habitat increases with increase in the number of different biotopes. The "Hördter Rheinaue" has a great diversity of biotopes.

The "Hördter Rheinaue" is situated in the meander-belt of the Upper Rhine Valley. This means that ostracods which live in the drainge area of the Rhine river can be transported by water in the "Hördter Rheinaue". The nature reserve "Taubergießen" is situated 105 km upstream in the meander-belt of the Rhine. Unfortunately, the ostracod fauna of "Taubergießen" is unknown. Because of the great diversity of the waters in this area it is probable that there are many ostracod species, perhaps more than in the "Hördter Rheinaue". In 1984 Meisch (pers. comm.) found *Candona sarsi* in the meander-belt of the Rhine, a few kilometres away from "Taubergießen". Wolf (1919) took samples from an oxbow lake with many water plants, situated on an island in the Rhine river near Basel, Switzerland, about 190 km upstream of the "Hördter Rheinaue" and found 18 ostracod species. With the exception of *Potamocypris villosa*, all the other species are present in the "Hördter Rheinaue". Further upstream is Lake Constance which can also provide a faunal influence. For the ostracod fauna of Lake Constance see Kuttner (1924) and Löffler (1969).

The "Hördter Rheinaue is situated on a bird migration route; for the birds of the "Hördter

Rheinaue" see Niehuis (1977) and Froehlich (1977). Löffler (1964) carried out experiments in which he fed ducks with Crustacea of different groups. 10% of the eggs of *Cypris pubera* survived the journey through the intestine of the ducks. The eggs of *Cypris pubera* developed normally even when they were stored some days in the ducks's intestine. The Mallard *Anas platyrhynchos* can fly at least 380 km a day. This means that a Mallard can reach the "Hördter Rheinaue" in two days from the Mediterranean region or from Scandinavia. In the warm summer of 1976 a large parthenogenetic population of *Cypris bispinosa* was found a few kilometres further south of the "Hördter Rheinaue" (Prof. Dr. G. Preuss kindly provided some specimens of this population) (Scharf, in prep.). *Cypris bispinosa* is frequent in the Mediterranean region (Stephanides, 1948; Ghetti and McKenzie, 1981), but until now it has not been found in Germany. It seems certain that *Cypris bispinosa* was transported by birds from the Mediterranean region to Germany. The animals found an adequate biotope within a dense population of the water nut *Trappa natans*. Perhaps the winter was too hard for them to survive, but whatever the cause in the following year the population of *Cypris bispinosa* died out.

It is also suggested here that *Notodromas persica* in the "Hördter Rheinaue" and a so far undetermined *Cyprinotus* species found about 60 km further north of the "Hördter Rheinaue" in the upper Rhine Valley (Scharf, in prep.) were brought by birds to Germany too.

The transport of ostracods by birds and insects can be very effective (Keyser, 1976:64; Fryer, 1978).

The transport of ostracods by water, birds or insects provides an opportunity for distribution, but on the other hand there is a great risk involved. As a result the high percentage of subfossil valves in the running waters of Michelsbach (No. 7) and Sondernheimer Altrhein (No. 13) is interpreted as the result of the drifting of ostracods during high water from stagnant water into running water. There the single individual did not find an adequate biotope and could not form a population.

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This paper is dedicated to my honoured teacher and mentor Prof. Dr. Harald Sioli on his 75th birthday

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DISCUSSION

De Deckker: In regard to your description of the four quarries which were opened up at different times, could you perhaps say that the diversity of ostracods instead of being a result of the age of the quarry is in fact the result of a chemical evolution of the quarry water?

Scharf: No, I do not think so. With increasing age, the diversity of the habitats grows. For example, there are more species of water plants and there is mud on the bottom of the older loam-pits, which is absent in the youngest loam-pit. In 1975 only *Chara* species was present in the youngest loam-pit. In 1985, *i.e.* 10 years later, I visited the loam-pit again. Unfortuantely the localities were changed so that a comparison was not possible.

Keyser: Is there a difference between the parthenogenetic reproduction time compared to the bisexual reproduction time?

Scharf: According to the presented data a general answer is not possible. There are species with parthenogenetic reproduction (*Candona candida*) and species with bisexual reproduction (*Candona neglecta*) with only one generation a year. On the other side there are examples of other kinds of reproduction with more than one generation a year (*Cypridopsis vidua* and *Candonopsis kingsleii*).

McKenzie: Did you find males frequently or not?

Scharf: In some species like *Candona hartwigi, Candonopsis kingsleii* or the *Cyclocypris* and the *Cypria* species I found males very frequently. In other species males are rare or absent.

McKenzie: How long can ostracods survive within a duck?

Scharf: The eggs of ostracods can survive several days in the intestine of a duck. For further details please see Löffler (1964).

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Distribution of the Brackish-Salt Water Ostracods in Northwestern Qinghai Plateau and Its Geological Significance

FAN YANG
*Research Institute for Petroleum, Qilizhen, Dunhuang,
Gansu, P.R. China*

ABSTRACT

The climate in northwestern Qinghai Plateau is cold and dry. Most of the waters there are more or less saline.

In this part of the world there live ostracod faunae composed mainly of *Eucypris inflata, Limmocythere inopinata, Heterocypris salina, Eucypris gyirongensis, Ilyocypris biplicata, Candona neglecta, Candona candida* and *Candoniella lactea.* They are all stenotherms cold-loving (or eurythermic), halophylous (or euryhaline) species.

As is the same with the other areas, the ostracod associations in northwestern Qinghai Plateau differ from each other with the change of the environment.

The present climate is similar with the palaeo-climate in the Tertiary period in this area. According to the law that governs the distribution of the ostracod associations at present time, the associations of the ostracod fossils in the Tertiary period may be used to indicate the palaeo-environment in the same period.

INTRODUCTION

The Qinghai Plateau in northwest China is generally 2,500–4,500 metres above sea level. The climate there is that of the cold-temperate zone, with a cold winter and a cool summer. Average annual temperature is between $-5°$ C and 8° C. The northwestern part of the plateau located in the arid zone of the Northern Hemisphere has an annual average precipitation of 50–400 mm. Thanks to greater evapotranspiration, waters in this area are generally saline. Many rivers and lakes are either brackish or saline. In the waters there live ostracoda fauna with distinctive features different from those living in seas and waters near the sea as well as from the inland infrahaline species. They are composed overwhelmingly of the inalnd halophilous species and euryhaline species. The overwhelming majority of them are also stenothermal cold-loving species and eurythermal species. The infrahaline and stenothermal warmth-loving species are deficient. River or lake bottom matter sample analysis indicates that the distribution of Ostracoda in this area is heavily influenced by the varying environmental factors. From studying the relationship between the influential environmental factors and ostracod faunas and their taphocoenose we may infer the indicator role of ostracod fossils for ancient sedimentary environments, which is of very important geological significance.

INFLUENCE OF THE ENVIRONMENTAL FACTORS UPON THE DISTRIBUTION OF OSTRACODA

Salinity

The changes in salinity of the waters in the northwestern Qinghai Plateau strictly control the distribution of Ostracoda. This finds expression in the species of the taphocoenose, the diversity index of species and genera and the number of valves.

Table 1 shows the monotonousness of ostracod species in the infrahaline waters in this area. Only a small number of *Ilyocypris biplicata* (Koch) and *Eucypris gyirongensis* Huang were found. In the oligohaline waters 27 species of 15 genera were discovered in large numbers, and there were 100–300 valves in every 100 grams of bottom matter sample. The whole association is composed mainly of *Eucypris gyirongensis, Ilyocypris biplicata, Patamocypris smaragdina* (Vavra), *Candona neglecta, Candoniella lactea* (Baird) and *Limnocythere inopinata.* In addition, there are *Ilyocypris gibba* (Ramdohr), *C. candida, Subulacypris trapezoidea* sp. nov., *Potamocypris fulva* (Brady),

TABLE 1—ABUNDANCE OF OSTRACODS IN WATERS OF VARYING SALINITY

Salinity / Species	Infrahaline $s < 0.5‰$	Oligohaline $s = 0.5–5‰$	Mesohaline $s = 5–18‰$	Poly-Euhaline $s = 18–40‰$	Ultrahaline $s > 150‰$
Darwinula ? sp.					
Ilyocypris gibba		○			
I. biplicata	+	■■■■			
I. aff. *inermis*		•			
Candona candida		○			
C. neglecta		■■■■			
C. caudata		+			
C. marchica		+			
C. houi		○			
C. compressa		+			
Candoniella albicans		+	•		
C. lactea		**			
Pseudocandona sp.		•			
Eucypris moguntiensis		○			
E. gyirongensis	+	■■■■			
E. inflata		+	**	○	○
Heterocypris incongruens		○			
H. salina		○			
Cyclocypris serena		+			
Potamocypris fulya		○	•		
P. smaiagina		■■■■			
P. villosa		+			
Cypridopsis vidua		+			
C. aculeata		+			
Prionocypris gansenensis		■■■■			
Subulacypris trapezoidea		■■■■	•		
Megazonocypris fragilis		+			
Stenocypris hodgsoni		•			
Limnocythere inopinata		**	**	+	+
Cyprideis littoralis		+			

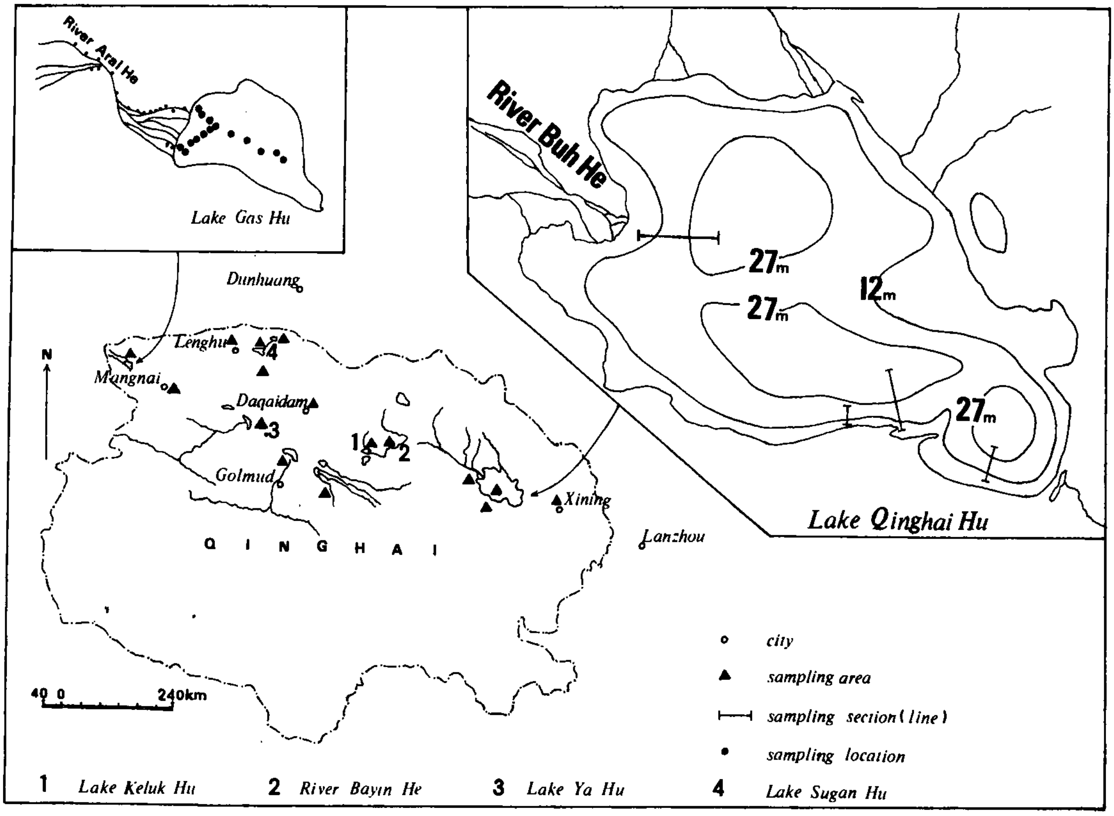
•, very few; +, a few; ◉, quite a few; ■■■■, a large quantity; **, a very large quantity.

Prionocypris gansenensis Huang, *Eucypris moguntiensis, Heterocypris incongruens* and *Cyclocypris serena,* as well as a small number of *Candona caudata, Candona marchica, Candona compressa, Candoniella albicans* (Brady), *Pseudocandona* sp., *Megazonocypris fragilis, Eucypris inflata, Cyprideis littoralis, Cypridopsis vidua* (O.F. Müller), *Cypridopsis aculeata* (Lilljeborg), *Potamocypris villosa* (Jurine), *Ilyocypris* aff. *I. inermis* and *Stenocypris hodgsoni.* Samples of live species or species with appendages taken together with salinity of the waters include:

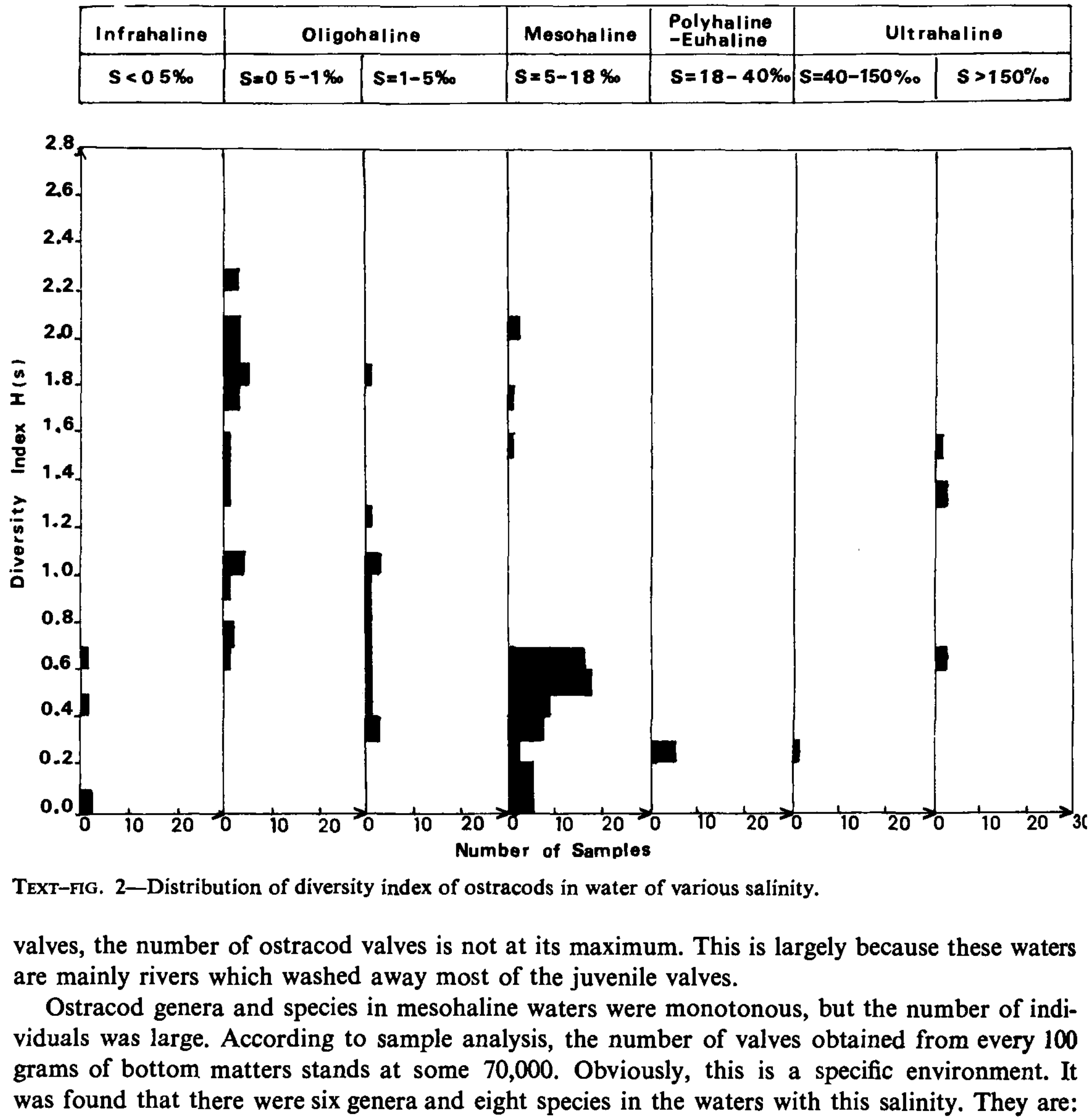
Candona houi	$S = 0.844$‰
Cyclocypris serena	$S = 0.714$‰
Ilyocypris biplicata	$S = 0.981$‰, 1.547‰
Candona neglecta	$S = 0.636$‰, 0.981‰
Candoniella lactea	$S = 0.981$‰. 3.251‰
Prionocypris gansenensis	$S = 3.335$‰
Eucypris gyirongensis	$S = 0.875$, 3.251, 3.335‰
Heterocypris incongruens	$S = 0.875$‰
Heterocypris salina	$S = 0.727$, 1.536, 3.251‰
Limnocythere inopinata	$S = 0.981$, 1.009, 3.335‰

Text-figure 2 shows that samples of genera and species with the highest diversity index could be found in waters whose salinity ranges from 0.5‰ to 1‰. This indicates that waters with this salinity are the most ideal for ostracod faunas.

Text-figure 3, however, shows that although waters with this salinity teem with the ostracod



Text-fig. 1—Map of sampling locations in the Qinghai Plateau.



TEXT-FIG. 2—Distribution of diversity index of ostracods in water of various salinity.

valves, the number of ostracod valves is not at its maximum. This is largely because these waters are mainly rivers which washed away most of the juvenile valves.

Ostracod genera and species in mesohaline waters were monotonous, but the number of individuals was large. According to sample analysis, the number of valves obtained from every 100 grams of bottom matters stands at some 70,000. Obviously, this is a specific environment. It was found that there were six genera and eight species in the waters with this salinity. They are: *Limnocythere inopinata* (the smooth type is the majority and the tuberculate type accounts for no more than 8/10,000), *Eucypris inflata* (G. O. Sars), *Cadoniella albicans, Candoniella lactea, Ilyocypris biplicata, Ilyocypris gibba, Potamocypris fulva, Subulacypris trapezoidea* sp. nov. Among them, *Limnocythere inopinata* and *Eucypris inflata* make up 96 percent of the members of this association. The remaining six were found sporadically in some river mouths, such as the mouths of the River Buh and River Aral. They were transported there by these rivers. Therefore, in waters with this salinity there were only *Limnocythere inopinata* and *Eucypris inflata,* or one of the two.

Few ostracod valves were found in the polyhaline, euhaline and ultrahaline waters, with the exception of Lake Yahu ($S = 48.46‰$) and Lake Sugan ($S = 36.3‰$). A total of 18–1160 *Eucypris inflata* valves, plus a few *Limnocythere inopinata* valves, were found in every 100 grammes of bottom matter taken from the two lakes. No ostracod valves were discovered in most of the other samples, except for a few juvenile ones washed in by river or lake waters.

Temperature

Little data about living ostracods and temperature are available, but judging from the taphocoenose members, the stenothermal cold-loving species and the eurythermal species were in the majority. The former includes *Candoniella lactea, Candona neglecta* and *Candona candida* (O. F. Müller). The latter includes *Limnocythere inopinata, Cyprideis littoralis* (Brady), *Cyclocypris serena, Cypridopsis vidua, Candoniella albicans* and others. While taking samples, Sun Zhengchen, my colleague, and I discovered dead *Ilyocypris biplicata* with appendages in a frozen pond (0.4 metres deep), which shows that the species was resistant to low temperature. Here are those live ostracoda (or ostracod samples with appendages) which we have managed to obtain together with data on temperature:

Eucypris gyirongensis	Bottom water temperature: 14° C
Candona neglecta	Silt temperature: 9° C, 11° C
Limnocythere inopinata	Silt temperature: 11° C
Candoniella lactea	Bottom water temperature: 14° C, 11° C
Heterocypris salina	Bottom water temperature: 14° C
Heterocypris incongruens	Bottom water temperature: 13° C
Ilyocypris biplicata	Silt temperature: 11° C
Cyclocypris serena	Silt temperature: 11° C
Candona houi	Silt temperature: 11° C

Thus far we have never found any live stenothermal warmth-loving species or their valves.

Bottom Matter

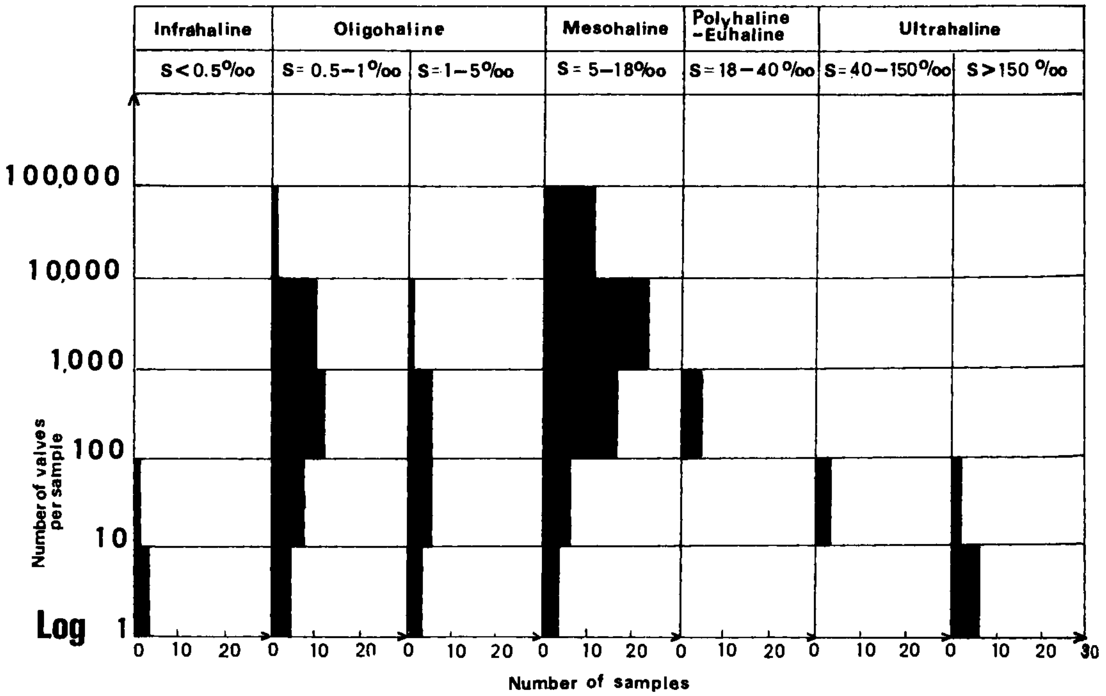
Most of the ostracod valves were discovered in samples of medium-fine sand, powdered sand and argillaceous sediments in this area. However, on water bottoms composed mainly of coarse sand or gravels, we found ostracod valves only from some samples of coarse sand, not from all the samples we examined. Judging from the available materials, *Eucypris gyirongensis, Subulacypris trapezoidea, Ilyocypris biplicata, Ilyocypris gibba* and *Potamocypris smaragdina* were concentrated on silt sand bottoms; while *Prionocypris gansenensis, Candona neglecta, Candoniella lactea, Limnocythere inopinata* and *Eucypris inflata* were scattered on powdered sand and fine sand or silt bottoms. Among them, bottom matter colonised by waterweeds contained more *Eucypris inflata* than other material.

Water Power

From the species discovered in the bottom matter samples, living Ostracoda live mainly in waters with weak water power conditions. According to the research of Wang, P. X., the ratio of carapaces to valves in the ostracod taphocoenose is in direct proportion to the speed of the deposit. The theory has been proved correct by materials available in this area. The carapaces to valves ratio becomes lowest in areas far away from the river mouths and in lakes which are pretty deep or have no compensation for their scarcity of water, such as southeastern Lake Qinghai where thousands of valves were found from the bulk of the samples with a 0 – 0.12 ratio of carapaces to valves. Judging from genera and species, those located in rivers with strong water power conditions include *Ilyocypris gibba, Ilyocypris biplicata, Potamocypris smaragdina, Eucypris gyirongensis, Subulacypris trapezoidea, Candona neglecta* and *Candoniella lactea.* In the relatively still swamps and ponds, *Candoniella lactea* and *Limnocythere inopinata* were in the majority, while *Heterocypris salina, Prionocypris gansenensis, Eucypris inflata, Candona neglecta, Candona candinda, Ilyocypris biplicata* and *Heterocypris incongruens* were in the minority.

Depth

The 27 metre deep Lake Qinghai is the deepest in the area while Lake Keluke is 18 metres deep.



TEXT-FIG. 3—Distribution of number of valves in water of varying salinity.

All the other lakes are pretty shallow. In Lake Qinghai, the diversity index of genera and species goes down with the deepening of the water (see Text-figs. 4 and 5). The carapace-valve ratio also reduces as the water deepens.

CHARACTERISTICS OF THE OSTRACOD TAPHOCOENOSE IN VARIOUS SEDIMENTARY ENVIRONENTS

Rivers

Braided streams on the upper reaches of the river

Characteristics of the association of genera and species: monotonous in species and few individuals.

Association:

Eucypris gyirongensis	common
Ilyocypris biplicata	common
Candona neglecta	rare
Heterocypris sp. (indet.)	rare

Diversity Index H(S)*: 0 – 0.80, averaging 0.45.

Carapace - Valve Ratio(%): very low, mostly zero.

Juv. - Adult Ratio: 0 – 1, averaging 0.32.

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* $H(S) = -\Sigma PiLnPi$

Valves Obtained From Every 100 grams of Bottom Matter Sample: 1–10.

Other Calcareous invertebrates and Oogonia of Charophytes Associated with Ostracoda: a few Gastropoda.

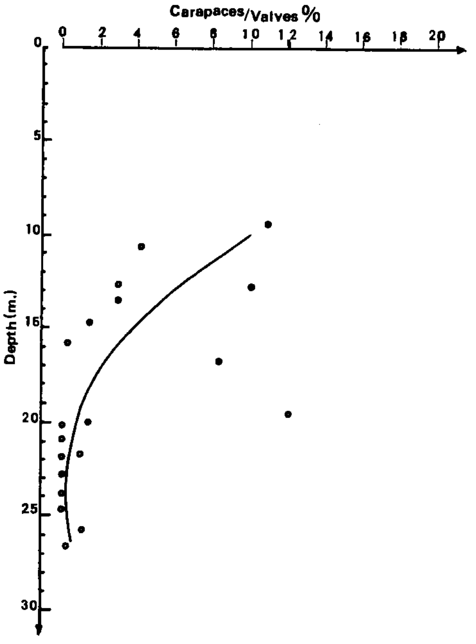
Meander streams on the middle reaches of the river

Characteristics of the association of genera and species: a variety of species and large numbers of individuals.

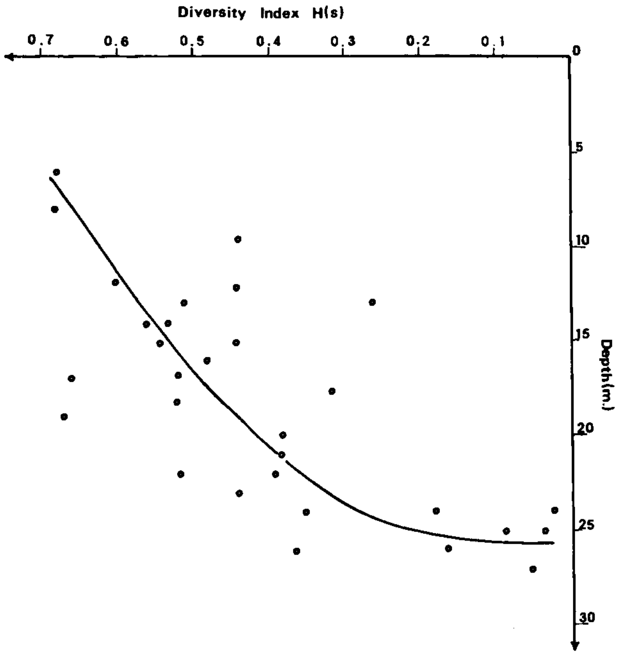
Association(%) (Obtained from 17 samples taken from the River Aral):

Eucypris gyirongensis	0–38.8, averaging 20.5
Ilyocypris gibba	
Ilyo. biplicata	3.5–33.3, averaging 17.2
Potamocypris smaragdina	0–56.3, averaging 17.6
Candona neglecta	
C. candida	3.7–33.3, averaging 17.6
Candoniella lactea	
C. albicans	8.3–26.3, averaging 13.3
Subulacypris trapezoidea	0–27.8, averaging 5.5
Limnocythere inopinata	0–6.6, averaging 1.6
Cypridopsis vidua	a few
C. aculeata	a few
Prionocypris gansenensis	a few
Heterocypris salina	a few
Potamocypris villosa	a few
Potamocypris fulva	a few
Eucypris moguntiensis	a few

In the branch streams on the lower reaches of the River Bayin, besides species similar to the above association members there were a small number of *Eucypris inflata, Cyprideis littoralis, Candona caudata, Candona marchica, Cyclocypiris serena* and *Pseudocandona* sp. (?).



TEXT–FIG. 4—Carapace - valve ratio in various water depths.



TEXT-FIG. 5—Diversity index in various water depths.

Diversity Index H(S): 0.7356–1.9884, averaging 1.6560 (middle reaches).
1.7276–2.2846, averaging 2.010 (lower reaches).

Carapaces - Valves Ratio: 0–5% (six samples), 6–10% (three samples), 16–48% (six samples).

Juv. - Adult Ratio: <1 (eight samples), 1–2 (seven samples), 3–3.3 (two samples).

The fairly low juvenile-adult ratio serves as an indication that most of the juveniles may have been washed away by rapid waters.

The number of valves obtained from every 100 grammes of bottom matter sample varies. Except in the case of a few samples, the general trend is an increase from the middle reaches to the lower reaches. For the River Aral the number of valves goes from 8 in the middle reaches to 300 in the lower reaches. The number of valves in the branch stream on the lower reaches of the River Bayin stands as high as some 1,300.

Other calcareous invertebrates and oogonia of charophytes associated with Ostracoda: large numbers of Gastropoda and some Chara.

River Mouths

Salinity in the river mouths in this area is higher than in the rivers because of the influence of the salt water lakes. For example, the salinity of the River Aral is less than 1‰, but in the area of the river mouth it goes up to 1.47–10.86‰. Therefore, the ostracod taphocoenose is different than that in the rivers.

Characteristics of the association of genera and species: a mixed feature shaped by two environments—river and lake.

Association:

Limnocythere inopinata (major member)
Candoniella lactea
Subulacypris trapezoidea
Potamocypris fulva
Potamocypris smaragdina
Heterocypris incongruens
Ilyocypris gibba
Ilyocypris biplicata
Eucypris inflata (River Buh's mouth)
Candoniella albicans (*ibid.*)
Prionocypris gansenensis (River Aral's mouth)
Eucypris moguntiensis (*ibid.*)
Candona candida(?) (*ibid.*)

Diversity Index H(S): 0.3186–2.0068, averaging 0.6123.

Carapaces-Valves Ratio: 0–67%.

Juv.-Adult Ratio: 0–0.6, very low.

Number of valves obtained from every 100 grammes of bottom matter sample: 2–1215.

Other calcareous invertebrates and oogonia of charophytes associated with Ostracoda: a small number of Chara and no Gastropoda.

Lakes

Shallow lake (0–12 metres deep)

Characteristics of the association of genera and species:

Infrahaline shallow lake – Ostracod material in this environment in this area is deficient.

Oligohaline shallow lake – A variety of species and a lot of individuals.

Mesohaline shallow lake – Monotonous in species and large numbers of individuals.

Polyhaline-Ultrahaline shallow lake – Monotonous in species and the number of individuals decreases as the salinity rises.

Association:

Oligohaline shallow lake – In this kind of lake there are mainly *Limnocythere inopinata, Candoniella lactea* and *Ilyocypris biplicata.* In addition, there are also *Candona neglecta, Eucypris moguntiensis, Ilyocypis gibba* and *Candona dandida,* plus a small number of *Eucypris inflata, Heterocypris salina, Prionocypris gansenensis, Candona houi* Huang, *Candona caudata, Cyclocypris serena, Cyprideis littoralis* and *Megazonocypris* sp. (indet.).

Mesohaline shallow lake – In this kind of lake there are almost only *Limnocythere inopinata* and *Eucypris inflata.* There are also a few *Candoniella albicans, Candoniella lactea, Ilyocypris biplicata, Ilyocypris gibba, Potamocypris fulva* and *Subulacypris trapezoidea.*

Polyhaline-Euhaline-Ultrahaline shallow lake – Only *Eucypris inflata* and *Limnocythere inopinata* occur, but the number of the latter plummets as the salinity rises.

Diversity Index H(S): Oligohaline shallow lake—0.78–1.45.
Mesohaline shallow lake—0.44–0.68.
Polyhaline-Ultrahaline shallow lake—<0.4.

Carapaces-Valves Ratio (%): Oligohaline shallow lake—1.1–6.7%.
Mesohaline shallow lake—0–11%. averaging 2.4%.

Juvenile-Adult Ratio: Oligohaline shallow lake—1.3–2, averaging 1.7.
Mesohaline shallow lake—18–42.

Number of valves obtained from every 100 grammes of bottom matter: Oligohaline shallow lake—376–17,626.

Measohaline shallow lake—3,065–69,748, averaging 59,089.

Other calcareous invertebrates and oogonia of charophytes associated with Ostracoda:

Oligohaline shallow lake—large numbers of *Chara* and a small number of Gastropoda and *Corbicula* sp.

Mesohaline shallow lake—a few *Chara*.

Mesohaline semi-deep and deep lake (upwards of 12 metres)

Ostracod material in infrahaline and oligohaline semi-deep and deep lakes in this area is deficient (the following therefore only concerns mesohaline semi-deep and deep lakes): monotonous in species, but an abundance of individuals.

Characteristics of the association of genera and species:

Association: only *Limnocythere inopinata* and *Eucypris inflata*.

Diversity Index H(S): 0.02–0.66.

Carapaces-Valves Ratio (%): 0–16, averaging 2.4%.

Juvenile-Adult Ratio: 12-very high (all are juveniles).

The number of valves obtained from every 100 grammes of bottom matter: 2,165–70,310, averaging 26,384.

Other calcareous invertebrates and oogonia of charophytes associated with Ostracoda: No *Chara* or molluscs.

Mud Lake Beaches

Characteristics of the association of genera and species: Close to oligohaline shallow lakes. Sometimes there are a small number. It varies greatly from time to time.

Association: Close to oligohaline shallow lakes. But there are a comparatively large number of *Prionocypris gansenensis*, *Heterocypris salina* and *Heterocypris incongruens*.

Diversity Index H(S): 0.45–1.81, averaging 0.99.

Carapaces-Valves Ratio (%): It varies. 0–140.

Juvenile-Adult Ratio: 0–7, averaging 1.2%.

The number of valves obtained from every 100 grammes of bottom matter: It varies. 33–3,008.

Other calcereous invertebrates and oogonia of charophytes associated with Ostracoda: Large numbers of *Chara* and a small number of Gastropoda.

GEOLOGICAL SIGNIFICANCE—INDICATOR ROLE OF THE ENVIRONMENT

According to the research of Zhao Xiulan and Zhu Zonghao on Tertiary spores and pollen, the Tertiary climate in this area was dry and arid. After the Oligocene Period, it became colder and colder so that the climate in the Tertiary Era in this area, especially during the Neogene was similar to the present climate. From this we may say that an analogy does exist between the sedimentary environment at present and the sedimentary environment in the Tertiary period. From the Principle of Uniformitarianism, it is safe to infer the ancient sedimentary environment from the association of ostracod fossils and the ostracod taphocoenose. The following points may be used to judge the palaeoenvironment.

Monotonous genera and species, low diversity index and small number of individuals—indicating upper reaches of the river when composed of the infrahaline or oligohaline species; indicating ultrahaline lakes when composed of the halophilous or euhaline species.

Monotonous genera and species, low diversity index and large number of individuals — indicating mesohaline lakes.

A variety of genera and species and large number of individuals — indicating the middle and lower reaches of the river when the Diversity Index H(S) is high, averaging 1.65–2.0; indicating the oligohaline shallow lakes when the Diversity Index H(S) is lower, averaging 1.0–1.4.

Carapace-Valve Ratio (%) — indicating river mouth when the ratio is high; indicating the middle and lower reaches of the river when the ratio is medium; indicating the upper reaches of the river or the lake when the ratio is low.

Juvenile-Adult Ratio — indicating the fact that they were moved here from other places or lakes when the ratio is extremely high; indicating rivers when the ratio is low.

Other Calcareous Invertebrates and Oogonia of Charophytes Associated with Ostracoda — indicating rivers when there are many Gastropoda; indicating oligohaline shallow lakes and mud beaches of lakes when there are large numbers of *Chara*; indicating mesohaline waters or waters with higher salinity when there are no *Chara* or Gastropoda (with the exception of the existence of *Lamprothamnium*, sp.).

DESCRIPTION OF NEW SPECIES

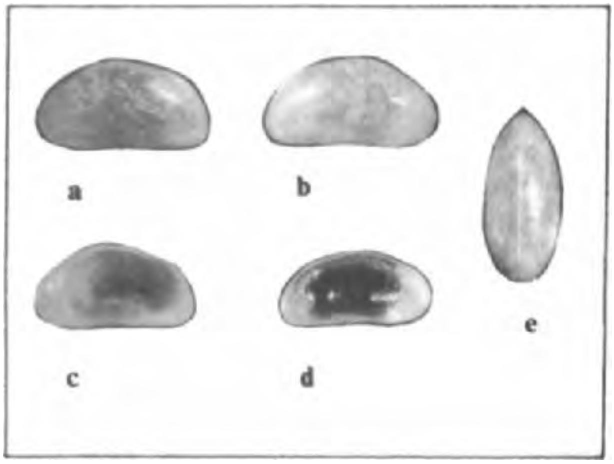
SUBULACYPRIS TRAPEZOIDES sp. nov.

(Text-figs. 6a–e)

Irregular trapezoidal in side view, highest at one-third of the length from the anterior and, whence it slopes down posteriorly; the two sides of the carapace look parallel in dorsal view. The duplicate is widest at about one-quarter the length of the carapace.

The new species and *S. subtilis* are alike, but the latter is shorter in width and higher in height. Holotype length; 690 μm; height: 360 μm; width: 310 μm.

Occurrence: Existing infrahaline-oligohaline river and lake sediments in the Qaidam Basin and the Lake Qinghai area.



TEXT-FIG. 6—*Subulacypris trapezoides* sp. nov. ×33. a, left outer view; b, right outer view of the same carapace; c, left inner view; d, right inner view; e, dorsal view.

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DISCUSSION

Hartmann: You used in your paper the term "living". How should this term be understood? Were the ostracods really living—that means "moving"? (Did they all have soft parts?)

Yang: The term "living" in my paper means "the ostracods were alive" or soft parts, mainly appendages, were preserved when I collected them.

McKenzie: Are comparable data available for your area in such groups as molluscs and dinoflagellates?

Yang: I've collected some molluscs such as genera *Gyraulus, Succinea. Galba* and *Corbicula* associated with the ostracods in oligohaline water bodies, especially in the Aral River, but no dinoflagellates have been found up to now. I have not yet studied these molluscs.

VI
Palaeoecology

The Iperk Sequence (Plio-Pleistocene) and its Ostracod Assemblages in the Eastern Beaufort Sea

QADEER A. SIDDIQUI
St. Mary's University, Halifax, Canada

ABSTRACT

Ostracods from the Iperk Sequence (Plio-Pleistocene) of five offshore wells in the Eastern Beaufort Sea have been shown to occur in four recognisable assemblages, three marine and one fresh water.

The wells, Adgo F-28, Netserk B-44 and F-40, Tarsiut A-25 and Nektoralik K-59 extend in a 110 km. (68 mile) line from south to north. The first four wells are close together on the continental shelf, but Nektoralik K-59 lies about twice as far from land.

The occurrences of certain typical species or genera, selected as indicators, have been tabulated to show the extent of the four assemblages. Nearly all of the taxa are still living.

The Iperk Sequence is the offshore equivalent of the Nuktak Formation of the MacKenzie Delta. It forms a thick lens-shaped deposit ranging in thickness from a few tens of metres in the south to about 5,000 metres in the north (Dietrich *et al.*, 1985). According to these authors the most rapid thickening of the sequence begins just north of the Tarsuit and Issungnak area.

The Cenozoic biostratigraphy based on Foraminifera has been worked out by MacNeil (1984, 1985). He found four foraminiferal assemblages from the Palaeocene to the Pleistocene; the Iperk Sequence asemblage is dominated by ***Elphidium*** spp., an euryhaline genus.

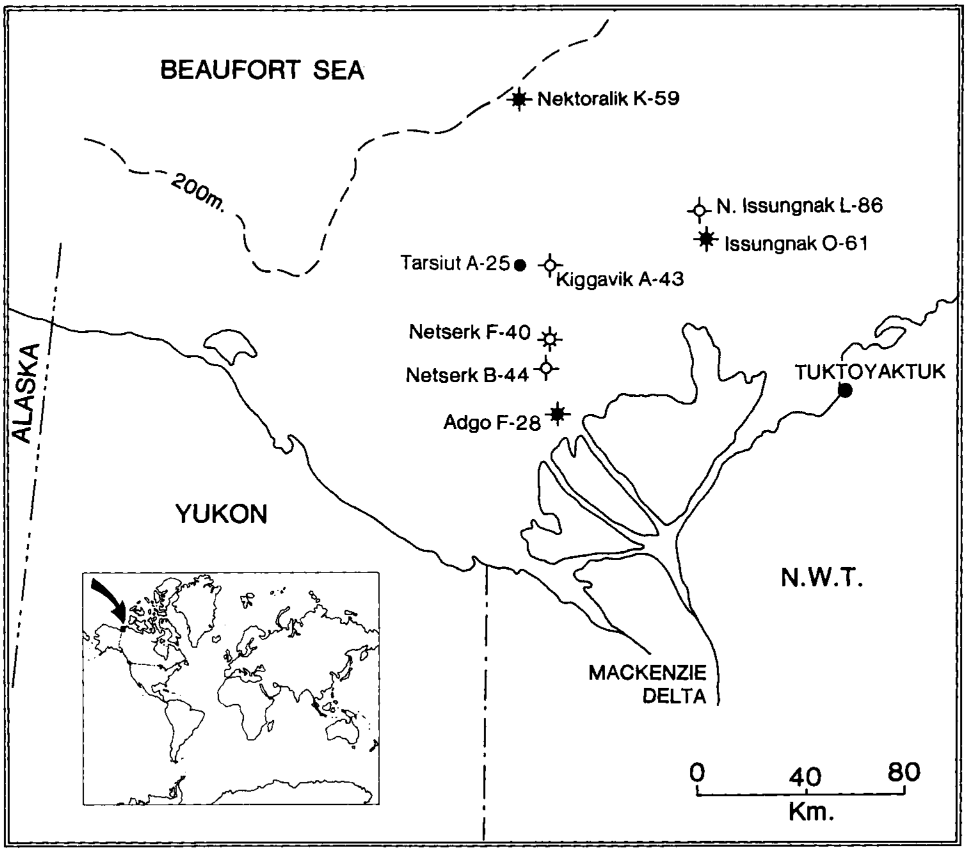
Organizations operating in the Eastern Beaufort Sea have provided samples from a number of wells in this area; these have yielded ostracod assemblages from the Iperk Sequence. The first conclusions based on material from five of these wells are presented in this paper.

The five wells were selected because they lie in a roughly south to north line from the coast near the MacKenzie Delta and so represent a series of sections through the Iperk Sequence (Text-fig. 1). The wells are:

Adgo F-28	Lat. 69° 27′ 16.6″ N	Long. 135° 51′ 15.8″ W
Netserk B-44	// 69° 33′ 03.0″ N	// 135° 55′ 56.0″ W
Netserk F-40	// 69° 39′ 22.7″ N	// 135° 54′ 21.0″ W
Tarsiut A-25	// 69° 54′ 10.0″ N	// 136° 20′ 20.0″ W
Nektoralik K-59	// 70° 28′ 35.9″ N	// 136° 16′ 59.0″ W

Nektoralik K-59 is twice as far from the Delta as Tarsiut and is situated on what was probably the edge of the continental shelf in Plio-Pleistocene times.

The general topography and the benthonic environment of this area are thought to have been much the same since Plio-Pleistocene times, the environment always having been harsh. During



TEXT-FIG. 1—Location map of the five wells and others in the Eastern Beaufort Sea. Inset map shows location of this area.

periods of glaciation, part of the shelf was exposed, ice-scoured and depopulated. During warmer periods the benthonic climate was characterised by annual swings in temperature and salinity, and the bottom was subject to ice gouging and rafting; such conditions become more extreme as the water becomes shallower towards land. Bernard (1979) summarizes the probable early environment from the biological point of view in a publication on bivalve molluscs in the Western Beaufort Sea. He suggests that the fresh water outflow of the MacKenzie River acts as a barrier to migration of benthonic species from east or west. It is not clear yet if this is true for ostracods and foraminifers; records so far suggest that it is not.

The ostracod fauna from these wells was identified; it comprised some 36 taxa, 26 of them forming a typical marine shelf assemblage dominated by *Heterocyprideis sorbyana, Paracyprideis pseudopunctillata* and *Rabilimis septentrionalis*. These are all tolerant of low salinity and range in depth from a few to at least 200 metres.

This agrees with what McNeil has reported for the foraminiferal assemblages of the Iperk Sequence. However, in addition to the marine species, there were about ten ostracod taxa from fresh water.

Once identified, the genera and species were grouped according to their known habitat preferences; this could be done with confidence because most are still living in the area. In addition,

TABLE 1—OCCURRENCE OF OSTRACOD ASSEMBLAGES IN FIVE BEAUFORT SEA WELLS: ADGO F-28, NETSERK B-44, NETSERK F-40, TARSIUT A-25, NEKTORALIK K-59. (LEGEND: F = fresh water; R = reduced salinity and depth; T = tolerant; M = marine; D = deep marine assemblages).

SEA LEVEL		ADG. F-28 FRTM	NET. B-44 FRTM	NET F-40 FRTM	TAR A-25 FRTMD	NEK K-59 FRTM
Ft.	M.					
			RTM	R		
		R	TM	T		
		R	F TM	FRT		
500		TM	RT	FRT	F TM	
		FRT	FRTM	F T	T	
		F T	F T	F T	TM	
		F T	F T	FRTM	FR	
		F T	RTM	FRTM	TM	
1000		F T		FRTM	FRTMD	
		T	FRT	T	RTM	
		T	F T	FRT	TM	TM
				F T	T	TM
		T	F TM	FRT	F TM	TM
1500			F TM		TM	TM
		T	F	T	T	RT
	500	T	F M	F T	RTM	RTM
		TM	TM	T		T
				TM	TM	TM
2000				F TM	T	T
				TM		
						TM
		T		TM		
					D	T
2500					D	TM
						T
		T				
3000						
	1000					M
		T				
3500						
4000						
4500						
5000	1500					M
5500						
						M

their ecology was discussed with W.M. Briggs, E.M. Brouwers, U.M. Grigg and R.M. Forester, who are familiar with recent marine and fresh water benthonic ostracods from this region. The material was easily divisible into four assemblages; three of these were marine, but the fourth, presumably derived, was from fresh water.

In order to simplify the data, the commonest species from each assemblage were selected as indicators of the presence of that assemblage. Any sample in which an indicator occurred was then plotted on a graph showing the locality and depth (Table 1).

In such an environment one might expect to find that the commonest species are those which are tolerant of the harsh and variable conditions inshore while also occurring in marine conditions on the continental shelf. From there replacements would be available to repopulate inshore areas where the fauna had been wiped out. In fact, the tolerant marine assemblage does contain the largest number of both species and specimens. The species selected as indicators are still abundant in modern benthonic samples (Briggs, Brouwers, Grigg, pers. comm.).

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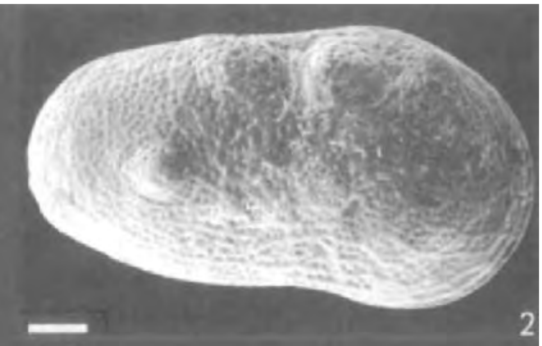

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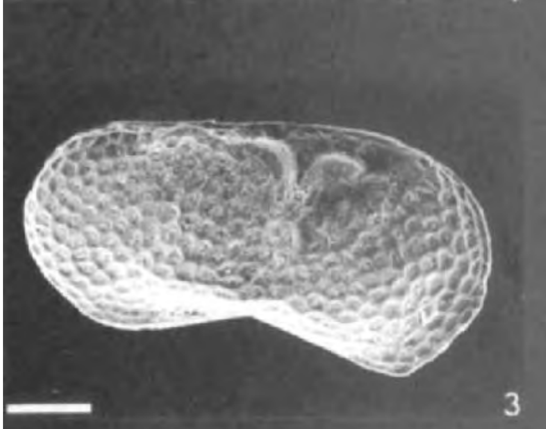

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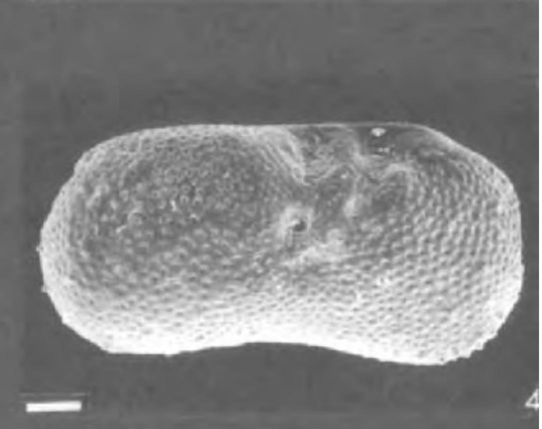

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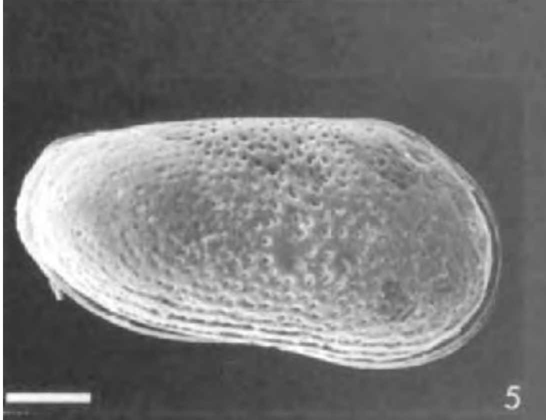

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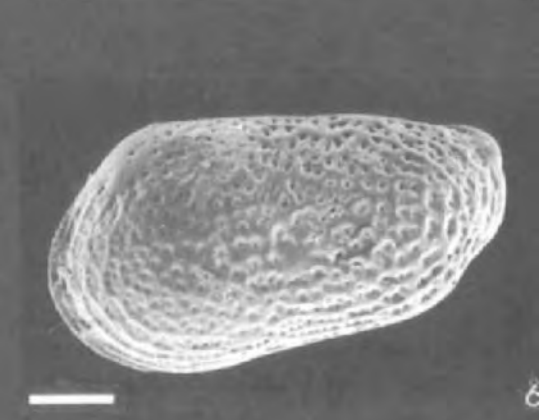

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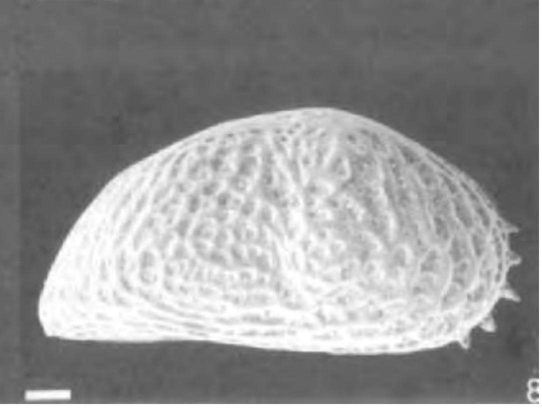

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The indicator species are:

Heterocyprideis sorbyana (Jones, 1865)
Paracyprideis pseudopunctillata Swain, 1963
Rabilimis septentrionalis (Brady, 1866)
Cytheretta teshekpukensis Swain, 1963
Sarsicytheridea bradii (Norman, 1865)

Of the other two marine assemblages, the inshore one contains few species, associated with shallow depths and reduced salinity.

The indicator species are:

Cytheromorpha macchesneyi (Brady and Crosskey, 1871)
Pteroloxa cumuloidea Swain, 1963

The offshore marine assemblage is defined as that in which the species are associated with marine salinities and sublittoral depths.

The indicator species are:

Cytheropteron spp.
Krithe glacialis (Brady, Crosskey and Robertson, 1874)
Rabilimis mirabilis (Brady, 1868)
Rabilimis paramirabilis (Swain, 1963)

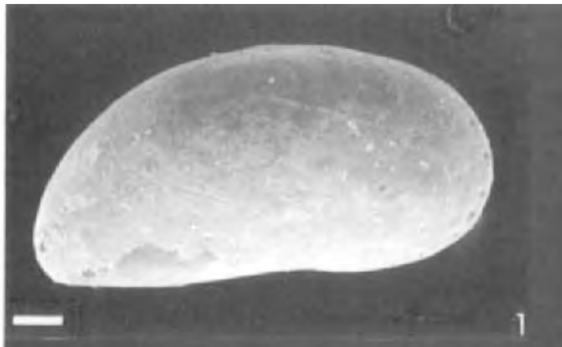
Fresh water ostracods found in these wells were presumably derived from the adjacent land drainage, especially the MacKenzie River system. All the genera represented were used as indicators of the fresh water assemblage; these are:

Candona spp.
Cytherissa sp. (*C. lacustris* (Sars, 1863))
Ilyocypris sp. (*I. bradyi* Sars, 1890)
Limnocythere spp.

The occurrences of these four assemblages, fresh water (F), inshore with reduced salinity (R), tolerant (T), and marine or offshore (M), in the five wells are shown in Table 1. The distances between the wells, from Adgo F-28 on the left, the most southerly, to Nektoralik K-59 on the right, the most northerly, are represented at approximately their actual distance apart. Depths are represented in 100 foot steps below sea level.

The tolerant assemblage occurs in all five wells and is the most prominent component in Adgo F-28. The marine assemblage increases in importance from Adgo F-28, where it is sparsely represented, to Tarsiut A-25 and Nektoralik K-59, in the latter of which it is the predominant component of the ostracod fauna. Conversely, the fresh water assemblage is present between 600 and 2000 feet in the three inshore wells, occurs sparsely between 500 and 1400 feet in Tarsiut A-25, and is absent from Nektoralik K-59, the furthest well from land.

PLATE 1—Fig. 1. *Candona rawsoni* Tressler, female left valve, GSC 68784, length 1220 μm, Netserk B-44, 1230 ft. below K.B. Fig. 2. *Cytherissa lacustris* (Sars), right valve, GSC 68785, length 860 μm, Netserk B-44, 1050 ft. below K.B. Fig. 3. *Limnocythere reticulata* Sharpe, right valve, GSC 68786, length 580 μm, Kiggavik A-43, 1246 ft. below K.B. Fig. 4. *Ilyocypris bradyi* Sars, right valve, GSC 68787, length 890 μm, Netserk B-44, 1230 ft. below K.B. Fig. 5. *Cytheromorpha macchensneyi* Brady and Crosskey, male carapace, right GSC 68788, length 580 μm, Netserk B-44, 470 ft. below K.B. Fig. 6. *Pteroloxa cumuloidea* Swain, male left valve, GSC 68789, length 530 μm, Netserk B-44, 230 ft. below K.B. Fig. 7. *Cytheretta teshekpukensis* Swain, right valve, GSC 68790, length 1110 μm, Netserk B-44, 590 ft. below K.B. Fig. 8. *Heterocyprideis sorbyana* (Jones), female right valve, GSC 68791, length 980 μm, Netserk B-44, 590 ft. below K.B.
(The bars on the figures represent 100 microns).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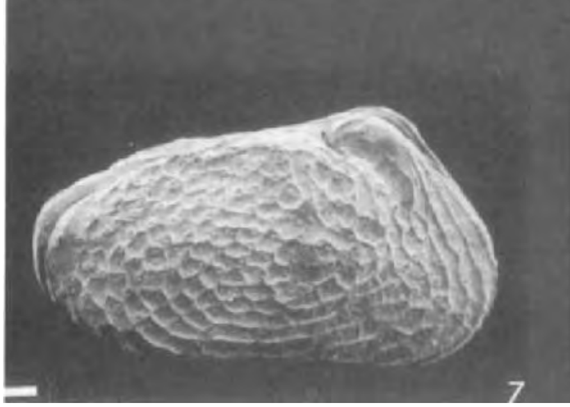
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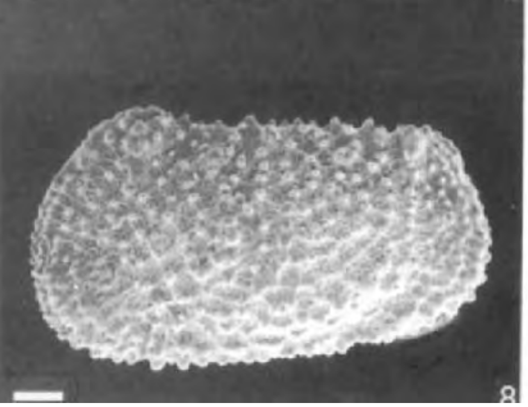
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The coastal assemblage is present in all five wells; it is not found abundantly anywhere, and is least well represented in Nektoralik K-59.

Tarsiut A-25 is the most difficult well to interpret. Perhaps an unusual amount of reworking has occurred in this area, for the occurrence of coastal and fresh water species is discontinuous. However, at 2500–2600 feet Tarsiut A-25 contains a very few speciments of an outer shelf marine assemblage (D in Table 1) characterised by *Henryhowella* sp. and *Muellerina abyssicola,* which may represent an older deposition. If so, the disconcerting appearance of a single valve of *Henryhowella* sp. at 1000 feet may be due to reworking; it is impossible to say. Another well in this area, Kiggavik A-43, has a few specimens of assemblage D at 2800, 3100 and 3900 feet. None of this assemblage has been found in Nektoralik K-59 in spite of the depth of that well; if it does represent an older fauna, its absence from Nektoralik K-59 might be explained by the much greater thickness of the Iperk Sequence at that site.

Although the material is scanty and has been reworked, it seems that the depositional environment of the Iperk Sequence can still be deduced from the assemblages of ostracods found there. If so, the distribution records of ostracods in the other wells from which samples have been obtained should combine to enhance understanding of this period considerably.

The specimens illustrated in this paper are deposited in the collection of the Geological Survey of Canada, Ottawa.

ACKNOWLEDGEMENTS

The ostracod material which formed the basis of this study was provided by Esso Resources Canada Ltd., Institute of Sedimentary and Petroleum Geology and Scott Geological Services, all from Calgary, Alberta. The author was fortunate to discuss this material with W. M. Briggs, Jr., E. M. Brouwers, and R. M. Forester. D. H. McNeil provided information on the stratigraphy of this area. U. M. Grigg read the manuscript.

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PLATE 2—Fig. 1. *Paracyprideis pseudopunctillata* Swain, male right valve, GSC 68792, length 880 µm, Netserk B-44, 350 ft. below K.B. Fig. 2. *Rabilimis septentrionalis* (Brady), female right valve, GSC 68793, length 1310 µm, Netserk B-44, 540 ft. below K.B. Fig. 3. *Sarsicytheridea bradii* (Norman), female right valve, GSC 68794, length 910 µm, Netserk B-44, 590 ft. below K.B. Fig. 4. *Cytheropteron montrosiense* Brady, Crosskey and Robertson, right valve, GSC 68795, length 490µm, Netserk B-44, 350 ft. below K.B. Fig. 5. *Krithe glacialis* Brady, Crosskey and Robertson, female left valve, GSC 68796, length 910 µm, Nektoralik K-50, 1400 ft. below K.B. Fig. 6. *Rabilimis mirabilis* (Brady), carapace right, GSC 68797, length 1170 µm, Nektoralik K-59, 1770 ft. below K.B. Fig. 7. *Rabilimis paramirabilis* Swain, male carapace, right GSC 68798, length 1220 µm, Netserk B-44, 1650 ft. below K.B. Fig. 8. *Henryhowella* sp, left valve, GSC 68799, length 880 µm, Kiggavik A-43, 2772-2788 ft. below K.B.
(The bars on the figures represent 100 microns.).

DISCUSSION

Cronin: What are the oldest occurrences of *Heterocyprideis sorbyana* and *Cytheromorpha macchesneyi*?

Siddiqui: *Heterocyprideis sorbyana* is one of the commonest ostracods in the Iperk Sequence. In several wells it occurs all the way down to the bottom at more than 3000 feet. The actual age of the Sequence at this depth is not known, but is most likely to be Pliocene (Dietrich *et al.*, 1985). *H. sorbyana* is present from the first appearance of this fauna.

Cytheromorpha macchesneyi only occurs infrequently, always in the top thousand feet in a few wells.

Hazel: Do you not find *Rabilimis paramirabilis* occurring before the other *Rabilimis* in the section? My report of it in the Recent off Alaska in 1967 was a clerical error. Its first and last occurrences are probably both good biostratigraphic data, although we don't know what the relationship of these are to the true Pliocene-Pleistocene boundary. *Rabilimis paramirabilis* may be the ancestor of both the shallow water form *R. septentrionalis* and the deeper form. *R. mirabilis.*

Siddiqui: No, I do not find *Rabilimis paramirabilis* occurring before the other *Rabilimis* species in the section. I have no evidence to suggest that it is ancestral to the other *Rabilimis* species; however, the Iperk Sequence is not perhaps the best formation for elucidating these relationships.

Plio-Pleistocene Ostracods from the Sogwipo Formation, Cheju Island, Korea

KWANG-HO PAIK AND EUI-HYEONG LEE
Korea University, Seoul, Korea

ABSTRACT

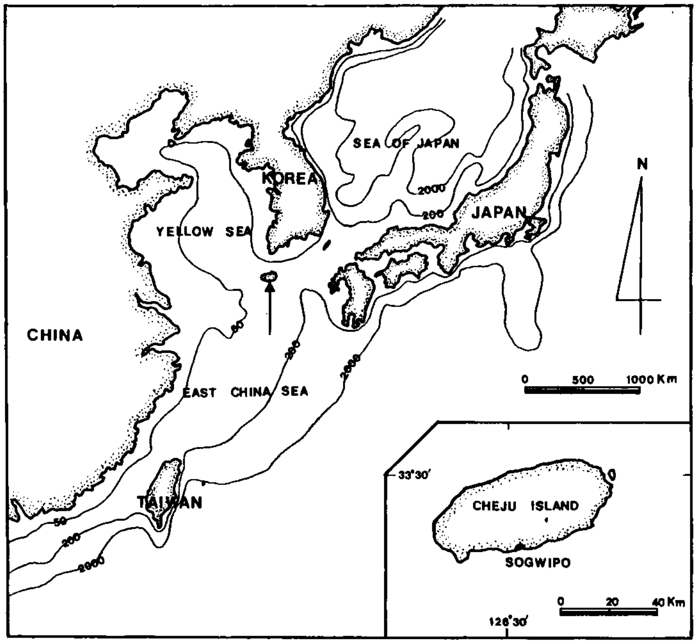
As a unique uplifted outcrop in the Yellow Sea and northern East China Sea, the Sogwipo Formation provides an unusual opportunity to study the palaeoceanographic history in this region during late Cenozoic time. It measures about 54 metres in thickness under the overlying volcanic complex and is characterised by near-shore, lagoon, barrier bar, offshore, tuffaceous sand, and volcanic conglomerate facies in ascending order. From nine samples taken from the lower half of the formation, 124 ostracod species belonging to 58 genera were recovered. The vertical occurrence data show that the palaeoenvironment of the formation varied from bay to open sea, was strongly influenced by a warm current and finally filled with volcanic sediments. The geological age of the formation is tentatively regarded as Plio-Pleistocene.

INTRODUCTION

The Sogwipo Formation, which is distributed in a narrow belt along the southern coast of Sogwipo City, Cheju Island is one of the important fossiliferous outcrops in Korea (Text-fig. 1). Cheju Island is located at the centre of the East Asian Continental Margin and at a point where the Kuroshio Current bifurcates, one branch flowing northward into the eastern Yellow Sea and the other through the Korean and Tsushima straits between the Korean Peninsula and Japan. The palaeontological study of the formation is, therefore, of great value in understanding the late Tertiary and Quaternary palaeoceanographical and tectonic history of the area.

Palaeontological studies of the formation have been made by several workers; in 1923, Yokoyama first reported Pliocene molluscan fossils from the formation. Haraguchi (1931) collected a prolific fauna of molluscs, brachiopods, echinoids, corals and fish teeth and considered its age to be Pleistocene. Recently, Kim (1972) recovered 72 species of benthonic and 18 species of planktonic foraminifers and concluded that the formation was Pliocene in age. No systematic study on its ostracod fauna has yet been made.

The purpose of the present study is firstly to record the fossil ostracod fauna of the formation and secondly to deduce the palaeo-environment and geological age of the formation.



TEXT-FIG. 1—Map showing the location of Cheju Island and the Sogwipo Formation.

MATERIAL

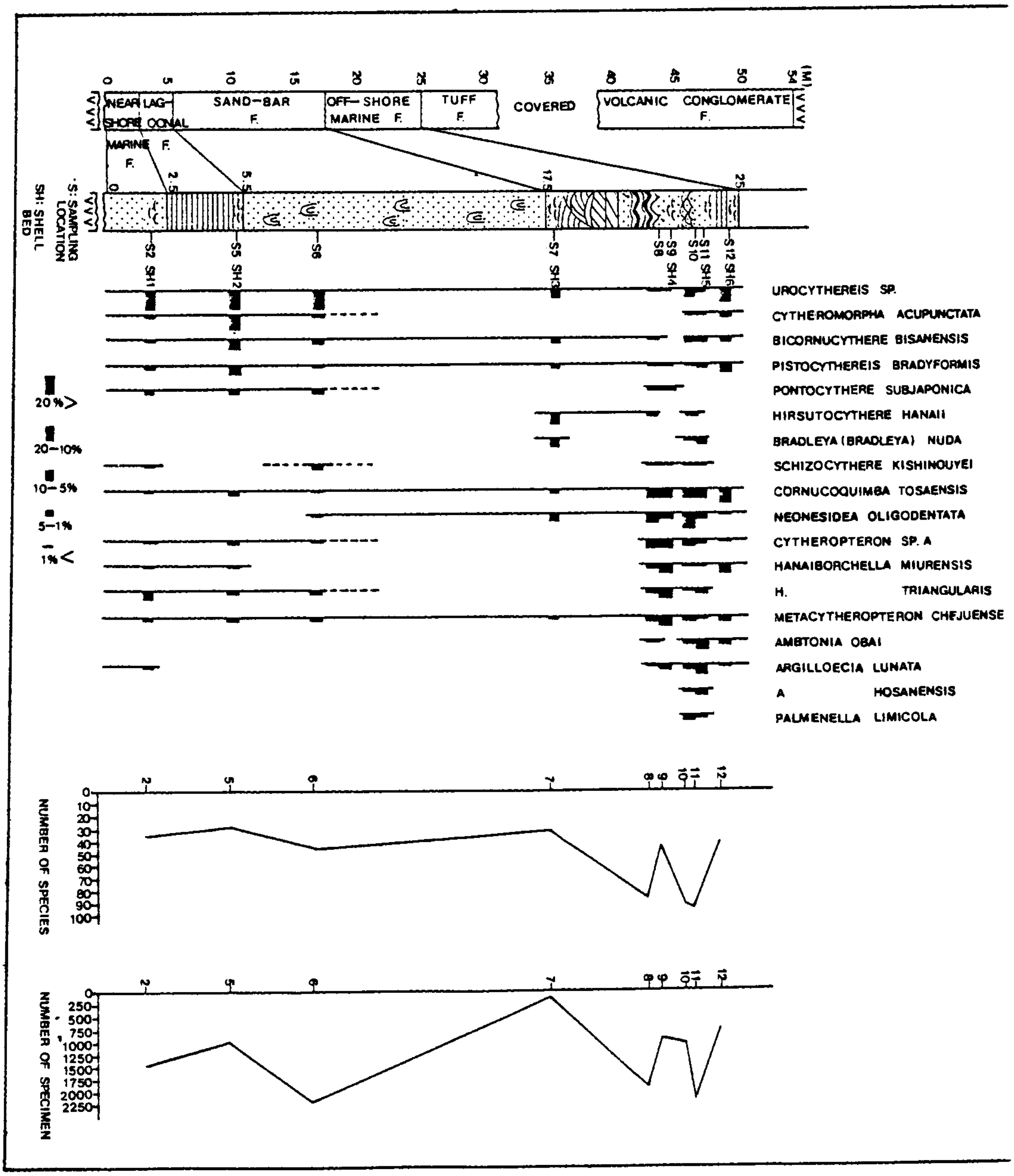
All of the samples used in this study were collected at the type locality in February, 1982 and in February, 1985 by the writers. A stratigraphical section was measured and 9 samples containing abundant ostracods were selected for the study (Text-fig. 2). In general 40-100 grams of dry material were taken from each rock sample and processed for the ostracod analysis. The gasoline method of Ferguson (1968) was modified by the writers and employed to disintegrate the samples. In washing, a 60-mesh screen (250 μm opening) and a 230-mesh screen (63 μm opening) were used. Ostracod species were identified from the published literature and from collections made from the sea floor around the Korean peninsula. Species counts were made for each sample, but adult and juvenile specimens were not differentiated.

SOGWIPO FORMATION

The Sogwipo Formation is exposed in a sea cliff, west of Sogwipo harbour. The extent of the formation is restricted to a narrow 1-km long belt along the coast. It overlies a volcanic lava flow and is overlain by a thick Quaternary basalt flow which forms the basement of Mt. Halla on the volcanic island of Cheju-Do. Unfortunately, the lowermost part of the formation is hidden under the sea. Thus the writers measured only the 50 metre thick section from sea level to the top of the sedimentary beds.

The formation strikes N 10° W and dips 8° to the west. It consists mainly of fine to coarse, light-grey sandstone but has occasional intercalations of siltstone and shale. Its characteristic structures are cross bedding, ripple marks, wavy bedding, worm burrows and other bioturbated structures suggesting shallow water conditions.

According to the nature of the sediments, six facies and six fossiliferous shell beds were identified. The section measured by the authors is given below and illustrated in Text-fig. 2.



Text-fig. 2—Sediment facies, stratigraphical distribution and relative abundance (%) of 18 dominant ostracod species from the measured section of the Sogwipo Formation.

6. Volcanic conglomerate facies	coarsening upward, overlain by basaltic lava flow	17 m
	————covered————	6 m
5. Tuffaceous sand facies	light grey, massive fine sandstone	6 m
4. Off-shore marine facies	wavy bedded, wave ripple laminated, trough cross-bedded, pebbly and coarse sandstone; well laminated, in the uppermost part fine to medium sandstone with 4 shell beds (3, 4, 5 and 6)	13.3 m
3. Sand bar facies	massive, well sorted, highly bioturbated, clean, light-grey sand	9.5 m
2. Lagoonal facies	well laminated, dark grey mudstone and fine sandstone with 1 shell bed (2)	3.0 m
1. Near-shore marine facies	alternating brown medium sandstone and grey coarse sandstone with 1 shell bed (1)	2.5 m

Six horizons with a prolific macrofossil fauna are used as marker beds for measuring and sampling. It is noteworthy that the samples taken adjacent to the shell beds yield abundant ostracod specimens.

Shell Bed 6	coarse, light-grey sandstone	0.3 m thick
Shell Bed 5	coarse, brownish-yellow sandstone	1 m
Shell Bed 4	coarse, light-grey sandstone with rounded basalt granules	2.5 m
Shell Bed 3	pebbly to coarse sandstone with rounded basalt pebbles	1 m
Shell Bed 2	fine to medium, light-grey sandstone	0.6 m
Shell Bed 1	poorly stored, medium to fine, light-brown sandstone	1 m

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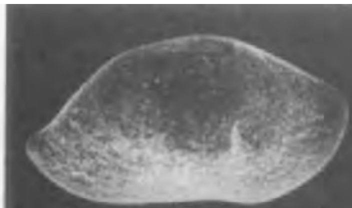
Plate 1—Fig. 1. *Neonesidea oligodentata* (Kajiyama, 1913). Lateral view of right valve (PLKU-O-301). Fig. 2. *Argilloecia* sp. [see Choe, 1985]. Lateral view of left valve (PLKU-O-302). Fig. 3. *Argilloecia lunata* Frydl, 1982. Lateral view of left valve (PLKU-O-303). Fig. 4. *Pontocythere subjaponica* (Hanai, 1959). Lateral view of right valve (PLKU-O-304). Fig. 5. *Pectocythere* sp. A. Lateral view of left valve (PLKU-O-305). Fig. 6. *Munseyella hatatatensis* Ishizaki, 1966. Lateral view of right valve (PLKU-O-306). Fig. 7. *Munseyella oblonga* Chen, 1982. Lateral view of left valve (PLKU-O-307). Fig. 8. *Munseyella oborozukiyo* Yajima, 1982. Lateral view of left valve (PLKU-O-308). Fig. 9. *Callistocythere reitculata* Hanai, 1957. Lateral view of left valve (PLKU-O-309). Fig. 10. *Callistocythere subjaponica* Hanai, 1957. Lateral view of left valve (PLKU-O-310). Fig. 11. *Callistocythere tateyamensis* Frydl, 1982. Lateral view of left valve (PLKU-O-311). Fig. 12. *Callistocythere undulatifacialis* Hanai, 1957. Lateral view of right valve (PLKU-O-312). Fig. 13. *Cythere* sp. Right valve view of carapace (PLKU-O-313). Fig. 14. *Schizocythere hatatatensis* Ishizaki, 1966. Lateral view of left valve (PLKU-O-314). Fig. 15. *Schizocythere kishinouyei* (Kajiyama, 1913). Lateral view of right valve (PLKU-O-315). Fig. 16. *Hanaiborchella miurensis* (Hanai, 1970). Left valve view of carapace (PLKU-O-316). Fig. 17. *Hanaiborchella triangularis* (Hanai, 1970). Lateral view of left valve (PLKU-O-317). Fig. 18. *Hanaiborchella* sp. Left valve view of carapace (PLKU-O-318). Fig. 19. *Palmenella limicola* (Norman, 1865). Left valve view of carapace (PLKU-O-319). Fig. 20. *Spinileberis* sp. Lateral view of left valve (PLKU-O-320). (bar = 100 μm)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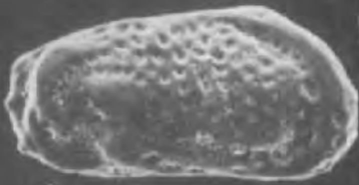
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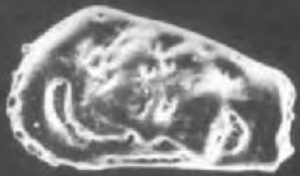
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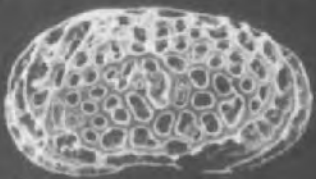
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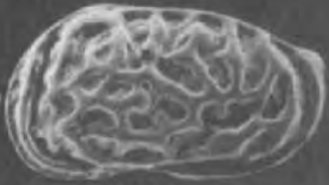
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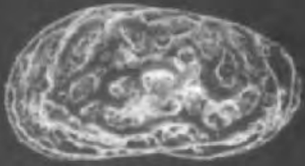
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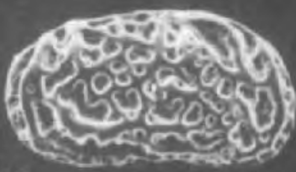
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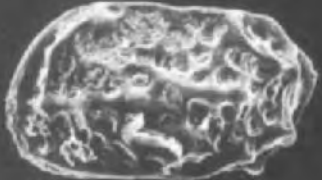
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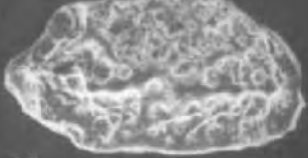
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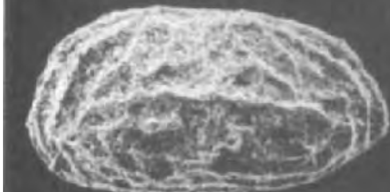
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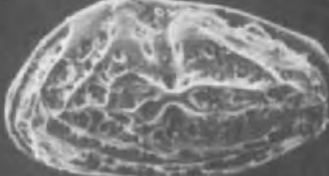
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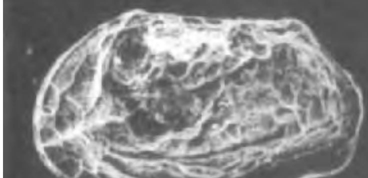
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OSTRACOD ASSEMBLAGE

A total of 124 species belonging to 58 genera was recovered from the 9 samples of the measured section. The number of ostracod specimens per 100 grams of rock samples ranges from 173 to 2221; the maximum number occurs in sample no. 11 from the fine-grained, light-grey sandstone, whereas the minimum number occurs in no. 7 from the pebbly sandstone, presumably caused by bad preservation. The number of ostracod species ranges from 28 in sample no. 5 to 95 in sample no. 11. The vertical distribution and population composition of Sogwipo ostracods are given in Table 1.

TABLE 1—RELATIVE ABUNDANCE(%) AND DISTRIBUTION OF OSTRACODS FROM THE SOGWIPO FORMATION

Species Sample number	2	5	6	7	8	9	10	11	12
Neonesidea oligodentata (Kajiyama, 1913)			*	5.8	7.6	4.1	10.7	2.8	*
Macrocypris sp.					1	1.1	1.3	2	
Propontocypris (*Propontocypris*) sp. A					*		*	*	*
P. (*P.*) sp. B					*		*	*	
Argilloecia lunata Frydl, 1982	*				*	1.1	2.4	6.6	*
A. sp. [see Choe, 1985]							*	1.1	
Paracypris sp.			2.1	*	*		*	*	
Pontocythere subjaponica (Hanai, 1959)	2.1	2	6.9		*	*			
Krithe sp.				2.2					
Parakrithella pseudadonta (Hanai, 1959)							*		
Pectocythere sp. A	11.8	1.5	4.2		*		*	*	
P. sp. B	*				*	1.1	*	*	
P. sp. C								*	
Munseyella hatatatensis Ishizaki, 1966		1	*		*		*	*	*
M. japonica (Hanai, 1957)					1.1		*		
M. oblonga Chen, 1982	*		*		1.4	1.9	*	*	3
M. oborozukio Yajima, 1982						*	*	2.1	
Eucythere sp.			*		*	*	*	*	
Callistocythere reticulata Hanai, 1957	1	*	*		*	*	1.1	*	*
C. subjaponica Hanai, 1957							*	*	
C. tateyamensis Frydl, 1982	2.7	1.2	*		*	2.6			
C. undata Hanai 1957								*	
C. undulatifacialis Hanai, 1957							*	*	2.2
C. sp.					*			*	
Cythere sp.			5	5.1	*	*	1.9	1	1.1
Schizocythere hatatatensis Ishizaki, 1966	*		3.7		*	*	*	*	
S. kishinouyei (Kajiyama, 1913)	5.4	*	2.5	3.6	6.6	12.2	4.8	3	7.1
Hanaiborchella miurensis (Hanai, 1970)	1.8	1			1.1	7.5	*	*	1.7
H. triangularis (Hanai, 1970)	9	2	2.3		2.8	6.7	*	1.3	
H. sp.			6						
Palmenella limicola (Norman, 1865)							1	*	
Spinileberis sp.			1						
Aurila corniculata Okubo, 1980		*	2.9	5.8	4.4	4.7	5.7	4.3	5.2
A. hataii Ishizaki, 1968		*	*		*		1.1	*	*
A. uranouchiensis Ishizaki, 1968	*	3.7	2.1	3.6	3.5	2.8	1.2	1	5.8
A. sp. [see Choe, 1985]	*	*	*	1.5	2.2	2.2	1.2	*	
A. sp. A				1.5	1.7	*	2.5	1.2	1.4
A. sp. B					*		*	*	
A. sp. C	*		*	4.4	5.2	2.4	6.7	2.1	1.4
Mutilus assimilis (Kajiyama, 1913)		*			*		*	*	

(*Continued*)

TABLE 1—*Continued*

Species Sample number	2	5	6	7	8	9	10	11	12
Pseudoaurila japonica (Ishizaki, 1968)							*	*	
Pokornyella sp.					*		*	*	*
Finmarchinella (*F.*) *uranipponica* Ishizaki, 1969				•					
F. (*F.*) sp. [see Choe, 1985]			3.6		*	*	*	*	
F. (*Barentsovia*) *japonica* (Ishizaki, 1966)	1.3	1	4.4		*	*	*	*	1.7
Urocythereis sp.	27.3	30.5	23.4	9.4	*	*	7.1	2.9	15.1
Ambostracon ikeyai Yajima, 1978	•				*	*	*	*	
Cornucoquimba tosaensis (Ishizaki, 1968)	*	3.9	*	4.4	8.9	6.9	5.7	7.6	16.5
C. sp. A					*		*	*	
C. sp. B							1.3		
Bradleya (*Bradleya*) *nuda* Benson, 1972				7.3			*	1	
Trachyleberis scabrocuneata (Brady, 1880)					*		*	*	
T.? *tosaensis* Ishizaki, 1968					*		*	*	
T. sp. A	1.4			6.5	3.2	1.3	•	7.3	2.8
T. sp. B	6.4	8.9	2.4	2.9	1.4	*	2	2.9	2.2
T. sp. C					3.2		1.3	1.2	*
T. sp. D					•			*	
T. sp. E					1			*	
Actinocythereis sp.	1		*		*	*	*	*	
Acanthocythereis munechikai Ishizaki, 1981				3.6	*				
A.? *mutsuensis* Ishizaki, 1971								*	
Hirsutocythere hanaii Ishizaki, 1981				8.7	*		*		
Ambtonia obai (Ishizaki, 1971)					*		1.6	7	1.9
Pacambocythere japonica (Ishizaki, 1968)						*	*	*	
Stigmatocythere sp.				1.5	*				
Pistocythereis bradyformis (Ishizaki, 1968)	1.3	7.1	*	2.9	*	*	*	1.2	5
Amphileberis nipponica (Yajima, 1978)	10.3		*	2.2	1.1	*	2.8	4.9	2.2
Bicornucythere bisanensis (Okubo, 1975)	*	9.6	4	2.9	*		2.8	3.3	2.5
Bythocythere exornata Gou, 1983		*	3.7		*				
Bythoceratina sp. [see Choe, 1985]					*	*	*	*	
B. sp. [see Choe, 1985]		*		*	*		*	*	
B. hanaii Ishizaki, 1968	*		*	*	*	2.4	1.2	*	*
B. sp. A					*	*	*		
B. sp. B					*				
B. sp. C							*		
B. sp. D								•	
Eucytherura utsusemi Yajima, 1982					*			*	
Hanaiceratina sp.					*		*		
Hemicytherura cuneata Hanai, 1957					1	1.7	*	1.3	3.3
H. sp. [see Choe, 1985]								*	1.1
H. sp. A	•		1.9						
H. sp. B					*		*	*	
Semicytherura henryhowei Hanai and Ikeya, 1977			*		•		*	*	
S. minaminipponica Ishizaki, 1981					*		*	*	
S. sp. A					*		*	*	
S. sp. B			*		*		*	*	
S. sp. C								*	*
S. sp. D					*		*		
S. sp. E							*	*	
S. sp. F					*		*	*	

(*Continued*)

TABLE 1—*Continued*

species Sample Number	2	5	6	7	8	9	10	11	12
S. sp. G							*	*	
Cytheropteron chejuense Choe, 1985	2.8		2.4	1.5	1.6	*	1	2.3	
C. miurense Hanai, 1957	2.2	*	1.2		2	4.1	2.4	1.6	2.5
C. uchioi Hanai, 1957	1.3	1.2	*	2.9	2.6	1.3	*	2.3	
C. sp. A	*	*	*		5.8	7.5	1	*	*
C. sp. B	1.4	1	1.4	1.5	2.8	3.2	1.3	1.1	*
C. sp. C							*		
Kobayashina hyalinosa Hanai, 1957					*		*	*	*
Hetacytheropteron chejuense Choe, 1985	4.7	3.4	3.1	2.2	3.5	8.4	2.4	*	1.4
Mangarina abyssicola (G. W. Muller, 1894)					*		1	*	
Paracytheridea SP. A				*					
Loxoconcha japonica Ishizaki, 1968							*	*	*
L. kattoi Ishizaki, 1968				*					
L. laeta Ishizaki, 1968			*		4	3	2.5	1.4	*
L. optima Ishizaki, 1968			*		*				
L. sp. A							*	*	
L. sp. B							*		
Loxocorniculum SP. A			*					*	
L. sp. B							*		
Nipponocythere SP.									*
Cytheromorpha acupunctata (Brady, 1880)	*	14.5	*				*	*	1.1
Xestoleberis hanaii Ishizaki, 1968				*			*	*	
X. sagamiensis Kajiyama, 1913	*			2.9	1.4	*	1.8	2.2	*
X. sp.					*			*	
Paradoxostoma SP. A					*			*	
P. sp. B							*		
P. sp. C								*	
Cytherois sp. A			*						
C. sp. B					*				
Paradoxostomatidae sp.								*	
Sclerochilus sp. A			*		*	*	*	*	*
S. sp. B					*		*	*	
Cytheroma hanaii Yajima, 1978							*	*	
Xiphichilus sp.					*	*	*	*	*
total number of specimen	1160	407	1746	138	1871	466	1022	2221	364
total number of species	34	28	46	32	84	45	92	95	42
weight of sample (in gram)	80	40	80	80	100	50	100	100	50

In the nine samples from the measured section, eight species occur in all the samples. They are given below in order of abundance:

	Total No.	%
Urocythereis sp.	1068	11.4
Cornucoquimba tosaensis	521	5.5
Schizocythere kishinouyei	435	4.6
Tracyleberis sp. B	279	3.0
Metacytheropteron sp.	275	2.9
Aurila uranouchiensis	199	2.1
Cytheropteron sp. B	154	1.6
Pistocythereis bradyformis	118	1.3

The following species are found in 8 samples out of a total of 9 samples examined:

	Total No.	%
Aurila corniculata	338	3.6
Amphileberis nipponica	290	3.1
Aurila sp. C	238	2.5
Bicornucythere bisanensis	236	2.5
Cytheropteron sp. A	176	1.9
C. miurense	171	1.8
C. uchioi	140	1.5
Finmarchinella (*Barentsovia*) *japonica*	128	1.4
Aurila sp.	80	0.8
Bythoceratina hanaii	58	0.6
Callistocythere reticulata	55	0.6

The most prolific species is *Urocythereis* sp. which makes up more than 11.4% of the entire population. A major group made up of only 16 species, including *Urocythereis* sp., accounts for almost 60% of all the specimens.

PALAEOECOLOGY

The Sogwipo ostracod assemblage includes many modern species living in the shallow sea of the temperate zone on the Korean Margin, East China Sea and the Pacific coast of Japan. In order to deduce the palaeoenvironment of deposition, the data on the distribution of the modern living representatives were used. The palaeoecological interpretation of the fossil fauna is difficult, however, because there is not yet sufficient ecological data on some of the dominant species.

The checklist of the Japanese ostracods (Hanai *et al.*, 1977), and other ecological studies including those of the Korean Margin (Choe, 1985), Hamanako Estuary (Ikeya and Hanai, 1982) and Tateyama Bay (Frydl, 1982) were mainly referred to in this analysis.

The palaeoenvironment of each sample, deduced from the recent data of the major constituents of the fossil fauna, is inferred as follows.

Sample nos. 2, 5 and 6, occupying the lower part of the measured section are characterised by their exceptionally high content of *Urocythereis* sp. Unfortunately, its ecology is not known and so the palaeoenvironment of these samples can only be inferred by reference to subordinate species. Sample no. 5 shows a remarkable abundance of *Cytheromorpha acupunctata* (14.5%) and *Bicornucythere bisanensis* (9.6%), both of which are found abundantly in the inner part of bays with decreased inflow of open sea water (Ishizaki, 1968; Ikeya and Hanai, 1982; Choe, 1985). On the other hand, samples 2 and 6 are characterised by the decrease in abundance of these two species and, in return, increased numbers of the shallow open sea species such as *Amphileberis nipponica, Hanaiborchella triangularis, Pontocythere subjaponica, Schizocythere kishinouyei* etc. Consequently, samples 2 and 6 appear to be deposited near the bay mouth, influenced by open sea water, whereas sample 5 was close to the inner part of the bay.

In sample 7, the proportion of *Urocythereis* sp. (9.4%) decreases, but it is still the dominant species. The absence of *Cytheromorpha acupunctata* and the appearances of *Hirsutocythere hanaii* (8.7%), *Bradleya* (*Bradleya*) *nuda* (7.3%) and *Neonesidea oligodentata* (5.8%) are noteworthy. They are dominant species off-shore in the Cheju and Tsushima Straits area. *Neonesidea oligodentata* occurs abundantly in the offshore area of the Korean South Sea and sparsely in the near-shore area (Choe, 1985).

Sample nos. 8 and 9 are distinguished by the increased numbers of *Cytheropteron* sp. A,


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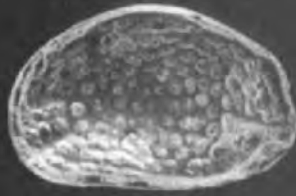
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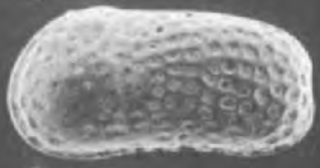
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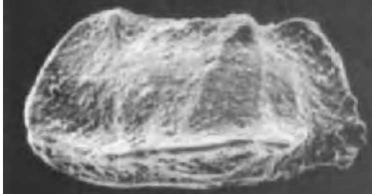
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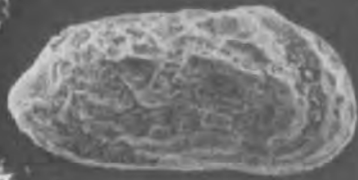
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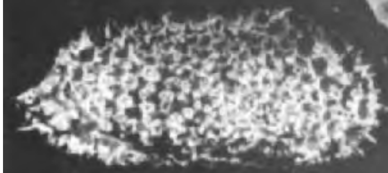
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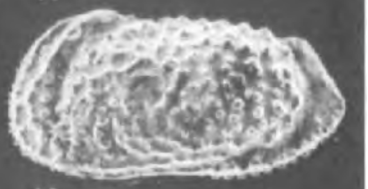
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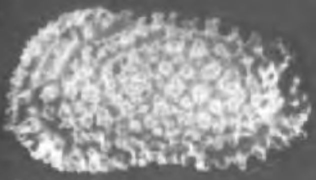
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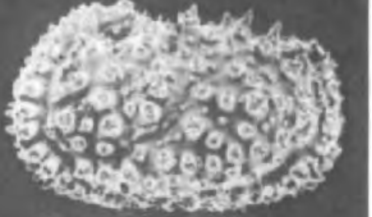
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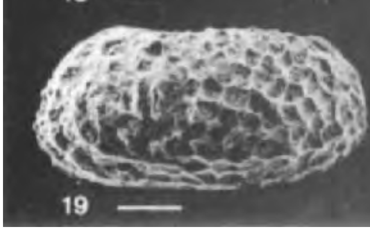
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Schizocythere kishinouyei, Cornucoquimba tosaensis and *Neonesidea oligodentata* and the near absence of *Urocythereis* sp. and *Bicornucythere bisanensis. Cytheropteron* sp. A is accompanied by *C. miurense* and *C. uchioi,* both of which were reported from the central part of Tateyama Bay, a wide open bay directly affected by the warm Kuroshio Current (Frydl, 1982) and the bay mouth—offshore in the South Sea of Korea (Choe, 1985). *C. uchioi* was recovered from the East China Sea in depths of 50 to 132 metres (Ishizaki, 1981). Yajima (1982) stated that the presence of *Cytheropteron* may suggest a sand bottom deeper than 30 metres. Similarly, the occurrence of *Cornuncoquimba tosaensis* is restricted to the Cheju Strait (Choe, 1985). To consider the occurrences of these species, samples 8 and 9 may have been adjacent to a wide open sea which was presumably more than 30 metres deep.

In sample 10, *Neonesidea oligodentata* (10.7%) increases in proportion and becomes the most prolific species. The number of *Urocythereis* sp. (7.1%) increases slightly, whereas *Cytheropteron* decreases greatly. This change in proportion of the major members may indicate that sample 11 was in shallower water and nearer to the open shore than samples 9 and 10.

In sample 11, the importance of *Cornucoquimba tosaensis* (7.6%) and *Ambtonia obai* (7.0%) increases, whereas *Neonesidea oligodentata* and *Urocythereis* sp. diminish in abundance. *Ambtonia obai* is the dominant species in the central part of Tateyama Bay in depths exceeding 30 metres and becomes more abundant with increasing depth and distance from the shore (Frydl, 1982). It also occurs abundantly in the Korean South Sea (Choe, 1985). Accordingly, the dominance of *Cornucoquimba tosaensis* and *Ambtonia obai* in sample 12 may indicate a deeper environment, presumably deeper than 30 metres, far from the open shore.

In sample 12, the number of *Urocythereis* sp. (15.1%) and *Cornucoquimba tosaensis* (16.5%) increases again, while the dominance of *Ambtonia obai* diminishes drastically. Accordingly, it may be suggested that sample 12 was formed in shallower water than sample 11.

Most of the living species of ostracods recovered from the measured section are warm water species distributed along the Korean Margin and the Pacific side of Japan influenced by the Kuroshio Current. Therefore, the Sogwipo Formation appears to have been deposited in warm water conditions. However, the presence of *Palmenella limicola* and *Agrilloecia* sp. in samples 10 and 11 probably indicate a slight cold water influence.

BIOSTRATIGRAPHY

Kim (1972) reported 72 species of benthonic and 8 species of planktonic foraminifers from the

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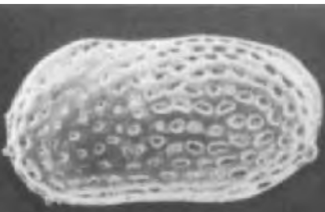
PLATE 2—Fig. 1. *Aurila corniculata* Okubo, 1980. Lateral view of right valve (PLKU-O-321). Fig. 2. *Aurila* sp. [see Choe, 1985]. Lateral view of right valve (PLKU-O-322). Fig. 3. *Aurila uranouchiensis* Ishizaki, 1968. Lateral view of right valve (PLKU-O-323). Fig. 4. *Aurila* sp. A. Lateral view of left valve (PLKU-O-324). Fig. 5. *Aurila* sp. B. Lateral view of left valve (PLKU-O-325). Fig. 6. *Aurila* sp. C. Lateral view of right valve (PLKU-O-326). Fig. 7. *Finmarchinella (Barentsovia) japonica* (Ishizaki, 1966). Lateral view of left valve (PLKU-O-327). Fig. 8. *Urocythereis* sp. Lateral view of left valve (PLKU-O-328). Fig. 9. *Cornucoquimba tosaensis* (Ishizaki, 1968). Lateral view of right valve (PLKU-O-329). Fig. 10. *Bradleya (Bradleya) nuda* Benson, 1972. Lateral view of left valve (PLKU-O-330). Fig. 11. *Trachyleberis scabrocuneata* (Brady, 1880). Lateral view of left valve (PLKU-O-331). Fig. 12. *Trachyleberis*? *tosaensis* Ishizaki, 1968. Lateral view of right valve (PLKU-O-332). Fig. 13. *Trachyleberis* sp. A. Lateral view of right valve (PLKU-O-333). Fig. 14. *Trachyleberis* sp. B. Lateral view of left valve (PLKU-O-334). Fig. 15. *Trachyleberis* sp. C. Lateral view of left valve (PLKU-O-335). Fig. 16. *Acanthocythereis munechikai* Ishizaki, 1981. Lateral view of left valve (PLKU-O-336). Fig. 17. *Hirsutocythere hanaii* Ishizaki, 1981. Lateral view of left valve (PLKU-O-337). Fig. 18. *Ambtonia obai* (Ishizaki, 1971). Lateral view of left valve (PLKU-O-338). Fig. 19. *Pistocythereis bradyformis* (Ishizaki, 1968). Lateral view of left valve (PLKU-O-339). Fig. 20. *Amphileberis nipponica* (Yajima, 1978). Lateral view of left valve (PLKU-O-340).
(bar = 100 μm)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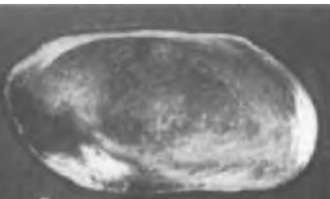
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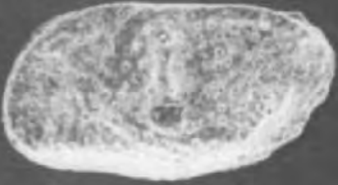
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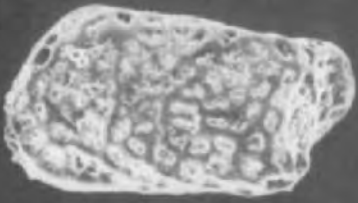
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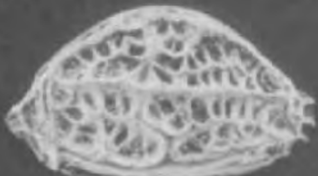
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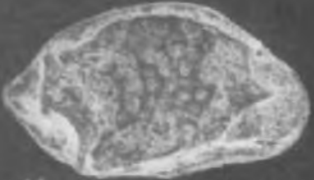
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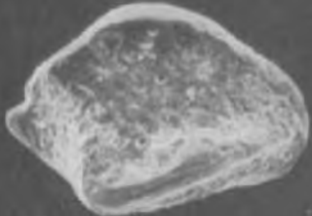
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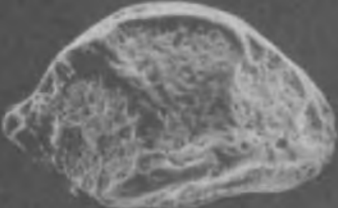
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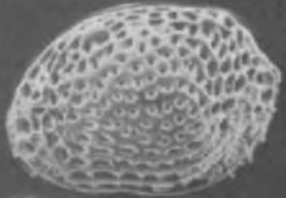
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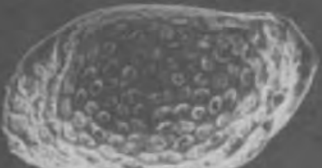
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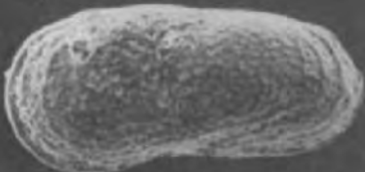
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Sogwipo Formation. He suggested that the age of the formation was Pliocene, judged from the occurrence of *Turborotalia numerosa, T. crassiformis* and *Pulleniatina obliquiloculata.*

Among the Sogwipo ostracod fauna, 64 species have so far been reported from the late Cenozoic strata, mostly in Japan (Text-fig. 3). Most of them, except for 5 species (*Ambostracon ikeyai, Cytheroma*? *hanaii, Eucytherura utsusemi, Museyella oblonga* and *M. obrozukiyo*), represent their life spans as known at present.

It seems evident that additional data will eventually revise some of the stratigraphical ranges of fossil ostracods in the future. Nevertheless, not a single species which became extinct in the Pliocene has been found in this study.

According to the data compiled in Text-Fig. 3, eleven species in this fauna have been reported as having their first appearence in the Miocene, 28 species in the Pliocene and eleven species in the Pleistocene.

To judge from the stratigraphical ranges of the Sogwipo ostracod fauna, it is not clear that the age of the formation can be restricted to the Pliocene alone. Consequently, the writers consider that the formation is also younger, at least in part, and it is presumed to be Plio-Pleistocene in age.

GENERAL CONCLUSION

The Sogwipo Formation, comprising about 54 metres of sedimentary rocks, shows several distinct sedimentary facies which vary from lagoon, barrier island, offshore and tuffaceous sand to volcanic conglomerate in ascending order.

The samples taken from the near-shore, lagoonal, barrier island and offshore facies yield abundant ostracod specimens, particularly from the samples adjacent to the six shell beds.

An ostracod assemblage representing 124 species belonging to 58 genera was recovered from the 9 samples taken from the measured section. Among them, 64 species are known to science and the rest, on which taxonomic work is at present in progress, appear to be new.

Because of the scarcity of late Cenozoic material available for ostracod study, the present data are largely incomplete and must be considered merely an introduction to any detailed biostratigraphical and palaeoecological studies to be accomplished in the future. Nevertheless it is noteworthy that striking changes in sedimentary facies are accompanied by changes in the ostracod faunas.

The faunal composition in samples 2 and 5 corresponds to sedimentary facies changes presumably related to the bay and bay mouth environment. A slight change in faunal composition in sample

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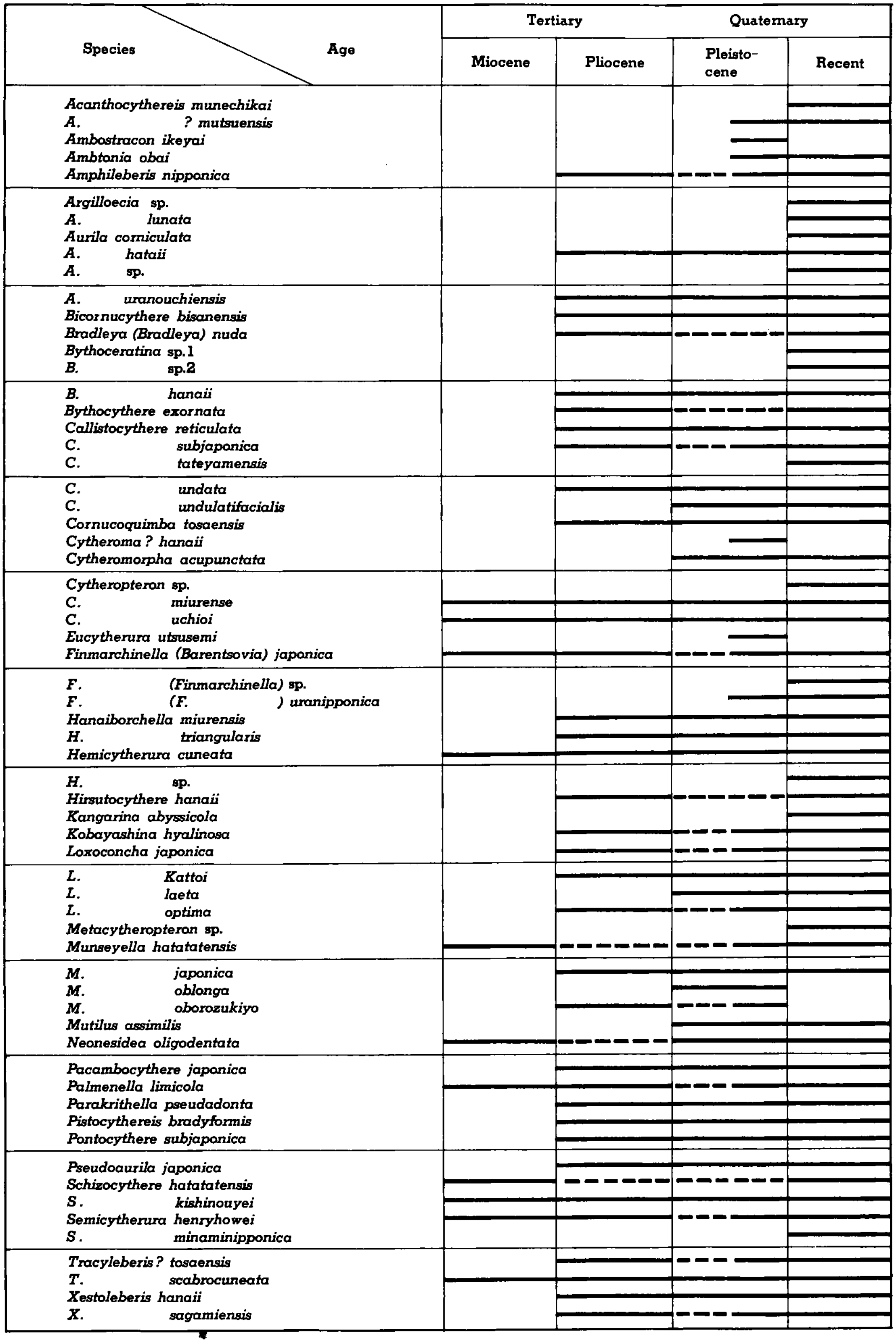
PLATE 3—Fig. 1. *Bicornucythere bisanensis* (Okubo, 1975). Lateral view of left valve (PLKU–O–341). Fig. 2. *Bythocythere exornata* Gou, 1983. Lateral view of right valve (PLKU–O–342). Fig. 3. *Bythoceratina* sp. 1 [see Choe, 1985]. Lateral view of right valve (PLKU–O–343). Fig. 4. *Bythoceratina* sp. 2 [see Choe, 1985]. Lateral view of right valve (PLKU–O–344). Fig. 5. *Bythoceratina hanaii* Ishizaki, 1968. Lateral view of left valve (PLKU–O–345). Fig. 6. *Eucytherura utsusemi* Yajima, 1982. Lateral view of left valve (PLKU–0–346). Fig. 7. *Hemicytherura cuneata* Hanai, 1957. Lateral view of right valve (PLKU–O–347). Fig. 8. *Hemicytherura* sp. [see Choe, 1985]. Lateral view of left valve (PLKU–O–348). Fig. 9. *Hemicytherura* sp. A. Lateral view of right valve (PLKU–O–349). Fig. 10. *Semicytherura minaminipponica* Ishizaki, 1981. Lateral view of right valve (PLKU–O–350). Fig. 11. *Cytheropteron* sp. [see Choe, 1985]. Lateral view of right valve (PLKU–O–351). Fig. 12. *Cytheropteron miurense* Hanai, 1957. Lateral view of right valve (PLKU–O–352). Fig. 13. *Cytheropteron uchioi* Hanai, 1957. Lateral view of right valve (PLKU–O–353). Fig. 14. *Cytheropteron* sp. A. Lateral view of right valve (PLKU–O–354). Fig. 15. *Cytheropteron* sp. B. Lateral view of right valve (PLKU–O–355). Fig. 16. *Metacytheropteron* sp. [see Choe, 1985]. Lateral view of left valve (PLKU–O–356). Fig. 17. *Loxoconcha japonica* Ishizaki, 1968. Lateral view of left valve (PLKU–O–357). Fig. 18. *Loxoconcha laeta* Ishizaki, 1968. Lateral view of left valve (PLKU–O–358). Fig. 19. *Cytheromorpha acupunctata* (Brady, 1880). Left valve view of carapace (PLKU–O–359). Fig. 20. *Xestoleberis sagamiensis* Kajiyama, 1913. Lateral view of left valve (PLKU–O–360).
(bar = 100 μm)



TEXT–FIG. 3—Biostratigraphical ranges of the known ostracod species of the Sogwipo Formation, based on the data from the Korean Margin, Japan and mainland China.

6 compared to the underlying samples reflects the facies shift from lagoon to barrier island, which was presumably affected by the warm Kuroshio water of the open sea. Six samples (nos. 7, 8, 9, 10, 11 and 12) are taken from the offshore facies. Among them, samples 8, 9 and 11 contain diagnostic species indicating a deeper environment farther away from the shore, whereas samples 10 and 12 have species hinting at shallower water closer to the open shore. This shows that a two-fold oscillation of water depth occurred during the deposition of the offshore facies. Above the offshore facies, two facies of volcanic sediment, namely tuffaceous sand and volcanic conglomerate in ascending order, indicate the evuentual filling in of the sedimentary basin.

Judging from the stratigraphical ranges of the 64 known species in the entire fauna, the age of the formation can be tentatively regarded as Plio-Pleistocene.

ACKNOWLEDGEMENTS

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DISCUSSION

Singh: What is the basis of dating the Pliocene-Pleistocene sediments in your area? Have you demarcated Pliocene-Pleistocene boundary in your area on the basis of ostracod assemblages?

Paik: I used the ostracod stratigraphical ranges already reported from Japan and China for dating the formation and couldn't define the boundary between the Pliocene and the Pleistocene in my section.

Pliocene-Pleistocene Palaeoenvironment and Fossil Ostracod Fauna from Southwestern Hokkaido, Japan

KEI-ICHI HAYASHI
Fussa Highschool, Tokyo, Japan

ABSTRACT

The Pliocene-Pleistocene Setana Formation occurs in the Kuromatsunai area of southwestern Hokkaido, Japan. This formation which consists of marine, brackish and freshwater sediments, is first analysed in terms of the palaeoenvironment, mainly on the basis of lithological characteristics, and second on the basis of the molluscan fossils found in the marine and brackish sediments of the formation. These sediments can be further divided into four marine and one brackish facies based on the fossil molluscan assemblages identifiable from field observation. In the field survey, eight sedimentary facies representing different palaeoenvironments can be distinguished in the formation: four cold-water marine, one brackish-water and three unfossiliferous freshwater facies. These sedimentary facies change vertically exhibiting two cyclical sequences of sedimentation. Each cycle is composed of marine (brackish in part), marine, and freshwater facies in ascending order.

Seven ostracod assemblages are distinguishable in the marine and brackish-water facies. The correlation between molluscan and ostracod assemblages is shown in Text-fig. 1. In the early stage of the first cycle, the *Cytheropteron sawanense* Assemblage appeared in the fairly deep water facies, and the *Schizocythere okhotskensis* Assemblage came out in the relatively high energy environment. As the deep water becomes shallower, the bank facies of coarse-grained sand was deposited containing an assemblage of very high species-diversity, in which *Schzocythere okhotskensis, Baffinicythere emarginata, Urocythereis*? sp. B and *Cytheropteron sawanense* predominate. The deep water and high energy environmental facies is then overlain by the embayment facies dominated by *Howeina camptocytheroidea* and *Cytheropteron* sp.—*Ruggieria* sp. Finally, the embayment facies passes vertically into the unfossiliferous freshwater facies.

In the second cycle, shallow near-shore facies appeared at the base suggesting that it is the lower limit of water depth of the second cycle. It contains two ostracod assemblages of high species-diversity and the *Schizocythere okhotskensis* Assemblage which is also found in the brackish-water facies. The second cycle terminates with the deposition of freshwater facies, without a trace of embayment facies.

INTRODUCTION

The Omma-Manganji fauna is one of the distinctive Pliocene-Pleistocene faunas of Japan. Its molluscs have been fully studied and known since 19th century. Some groups other than molluscs, however, have not been studied in detail and even the description of species is insufficient.

Accordingly the stratigraphic distribution, habitat and other aspects remains poorly known. One such group is the ostracods. In earlier studies, Okada (1979) and Tabuki (1980, MS.) reported on the ostracods of this fauna in the Oga and Tsugaru Peninsulas both of which is in Northeast Honshu, but other areas are still remain unstudied. Hokkaido is one such area situated in the northernmost part of the distribution of the Omma-Manganji fauna, and there is no published paper on the ostracods apart from the description of a few species by Hanai (1961). It is important to study the Pliocene-Pleistocene ostracods in Hokkaido, because the Omma-Manganji fauna represents cold-water conditions and has palaeoclimatic significance.

On Neogene fossil and living species of cold-water habitat of Japan, Ishizaki (1963, 1971) and others have described in detail many new species. They were studied in Hanai *et al.* (1977). Many other species, however, remain still undescribed.

Thus the study of cold-water ostracods remains at an elementary stage. Further, there is no study of the ostracod fauna and their relationship to the sedimentary environment in which they live. This study is the first attempt in that respect.

The area studied is situated in the "Kuromatsunai Lowland Belt" in the southwestern Hokkaido, Japan, which lies between Suttsu Bay (the Sea of Japan side) on the north and Funka Bay (the Pacific side) on the south. The lowland is bounded by mountains on the east and west. Its topography is controlled by the geological structure of the Neogene sediments (Ikeya and Hayashi, 1982) in that the lowland belt coincides with the structural depressions and is underlain by younger and poorly consolidated deposits, most of which belong to the Pliocene-Pleistocene Setana Formation. In this paper, sedimentary environments are clarified on the basis of the lithology and molluscan assemblages, and the accompanying ostracod assemblages are described and compared with these sedimentary environments.

SEDIMENTARY ENVIRONMENT AND MOLLUSCAN ASSEMBLAGES OF THE SETANA FORMATION

The Pliocene-Pleistocene Setana Formation is sporadically distributed in southwestern Hokkaido, Japan. The norhternmost part is in the "Kuromatsunai Lowland Belt" of which the central part is studied in terms of the palaeoenvironment in this paper. The formation in this area consists of marine, brackish, and freshwater sediments and is analysed mainly on the basis of lithological characteristics. The writer subdivided the formation into eight sedimentary facies in order to compare the different detailed palaeoenvironments with that of the ostracod assemblages. In addition the data provided by the molluscs found in the marine and brackish sediments allow four cold marine and one brackish facies to be recognized. Both the composition of fossil assemblages and the modes of fossil occurrence are taken into account for the interpretation of the sedimentary facies, as well as the characteristics of the sediments themselves. The unfossiliferous freshwater sediments are subdivided into three different freshwater facies, based on the detailed lithological characteristics and sedimentary structure.

The eight sedimentary facies are tentatively named Marine I–IV, Brackish, and Fresh-water I–III as shown in Text-fig. 1. Their stratigraphical relationships are shown in Text-figs. 2A, B, C (A: western area, B: middle area, C: eastern area), on which the distribution of molluscan and ostracod assemblages is also shown by symbols. In the stratigraphic sequence, these sedimentary facies change vertically exhibiting two cyclical sequences of sedimentation. Each cycle is composed of marine or brackish water, marine water, and freshwater facies in ascending order. The three-dimensional relationships between these facies for each cycle are shown schematically in Text-fig. 3.

	Facies	Fossil Molluscan Assemblage	Fossil Ostracod Assemblage
Upper Cycle	Fresh-w. III		
	Fresh-w. II		
	Brackish w.	◒ Crenomytilus grayanus A.	□ Schizocythere okhotskensis A.
	Marine II (near-shore, shallow)	⊖ Patinopecten yessoensis A.	◩ Semicytherura henryhowei – Finmarchinella "angulata" A. ◪ Schizocythere okhotskensis – Baffinicythere emarginata Urocythereis gorokuensis – Semicytherura henryhowei A.
Lower Cycle	Fresh-w. III		
	Fresh-w. II		
	Fresh-w. I		
	Marine IV (Bay)	⊗ Raeta yokohamaensis A. ● Macoma calcarea A. ⊕ Lucinoma annulata A.	■ Cytheropteron sp. – Ruggieria sp. A. ⊞ Howeina camptocytheroidea A.
	Brackish w.	◓ Crassostrea gigas A. ◒ Crenomytilus grayanus A.	
	Marine III	○ Chlamys islandica A.	□ Schizocythere okhotskensis A.
	Marine II (Bank, shallow?)	◎ Chlamys daishakaensis A.	◨ Schizocythere okhotskensis – Baffinicythere emarginata – Urocythereis? sp. B – Cytheropteron sawanense A.
	Marine I (fairly deep)	◑ Cryptonatica janthostomoides A. ◍ Acila divaricata A.	▩ Cytheropteron sawanense A.

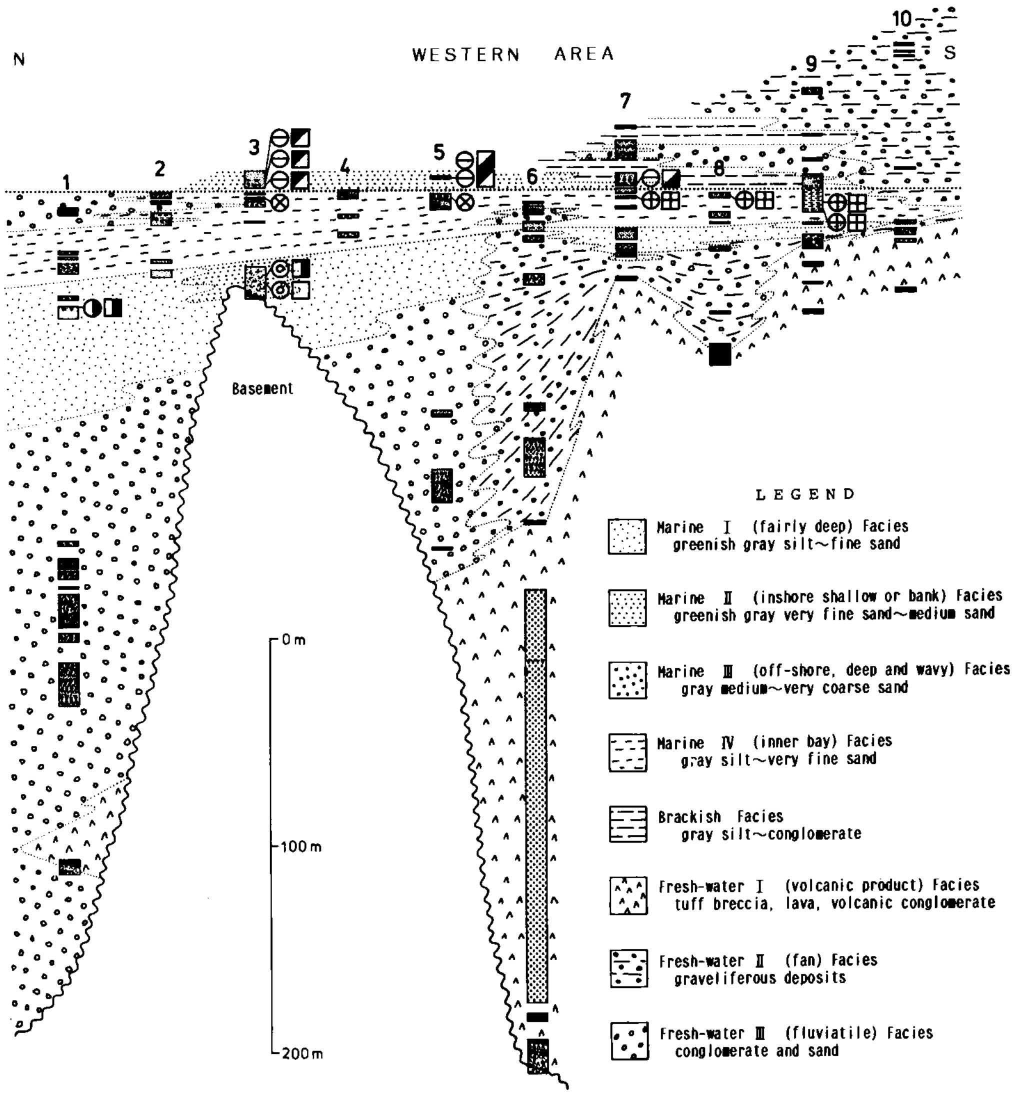
Text-fig. 1—Sedimentary Facies and Relationship between Ostracod and Molluscan Assemblages.

Lower (First) Cycle

A marine transgression after the folding and erosion of pre-Setana formations is inferred from the existence of marine fossils in the lower part of the Setana Formation in all areas except the western area. These fossils indicate continental shelf depths and open ocean conditions and deposited fine-grained sediments in the main part of the basin. The writer identified this sedimentary facies by two molluscan assemblages: the *Acila divaricata* Assemblage which is characterised by the dominance of articulated individuals of this bivalve in life position, and the *Cryptonatica janthostomoides* Assemblage that is meagre and composed of several species of small gastropods and bivalves. The *Acila divaricata* Assemblage indicates deeper conditions (tens of metres at least, perhaps 100 m or more, as inferred from the depths inhabited by the living *Acila divaricata*) than the *Cryptonatica janthostomoides* Assemblage. The latter assemblage might have been deposited in the depths of tens of metres, though this supposition is unwarranted because of allochthonous material. This sedimentary facies of fairly deep and low energy shelf environments is named Marine I facies.

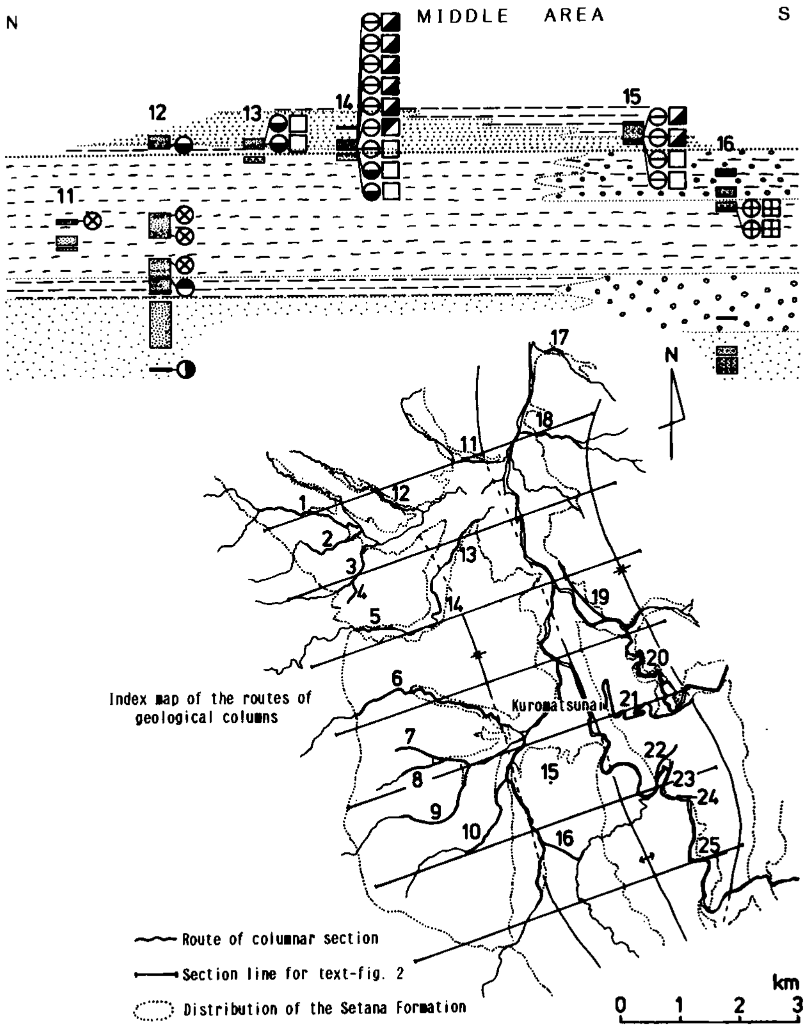
In the southeastern area, however, this facies grades laterally into another facies which is composed of coarse-grained sandstone including abundant allochthonous molluscan fossils (Text-fig. 2C). The molluscan assemblage is characterised by the abundance of *Chlamys islandica,* which accounts for more than 50% of the individuals. *Limopsis tokaiensis* and *Boreoscala yabei echigonum* are also characteristic constituents of the assemblage. The assemblage also contains *Chlamys daishakaensis, C.* (*Swiftopecten*) *swiftii* and *Monia macroschima.* These fossils are usually poorly preserved in cross-bedded layers. Because these fossils are almost allochthonous, it is difficult to infer the palaeoenvironment of deposition. The abundance of *Ostrea denselamellosa* may signify shallow water in the basal part, and *L. tokaiensis* may suggest fairly deep water in the lower part. The sea may have been as much as 200 m or more in places, because *Acesta goliath* in life position was found in the same assemblage (in the southern locality of route 25 in Text-fig. 2C). Consequently the depth range is too wide to characterise this sedimentary facies. Lithologically this facies is characterised by the cross-bedding of a relatively high energy environment such as that of a straight. It is named here Marine III facies.

Before marine inundation of the basin, volcanic activity had deposited thick layers of pyroclastics and lava flows in the southwestern area (Text-fig. 2A). The depositional environment of these volcanic deposits is uncertain, but it was certainly, in part, a freshwater environment, because the lowermost part of this facies consists of unfossiliferous, water-laid sediments. This facies is here

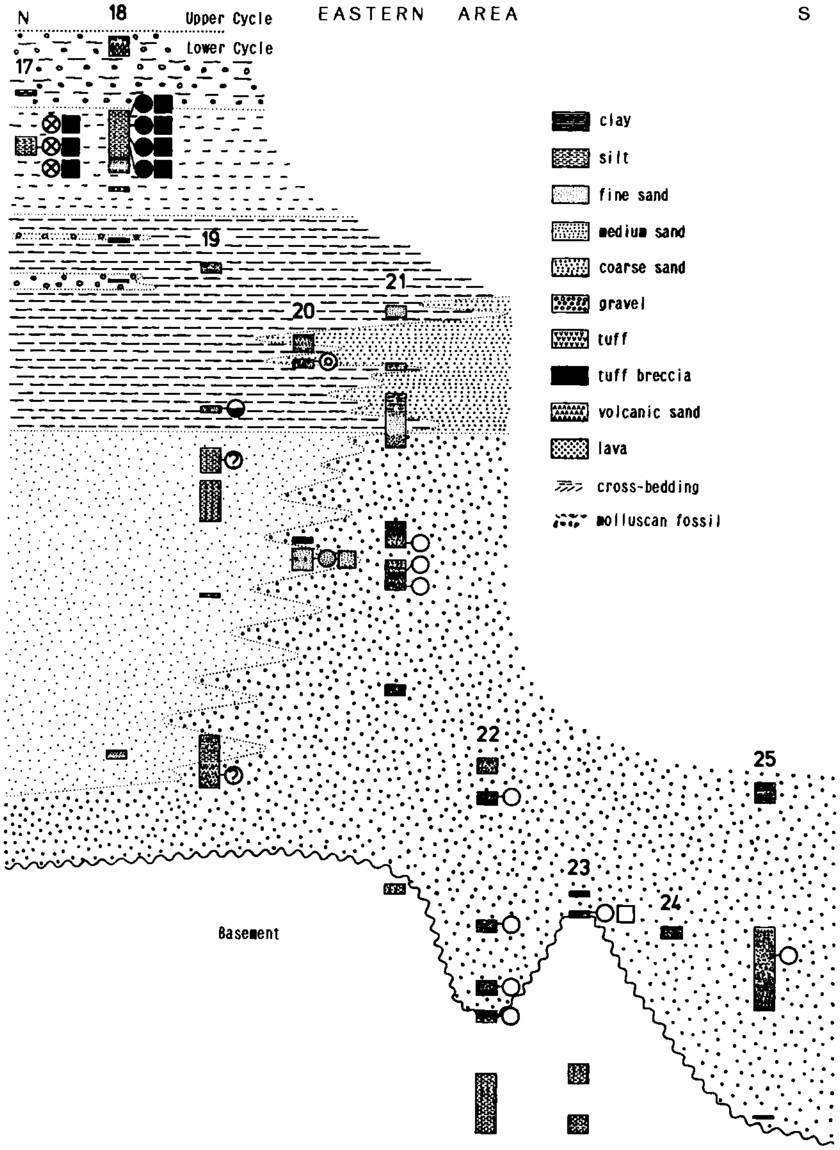


TEXT-FIG. 2A—Sedimentary facies and fossil assemblages (Western area). Square and circular symbols represent molluscan and ostracod assemblages respectively. Names of the assemblages refer to Table 1. Routes of columnar sections are shown in the index map.

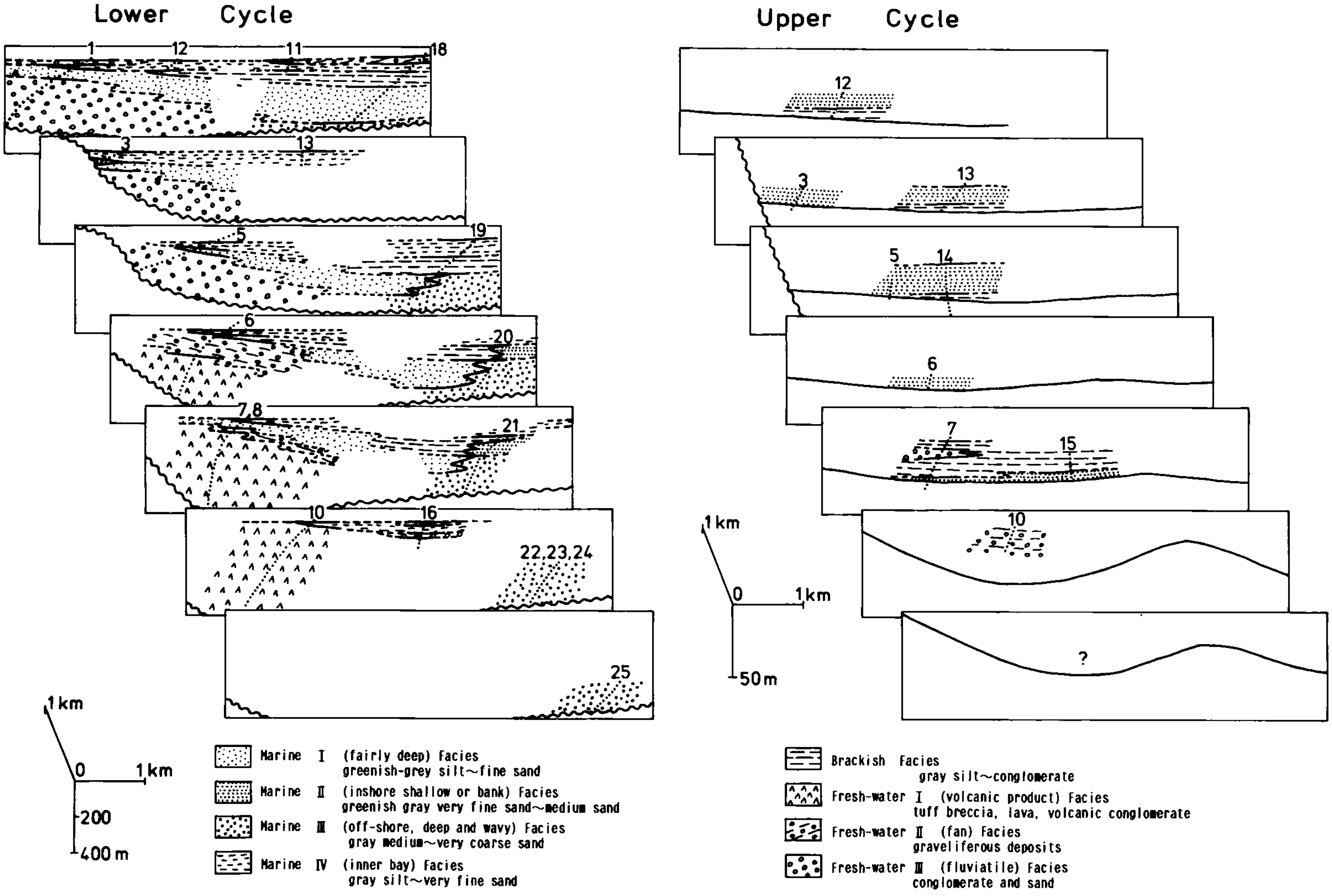
named Fresh-water Unit I. Above this facies, gravel accumulated forming fan deposits. The inclination of the gravelly layers indicates that the sediments were transported from the west. The gravels were presumably derived from the underlying volcanic products, because of their similar lithology. This facies represents re-sedimentation of the underlying volcanics by rivers flowing in from the



TEXT-FIG. 2B—*Continued* (Middle area).



TEXT-FIG. 2C—*Continued* (Eastern area).



Text-fig. 3—Three-dimensional relationships among sedimentary facies for each cycle. Section lines are shown in the index map of Text-fig. 1.

west. This fan facies is tentatively named Fresh-water Unit II. This facies grades laterally into cross-bedded conglomerate intercalated with thin layers of sandstone in the northwestern area. Original dips and imbrication structure found in the conglomerate signify a current from the west flowing in a direction varying between northeast and southeastward. This coarse-grained facies is regarded as fluviatile facies (delta or fan-delta), and called Fresh-water Unit III. No molluscan or ostracod fossils were found in these three Fresh-water facies.

Later, the sea presumably became shallower because of the infilling by sedimentation, and in the eastern and middle areas it became brackish (Text-figs. 2B, C). In some areas, near-shore shallows and bank environments appeared.

The Brackish-water facies is recognized in the eastern and middle areas, on the basis of the *Crenomytilus grayanus* and *Crassostrea gigas* Assemblages respectively. In this case, it is useful that these oysters are restricted to brackish water. The influx of freshwater has implications for the regression of the sea, depending on whether the source of freshwater was in the south or east. Though this facies is composed of fine-grained sediments, the oyster bank may have formed a stony bottom habitat for benthonic micro-organisms such as ostracods.

This facies changes laterally into fine- to medium-grained sandstone containing *Chlamys daishakaensis* primarily in the southeastern area (Text-fig. 2C). The coarseness of grain size and habitats of some species in the *Chlamys daishakaensis* Assemblage indicate a near-shore, shallow bottom of a high energy environment. High energy conditions persisted during the deposition of the Lower Cycle in this area, because the underlying Marine III facies is also a high energy facies too. This fact may hold critical clues to the direction of regression.

The same facies, including the same molluscan assemblage, is found in a small part of the northwestern area (Text-fig. 2A). The *Chlamys daishakaensis* Assemblage found in this area is characterised by the predominance of that species (about 70% of the total assemblage) which is accompanied by *Monia macroschima* and *Callista* (*Ezocallista*) *brevisiphonata*. Most of the fossils are well-preserved, though they are not in life position. Consequently, it is unlikely that the fossils have been transported far from their living sites. In the field, one can see that the sandstone of this facies abuts on a swell of rocky basement. The molluscs are considered to have lived around, or on, the submarine rocky swell which perhaps formed a bank, and to have fallen to the bottom near the bank.

During its final stage, the sea became an inner bay environment over most of the area and deposited very fine-grained sediments. In addition to the typical lithology of the bluish-grey siltstone and very fine-grained sandstone, this facies can be recognised by three distinctive inner bay assemblages of molluscs, the *Raeta yokohamaensis* Assemblage, the *Lucinoma annulata* Assemblage and the *Macoma calcarea* Assemblage. *Raeta yokohamaensis* is a characteristic fossil of the innermost bay environment and is widely distributed in the northern area (Text-figs. 2A, B, C). *Lucinoma annulata* indicates an inner bay environment and is found in the southern area (Text-figs. 2A, B). The *Macoma calcarea* Assemblage is found at the same horizon of the *Raeta yokohamaensis* Assemblage mentioned above at the adjacent outcrop in the northeastern area (Text-fig. 2C). The *Macoma calcarea* Assemblage is regarded as distinctive one of the inner bay because it is similar to the *Raeta yokohamaensis* Assemblage in species composition in spite of lacking of the diagnostic *R. yokohamaensis*. Judging from the habitat of some of the molluscs, the depth range of the bay was 30–50 m. This inner bay facies is here named Marine IV.

Fresh-water II and III, both of which are mentioned above, are partly distributed in the marginal area of the bay in the northwest and south. They may be attributed to the fluvial deposits of rivers discharging into the bay.

The geographical changes of the molluscan assemblages in the Marine IV facies and the distribution of the underlying Brackish and Marine II facies indicate that the sea probably retreated southeastward.

Upper (Second) Cycle

The second transgression following the infilling of the basin of the Lower Cycle is demonstrated by the presence of wide-spread marine sediments overlying the Marine IV facies at the top facies of the Lower Cycle.

In the early stage of the second transgression, a brackish water environment appeared in the central part of the basin (Text-fig. 2B). This Brackish facies is identified by the *Crenomytilus grayanus* Assemblage which is also found in the Lower Cycle. It is composed of fine-grained sandstone, with the basal part being conglomeratic.

The northern area of the "Kuromatsunai Lowland Belt" was inundated by a near-shore shallow sea. The area studied is situated in the southernmost part of that sea, and is overlain by the greenish-grey, very fine-grained sandstone containing abundant autochthonous or subautochthonous marine fossils. This sandstone is distributed throughout most of the area except the southernmost part (Text-figs. 2A, B). This fossiliferous sandstone yields *Patinopecten yessoensis* in abundance and is associated *Glycymeris yessoensis, Callista* (*Ezocallista*) *brevisiphonata, Chlamys* (*Swiftopecten*) *swiftii, C. farreri nipponensis, Homalopoma amussitatum, Cyclocardia crebricostata.* This assemblage which is named the *Patinopecten yessoensis* Assemblage is also composed of many other species and varies vertically and laterally. Consequently, small environmental changes were recognized by changes in composition and frequency of this molluscan assemblage. For example, the appearance of an environment similar to the inner bay is inferred by the occurrence of *Lucinoma annulata* in the early stage of the Upper Cycle. A similar environmental change can be traced by the lithological characteristics and modes of occurrence of the fossils. In the southwestern area, the coarseness of sediments and slightly transported molluscan fossils suggest more turbulent, perhaps shallower conditions than the other areas. On the whole, however, this assemblage indicates a near-shore shallow sea which becomes shallower southward and westward. This sedimentary environment is generally the same as that of the Marine II facies of the Lower Cycle.

Thereafter, Brackish facies gradually appeared again as shown by the diatoms studied by Ichikawa *et al.* (1967). This environmental change began in the southern area and spread northward, because the underlying Marine II facies is thick in the north and thin or thinning-out in the south (Text-figs. 2A, B). This northward spreading of the Brackish facies coincides with the northward thinning of intercalated peat layers. This fact suggests that the sea of the Upper Cycle retreated northward. No fossil molluscs and ostracods were preserved in this facies.

In the southwestern area, fan and fluviatile facies constitute the whole of the whole of the Upper Cycle, both of which have lithological characteristics similar to those of the Lower Cycle. The former is therefore attributed to the Fresh-water II facies, and the latter to the Fresh-water III.

OSTRACOD FAUNA AND PALAEOENVIRONMENT

One hundred and ninety one marine ostracod species among 56 genera were obtained from 44 sediment samples from the Setana Formation in the "Kuromatsunai Area". Sediment samples were treated by the sodium-sulphate-naphtha method, and washed on a 200 mesh sieve. About 200 individuals were picked up random from the aliquots of the samples, except in the case of several poorly fossiliferous samples. The characteristics of seven assemblages of fossil Ostracoda are described in the following section.

1. *Schizocythere okhotskensis* Assemblage

This assemblage is characterised by the abundance of *Schizocythere okhotskensis* (more than 20% of the total number of individuals) and low ratios of subordinate species (less than 10% in most species). Common species among these subordinate species are *Hemicythere orientalis, Baffinicythere emarginata, B. howei, Aurila uranouchiensis, Urocythere* sp. A, *Urocythereis*? sp. B, *Patagonicythere* sp., *Semicytherura henryhowei, S. miurensis, Cytheropteron sawanense* and *Xestoleberis iturupica*. This assemblage is represented by samples from the Marine II facies (Text-fig. 2A) and Marine III facies (Text-fig. 2C) of the Lower Cycle and from the Brackish and Marine II facies of the Upper Cycle (Text-fig. 2B). This is the only one assemblage that is found both in the Lower and Upper Cycles. The assemblage found in the Lower Cycle is accompanied by the *Chlamys daishakaensis* Assemblage in the Marine II facies and the *Chlamys islandica* Assemblage in the Marine III facies respectively. The assemblage belonging to the Upper Cycle coexists with the *Crenomytilus grayanus* Assemblage in the Brackish facies and the *Patinopecten yessoensis* Assemblage in the Marine II. Ostracods are abundant in the Marine II and Brackish facies which were presumably deposited on the shallow fine- to coarse-grained, sandy bottom of a bank and coast respectively. In contrast, ostracods are few in the Marine III facies which was deposited on the coarse-grained sandy bottom of a high energy environment. Consequently, it may be possible to divide this assemblage into two "sub-assemblages", it seems, however, that the palaeoenvironmental difference did not affect the composition of the ostracod assemblages. A palaeoenvironmental characteristic common to these facies is the coarse-grained bottom independently of depth.

2. *Cytheropteron sawanense* Assemblage

This is represented by one sample from the Marine I of the Lower Cycle (Text-fig. 2C). This assemblage is marked by the dominance of *Cytheropteron sawanense* (more than 30%) and fewer numbers of subordinate species (all of them are less than 10%). These subordinate species are *Cythere lutea, Schizocythere okhotskensis, Hemicythere nana, Baffinicythere emarginata, Howeina higashimeyaensis, Semicytherura henryhowei* and *Paradoxostoma* sp. D. This assemblage is inferred to have lived on the fine-grained sandy bottom of a fairly deep sea (perhaps 100 m or more), because it is accompanied by the *Acila divaricata* molluscan Assemblage.

3. *Schizocythere okhotskensis – Baffinicythere emarginata – Urocythereis*? sp. B – *Cytheropteron sawanense* Assemblage

This is represented by samples from the Marine I and Marine II facies of the Lower Cycle (Text-fig. 2A). This assemblage is characterised by the equally common occurrence of these four species (about 10% for each species). Common species are *Cythere lutea, Baffinicythere howei, Finmarchinella "angulata", F.* sp. A of Tabuki (1980, MS), *Urocythereis gorokuensis, Howeina higashimeyaensis, Loxoconcha optima, Loxocorniculum mutsuense* and *Xestoleberis* sp. F. The assemblage in the Marine I facies is contained in the greenish-grey very fine-grained sandstone that was presumably deposited in a several tens of metres of water and accompanied by the *Cryptonatica janthostomoides* Assemblage. The same ostracod assemblage in the Marine II is, however, found in the grey coarse-grained sandstone which was deposited on the bank mentioned above, and accompanies the *Chlamys daishakaensis* Assemblage. The ostracods constituting this ostracod assemblage are considered to be allochthonous from the mode of molluscan fossil preservation. The high species-diversity also suggests that the assemblage is allochthonous formed by the mixing of several near-shore assemblages.

4. *Schizocythere okhotskensis – Baffinicythere emarginata – Urocythereis gorokuensis – Semicytherura henryhowei* Assemblage

This assemblage is similar in species composition to the one above, though the last two species are replaced by *Urocythereis gorokuensis* and *Semicytherura henryhowei.* It is characterised by the equally common occurrence of these four species which make up about 40% of the total population. Subordinate species are small in numbers except for *Aurila uranouchiensis* and *Howeina higashimeyaensis.* Only *Hemicythere*? sp. A occurs in all eight samples belonging to this assemblage. The subordinate species which are common among most samples are *Cythere lutea, Aurila uranouchiensis, Finmarchinella "angulata", F.* sp. A of Tabuki (1980, MS), *F. nealei, Xestoleberis iturupica* and *Sclerochilus* sp. A. This assemblage is restricted to the Marine II facies of the Upper Cycle (Text-figs. 2A, B), and is exclusively accompanied by the *Patinopecten yessoensis* Assemblage. This suggests that this ostracod assemblage was deposited on the fine-grained sandy bottom of a near-shore shallow sea. The weak bottom current which is inferred from the mode of occurrence of the molluscan fossils must have played a distinctive role in forming the assemblage. The high species-diversity also signifies that this ostracod assemblage is allochthonous.

5. *Semicytherura henryhowei – Finmarchinella "angulata"* Assemblage

This is also restricted to the Marine II facies of the Upper Cycle and is exclusively associated with the *Patinopecten yessoensis* Assemblage as is the above assemblage (Text-figs. 2A, B). This assemblage is peculiar in its lack of dominant or abundant species and in its high species-diversity. Only very few species ever make up more than 10% of the total individual numbers. Species found in all samples are *Schizocythere okhotsukensis, Baffinicythere emarginata, Aurila uranouchiensis, Finmarchinella "angulata", Semicytherura henryhowei, Loxocorniculum kotoraformum* and *Xestoleberis* sp. F. This assemblage is here named after *Semicytherura henryhowei* and *Finmarchinella "angulata"* which are fairly abundant among these common species. This assemblage is similar to the one above, although *Schizocythere okhotskensis, Baffinicythere emarginata* and *Urocythereis gorokuensis* are rare. It is uncertain what palaeoenvironmental difference caused the difference in composition of these two ostracod assemblages. The higher species-diversity, however, may indicate the mixing of a larger number of original assemblages in this assemblage than that in the previous one. Accordingly, a shallow near-shore sea is considered to have deposited the assemblage in association with fine-grained sand.

6. *Howeina camptocytheroidea* Assemblage

All the samples yielding this assemblage are confined to the Marine IV facies of the Lower Cycle (Text-figs. 2A, B). This assemblage is characterised by the dominance of *Howeina camptocytheroidea* (more than 30%, and in some samples more than 50%). Subordinate species are usually small in numbers except for *Urocythereis gorokuensis.* Common species are *Cythere lutea, Schizocythere okhotskensis,* and perhaps *Hemicythere orientalis.* This assemblage is found in grey siltstone and is accompanied by the *Lucinoma annulata* Assemblage. It is, therefore, obvious that the ostracod assemblage was deposited in the calm environment of the inner bay. Conversely, this assemblage would be a valuable indicator of such an environment.

7. *Cytheropteron* sp. – *Ruggieria* sp. Assemblage

This is also represented by several samples from the Marine IV facies of the Lower Cycle. This assemblage is characterised by the abundance of *Cytheropteron* sp. and *Ruggieria* sp. (more than 40% of these two species), and the scarcity of subordinate species. Common species are *Pontocythere miurensis, P.* sp. of Hanai (1961), *Cythere lutea, Hemicythere*? sp. A, *Mutilus* sp. of Hanai (1961), *Finmarchinella "angulata", F. nealei, Howeina neoleptocytheroidea, Semicytherura henryho-*

wei and *Loxoconcha* sp. B of Okada (1976, MS.). This ostracod assemblage was clearly deposited in a calm environment of the innermost bay, because it is contained in the grey siltstone and is accompanied by the *Raeta yokohamaensis* and *Macoma calcarea* Assemblages.

In conclusion, the value of the comparison between ostracod assemblages and sedimentary facies based on the molluscan assemblages was strongly confirmed. In the cold water Pliocene-Pleistocene sediments of the northwestern Pacific, the fossil Ostracoda formed distinctly different assemblages from each other depending on the different sedimentary facies. This will be a useful information for future studies in other areas. Moreover, it will be possible to clarify what kind of species increased or decreased in what kind of environment, because almost all the species are still living at the present day.

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The writer wishes to express his sincere gratitude to Professor Emeritus Tetsuro Hanai, University of Tokyo, under whose direction this study was made. Gratitude is also expressed to Professor Kiyotaka Chinzei, the Department of Geology and Mineralogy, Faculty of Science, Kyoto University, who read the original manuscript and gave the writer instructions during laboratory and field work. The writer is much indebted to him for invaluable advice and encouragment which stimulated the writer's work. The writer is grateful to Associate Professor Noriyuki Ikeya of the Geoscience Institute, Faculty of Science, Shizuoka University, who gave the writer the opportunity to start this work. Dr. Tomas M. Cronin of the U. S. Geological Survey corrected English manuscript and gave advice.

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The Evolution of High Diversity in the Ostracod Communities of the Upper Pliocene Faunas of St. Erth (Cornwall, England) and North West France

C. MAYBURY AND R. C. WHATLEY
University College of Wales, Aberystwyth, Wales

ABSTRACT

The Upper Pliocene ostracod faunas from St. Erth (England) and Cotentin, Rennes, Redon, Nantes, Angers and Vendée (North West France) are the most diverse known (567 species) with simple species diversity within the families Cytheruridae, Loxoconchidae, Cytherideidae, Leptocytheridae and Paradoxostomatidae most unusually high. The faunal composition of each of the 7 regions is described and comparisons with other Neogene to Recent faunas made. The high diversity is probably due to favourable preservation, high abundance, efficient niche exploitation, the mixing of brackish, marine, cold and warm water species and some degree of allopatric speciation due to partial isolation of faunas because of the incomplete transgression of the Armorican and Cornubian massifs.

INTRODUCTION

The Upper Pliocene ostracod faunas from St. Erth and the 16 French localities shown in Text-fig. 1 exibit abnormally high diversity. From a total of only 81 samples, no less than 567 species belonging to 93 genera were recovered. Twenty-three samples from St. Erth yielded 378 species and 58 from North West France yielded 384 species. This represents a much higher level of species diversity than has been previously recorded in the literature for any stratigraphical interval or geographical region.

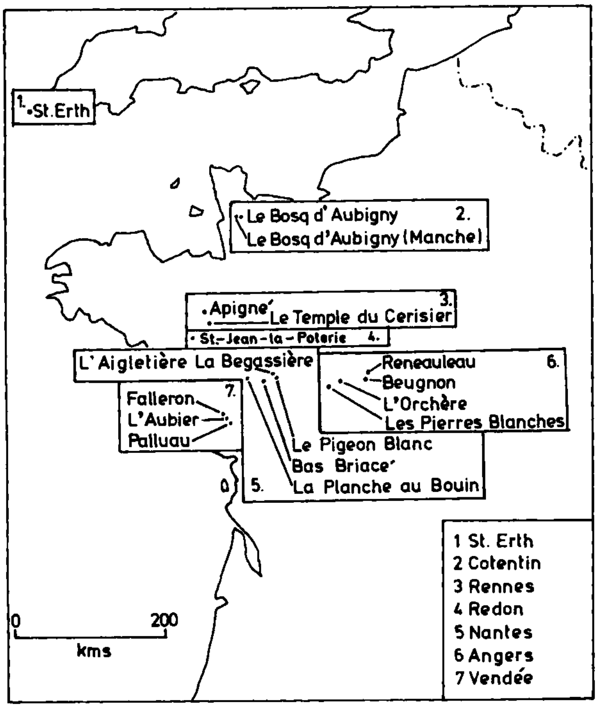
A further measure of the extraordinarily high diversity of these faunas, is that as many as 236 species were recovered from a single 50 gram wahsed residue sample at St. Erth and a sample of 49 grams washed residue at Le Temple du Cerisier yielded 240 species. This paper is devoted to the demonstration of this uniquely high diversity and also to a comparison with that of other selected Neogene to Recent faunas. In addition, a number of possible explanations are put forward to account for the richness of these faunas.

THE OSTRACODA OF ST. ERTH AND NORTH WEST FRANCE

Of the 378 species which occur at St. Erth, 183 (48%) do not occur in North West France and of the 384 species which occur in the latter area 189 (49%) do not occur at St. Erth. Thirty-four percent (195 species) of the total number of species from the two regions are common to both.

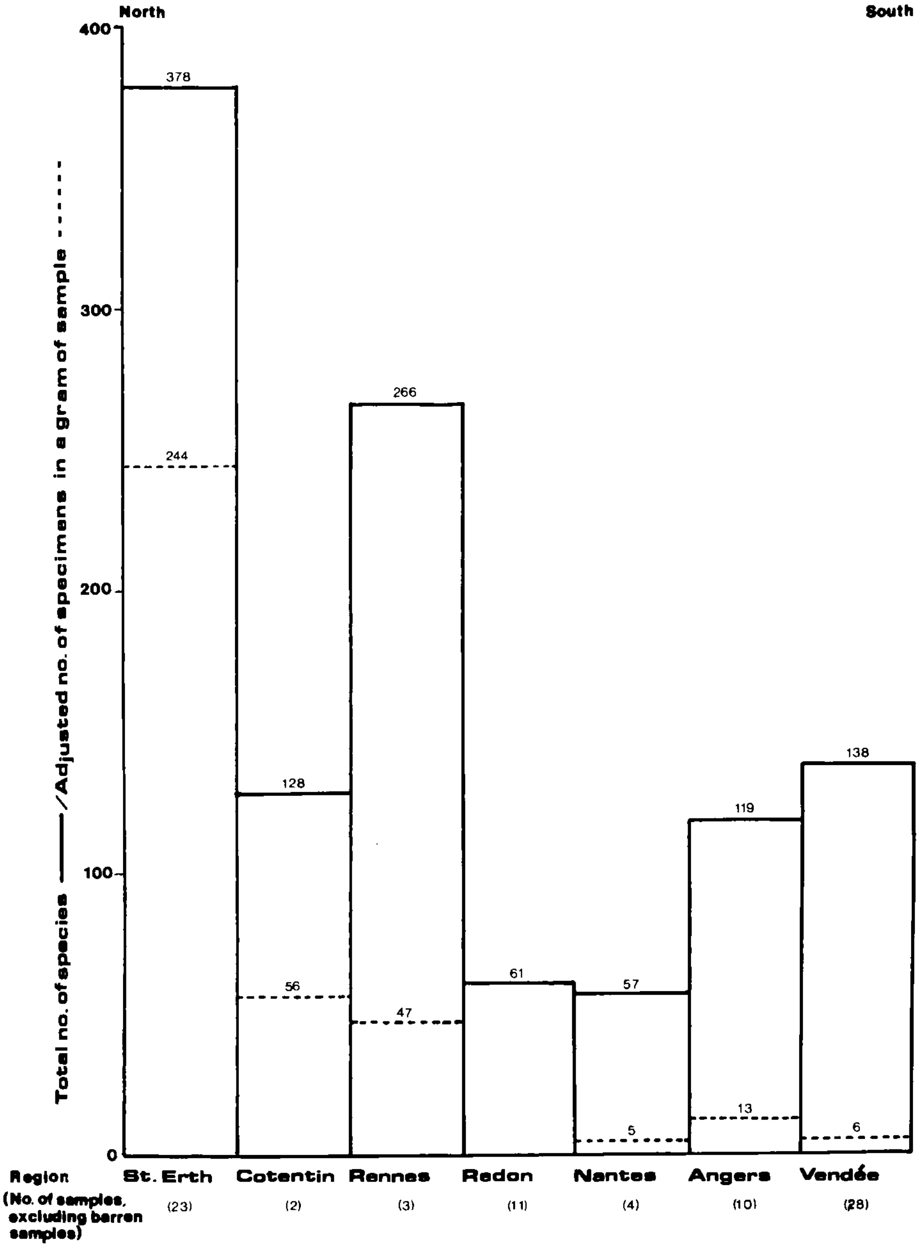
Given the fairly close proximity of the two regions, this percentage communality is relatively low and may be a pointer towards accounting for the overall high diversity of the faunas.

The localities in North West France are divided geographically into 6 regions: Cotentin, Rennes, Redon, Nantes, Angers and Vendée as shown in Text-fig. 1. These divisions were first made by Margerel (1968) in his study of Redonian Foraminifera and the sample localities occurring within each of the 6 regions in the present study are described in detail in this latter work and in Maybury (1985, MS.). The names and illustrations of all the 567 species quoted in this paper are also found in Maybury (1985, MS.).



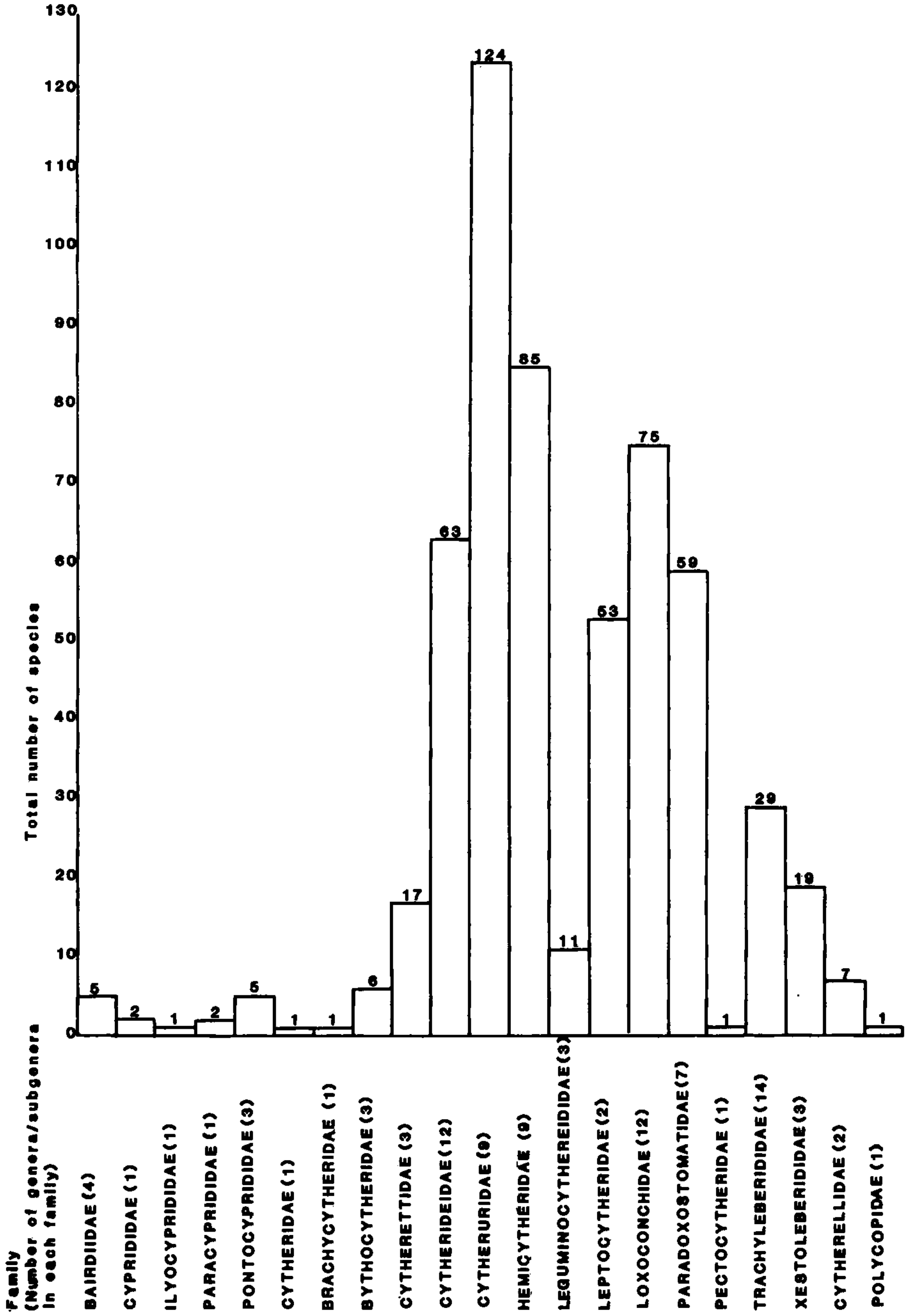
TEXT-FIG. 1—Sample localities and regions studied.

In Text-fig. 2 the total number of species for St. Erth and each of the 6 regions in France is given, together with the adjusted mean number of specimens per gram of washed residue. (It was necessary to calculate the latter value as not all the samples were of equal weight and there was not an equal number of samples from each of the regions studied). The simple species diversity of the St. Erth fauna is 30% higher than that of Rennes, the most diverse of the French localities. The mean diversity of all six French regions together is 128 species which is 34% less than that of St. Erth. However, the relatively large number of species from Rennes was from only 3 samples. It was not possible to adjust the weights of the washed residues from Redon, since the fauna was sent to the author in picked faunal slides. Text-fig. 3, however, shows clearly the remarkably higher incidence per gram at St. Erth when compared with the French localities. The mean number of specimens per gram of washed residue at St. Erth is 244 while the mean for the 5 French localities for which data is available is 25 specimens per gram or 90% less than at St. Erth. This is probably in large measure a function of the much finer grained lithology of the St. Erth deposit compared to the coarser, more arenaceous Pliocene "faluns" of North West France.



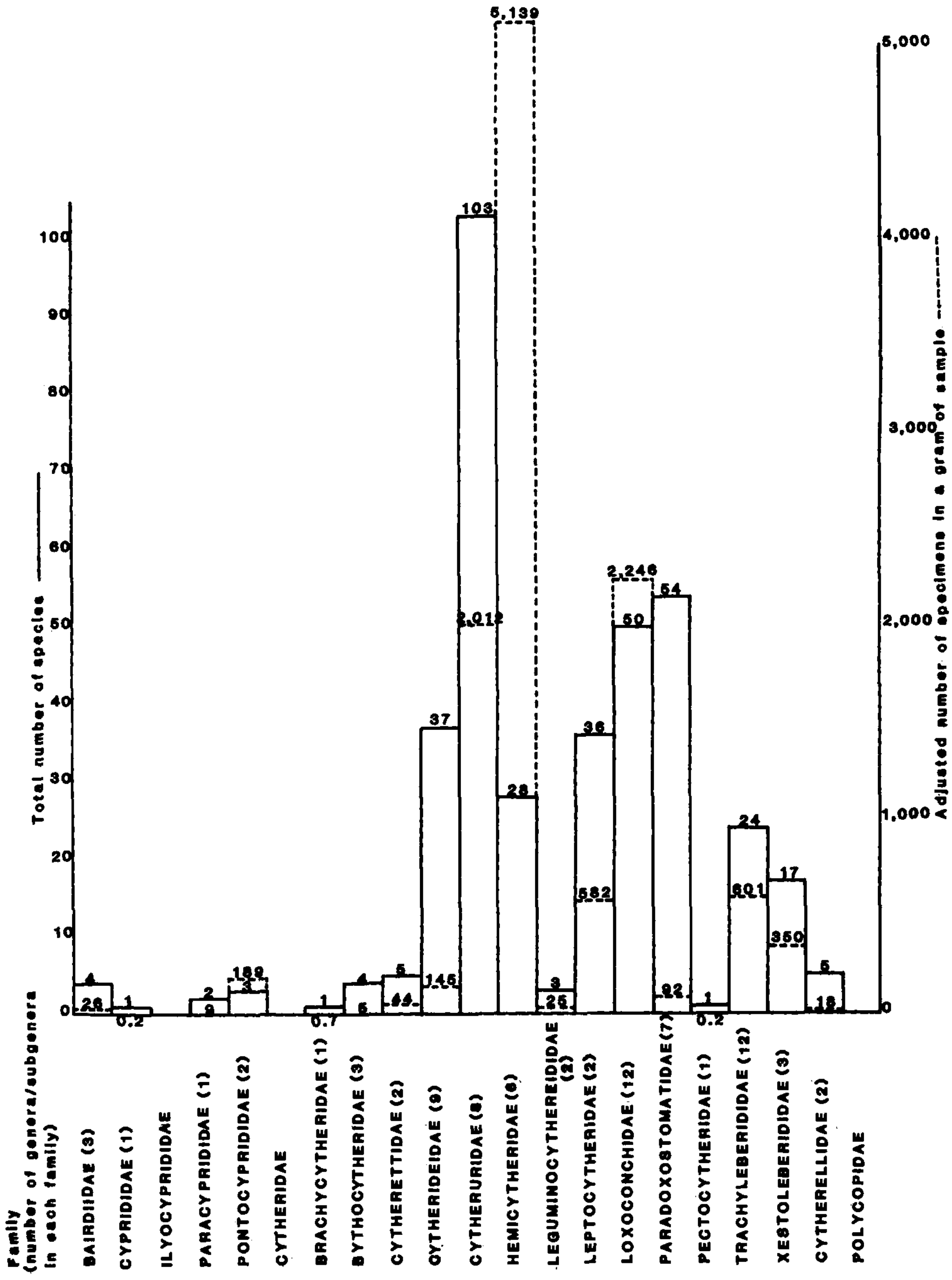
TEXT-FIG. 2—Species and specimen distribution.

Text-fig. 3 gives the total number of species in each family for both the Cornish and French faunas. The purpose of the histogram was to ascertain whether this high diversity was reflected across a wide or more restricted range of taxa. The histogram indicates clearly that the diversity is by no means equally distributed. Some families are very rare and others are only poorly represented. However, in the main, these latter families are those which one would not expect to have



TEXT-FIG. 3—Total number of species in each family based on all samples from St. Erth and North West France.

Total number of families = 21
Total number of genera/subgenera = 93
Total number of species/subspecies = 567
Total number of specimens* = 78,357



TEXT-FIG. 4—Total number of specics and adjusted number of specimens in a gram of sample in each of the families occurring at St. Erth calculated as a mean of all 23 samples which yielded Ostracoda.

Total number of families = 18
Total number of genera/subgenera = 77
Total number of species/subspecies = 378
Total number of specimens = 66,462

achieved prominence in a North West European, Upper Pliocene, shallow water environment. Those families on the left of Text-fig. 3 being prime examples. On the contrary the diversity of the Cytheruridae, Loxoconchidae, Cytherideidae, Leptocytheridae and Paradoxostomatidae is unusually high. That of the Hemicytheridae is also abnormally high, but this family in some other faunas often exhibits the highest diversity and it is perhaps surprising to see it ranking second to the Cytheruridae in the present study.

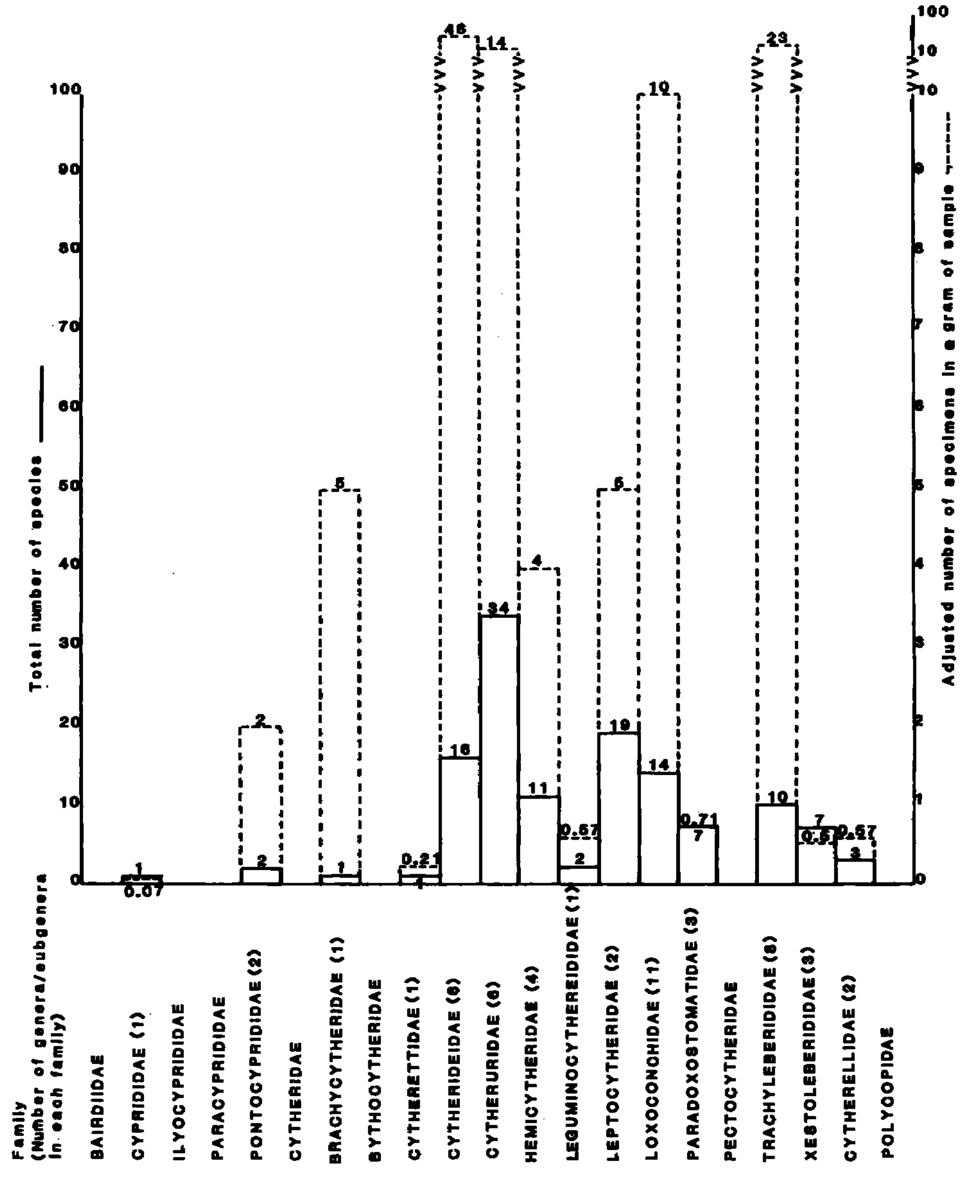
In Text-fig. 4, the total number of species and adjusted number of specimens per gram by family is given for the St. Erth fauna. The main difference between this histogram and that of Text-fig. 3, for the combined Cornish and French fauna is that, in the former, three families are absent (Ilyocyprididae, Cytheridae, Polycopidae) and that the most diverse family, the Cytheruridae is approximately 52% more diverse than its nearest rival, the Paradoxostomatidae. The 103 cytherurid species at St. Erth representing as they do 83% of the total of 124 cytherurid species of the entire study, must surely be in part a reflection of the fine grained nature of the St. Erth lithology and low energy levels of deposition since this group contains most of the "small" ostracod species in the study. It is, however, very surprising to find that the Paradoxostomatidae should be the second most diverse family with 54 species. Again this family's total number of species from the combined faunas is made up by a very high percentage from St. Erth (92%). The number of species of the Loxoconchidae (50 species), Cytherideidae (37 species), Leptocytheridae (36 species) are much higher than in other faunas known to the authors. The Hemicytheridae are sixth in the ranking order of families by species diversity (28 species). This is surprising since the first impression one gains in studying the ostracods of St. Erth is the overwhelming superabundance of the single hemicytherid genus, *Aurila*. This, of course, is reflected in the very high incidence per gram of the family. Also of significance is the high diversity of the Xestoleberididae at St. Erth. No less than 17 of the 19 total species for the combined faunas occur there (89%) and these, together with the paradoxostomatids, suggest a weed rich palaeoenvironment.

Text-fig. 4 clearly shows that there is no definite relationship between diversity and incidence. For example, the mean adjusted incidence per gram of washed residue for the most diverse family, the Cytheruridae is 2,246 specimens, while for the sixth most diverse family, the Hemicytheridae the enormously high figure of 5,139 is calculated. The Loxoconchidae, with 50 species and 22,146 specimens per gram are much more abundant than the Paradoxostomatidae with 54 species but only 92 specimens per gram. Similarly, the Leptocytheridae with 36 species and 582 specimens per gram are approximately 4 times more abundant than the Cytherideidae with 37 species but only 145 specimens per gram. The high incidence of the Pontocyprididae, with 189 specimens per gram, is not matched by their diversity of only 3 species.

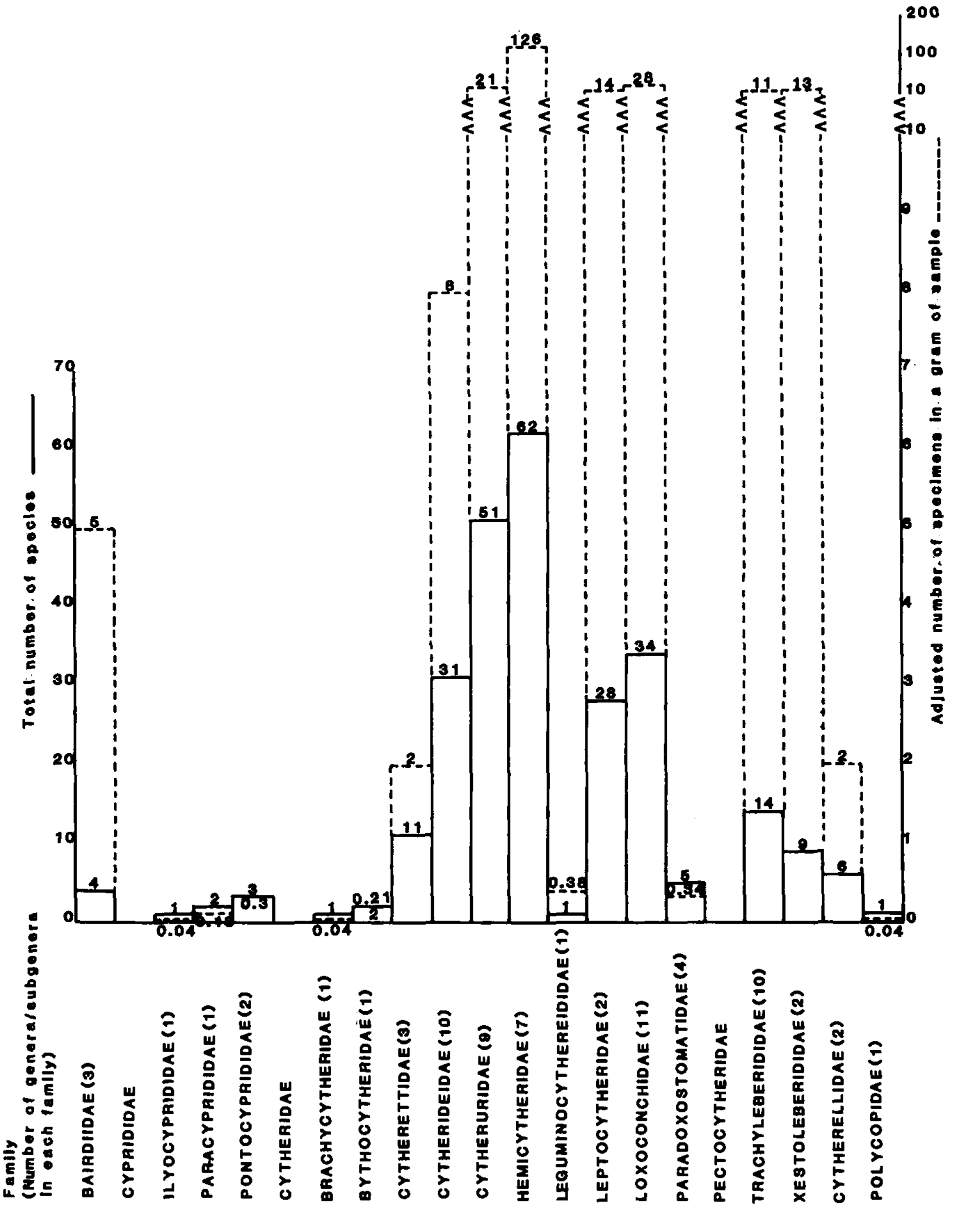
Text-fig. 5 shows, as a histogram, the distribution of the species among the 14 families which occur in the Cotentin Region and also gives the adjusted mean number of specimens which occur in one gram of washed residue. The Cytheruridae in this region are again the most diverse family although represented by only 34 species. The next most diverse family is the Leptocytheridae (19 species) followed by the Cytherideidae (16 species) and the Loxoconchidae (14 species).

The fauna of the Cotentin region with 128 species is much less diverse than that of St. Erth although it must be remembered that these 128 species were recovered from only 2 samples. By comparison with other faunas, as indicated later in this paper, this figure, nonethless, represents a high diversity fauna. The mean calculated incidence of the fauna is much lower than at St. Erth and overall there is a much closer relationship between incidence and diversity as Text-fig. 5 shows.

The distribution of species among the 18 families occurring in the 3 samples studied in the Rennes region and their calculated mean incidence per gram washed residue is given in Text-fig. 6. This is the first of the faunas analysed in which the Cytheruridae do not rank first; at Rennes they take second place to the Hemicytheridae. The Loxoconchidae, Cytherideidae and the Leptocytheridae respectively rank next after the Cytheruridae. The total simple species diversity of 266 is considerably higher than that of the Cotentin region as is the mean incidence. Both in the



TEXT-FIG. 5—Total number of species and adjusted number of specimens in a gram of sample in each of the families occurring in the Cotentin Region calculated as a mean of the 2 samples which yielded Ostracoda.
Total number of families = 14
Total number of genera/subgenera = 51
Total number of species/subspecies = 128
Total number of specimens = 1,572



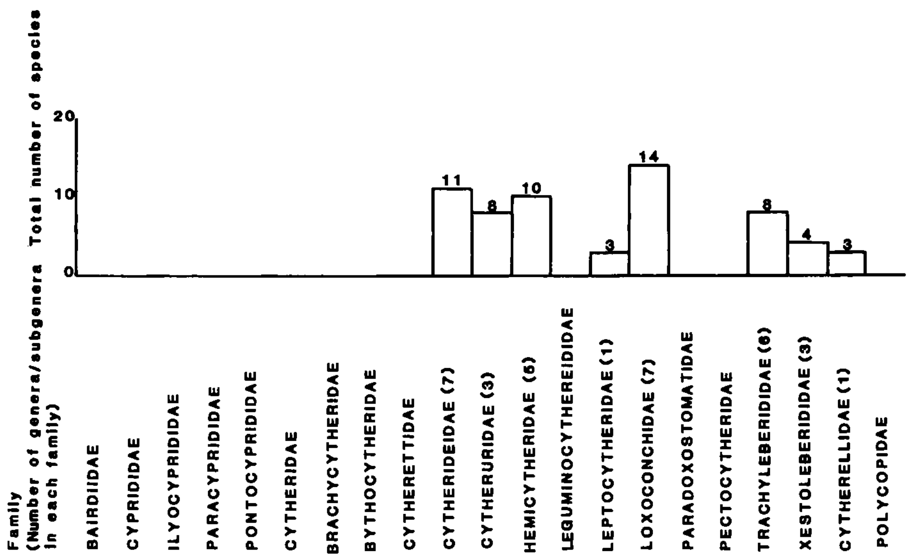
TEXT-FIG. 6—Total number of species and adjusted number of specimens in a gram of sample in each of the families occurring in the Rennes Region calculated as a mean of the 3 samples which yielded Ostracoda.

Total number of families	=	18
Total number of genera/subgenera	=	71
Total number of species/subspecies	=	266
Total number of specimens	=	5,475

Rennes and the Cotentin regions, the Paradoxostomatidae are notably less significant than they are at St. Erth.

As Text-fig. 7 demonstrates, the fauna of the Redon region, represented by only 61 species and 8 families is relatively impoverished. No data on incidence for the 11 samples is available for reasons already stated. In this region the 5 most diverse families are the Loxoconchidae, Cytherideidae and Hemicytheridae respectively with the Cytheruridae and Trachyleberididae joint fourth.

Within the context of this study, the fauna of the Nantes region, as demonstrated in Text-fig. 8 is also relatively impoverished. The 4 samples examined from this region yielded only 57 species belonging to 10 families. The Hemicytheridae is the most diverse family and is followed by the



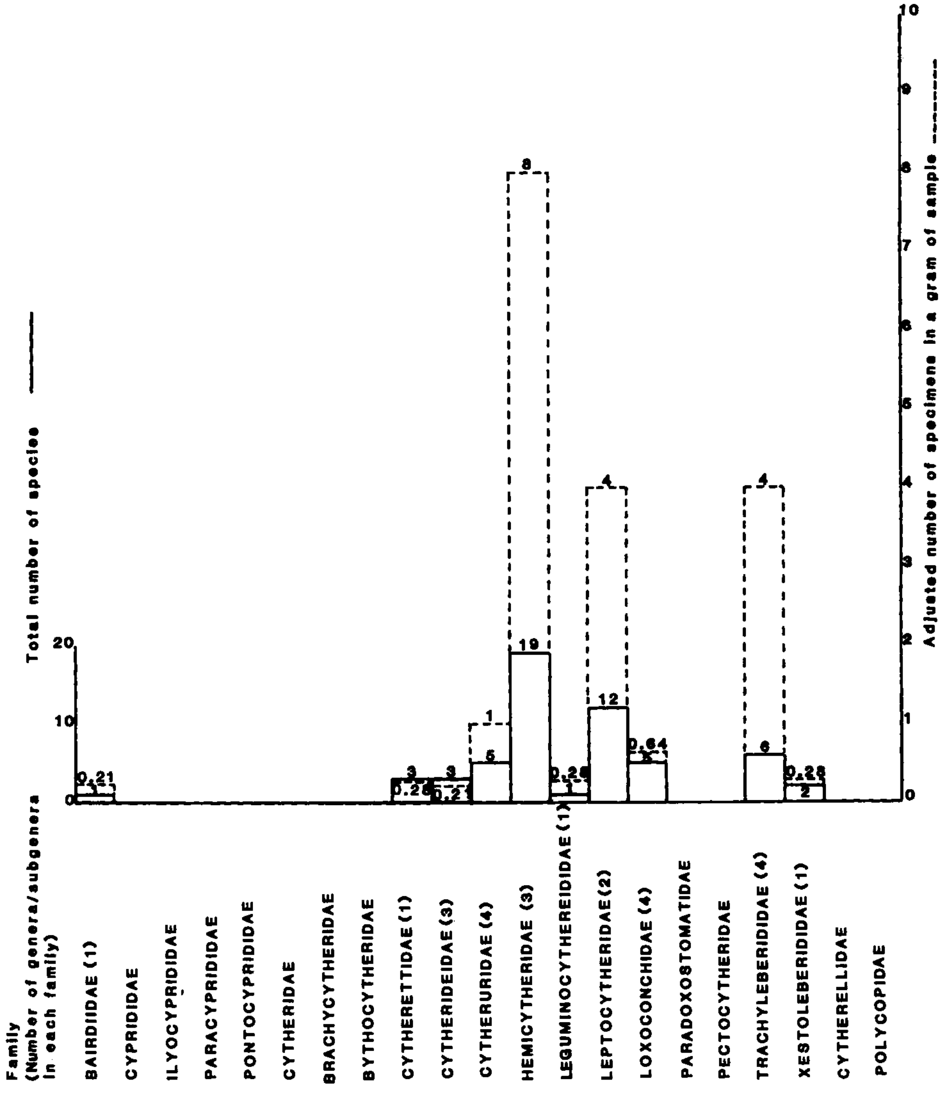
Text-fig. 7—Total number of species in each of the families occurring in the 11 samples which yielded Ostracoda in the Redon Region.
Total number of families = 8
Total number of genera/subgenera = 33
Total number of species/subspecies = 61
Total number of specimens = 260

Table 1—The Ten Most Diverse Families for St. Erth and North West France in Ranking Order (Number in brackets refer to the ranking position of the family in the other region).

St. Erth				North West France			
Cytheruridae	(2)	103 spp.	27.2%	Hemicytheridae	(6)	78 spp.	20.3%
Paradoxostomatidae	(8)	54	14.3	Cytheruridae	(1)	72	18.7
Loxoconchidae	(3)	50	13.2	Loxoconchidae	(3)	53	13.8
Cytherideidae	(4)	37	9.8	Cytherideidae	(4)	47	12.2
Leptocytheridae	(5)	36	9.5	Leptocytheridae	(5)	39	10.2
Hemicytheridae	(1)	28	7.4	Trachyleberididae	(7)	20	5.2
Trachyleberididae	(6)	24	6.3	Cytherettidae	(9)	15	3.9
Xestoleberididae	(9)	17	4.5	Paradoxostomatidae	(2)	14	3.6
Cytherettidae	(7)	5	1.3	Xestoleberididae	(8)	12	3.1
Cytherellidae	(11)	5	1.3	Leguminocythereididae	(13)	9	2.3

Leptocytheridae, Trachyleberididae, and the two equal fourth ranking families: the Cytheruridae and the Loxoconchidae. Diversity is low and is closely related to incidence per gram.

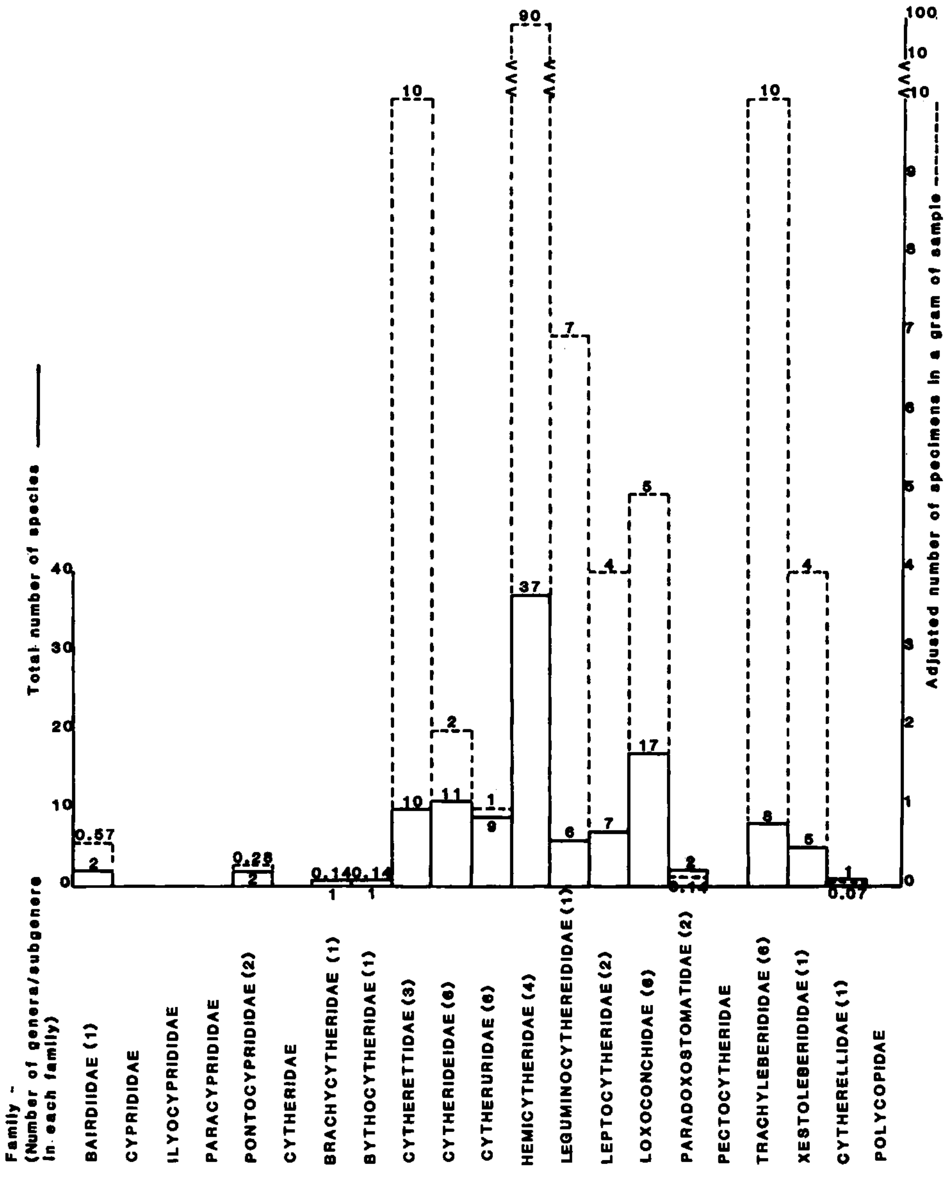
Text-fig. 9 is a histogram of the distribution of species by family and mean incidence per gram of washed residue for the 10 samples studied from the Angers region. The fauna is considerably more diverse than that of the Redon and Nantes regions with 119 species belonging to



TEXT-FIG. 8—Total number of species and adjusted number of specimens in a gram of sample in each of the families occurring in the Nantes Region calculated as a mean of the 4 samples which yielded Ostracoda.

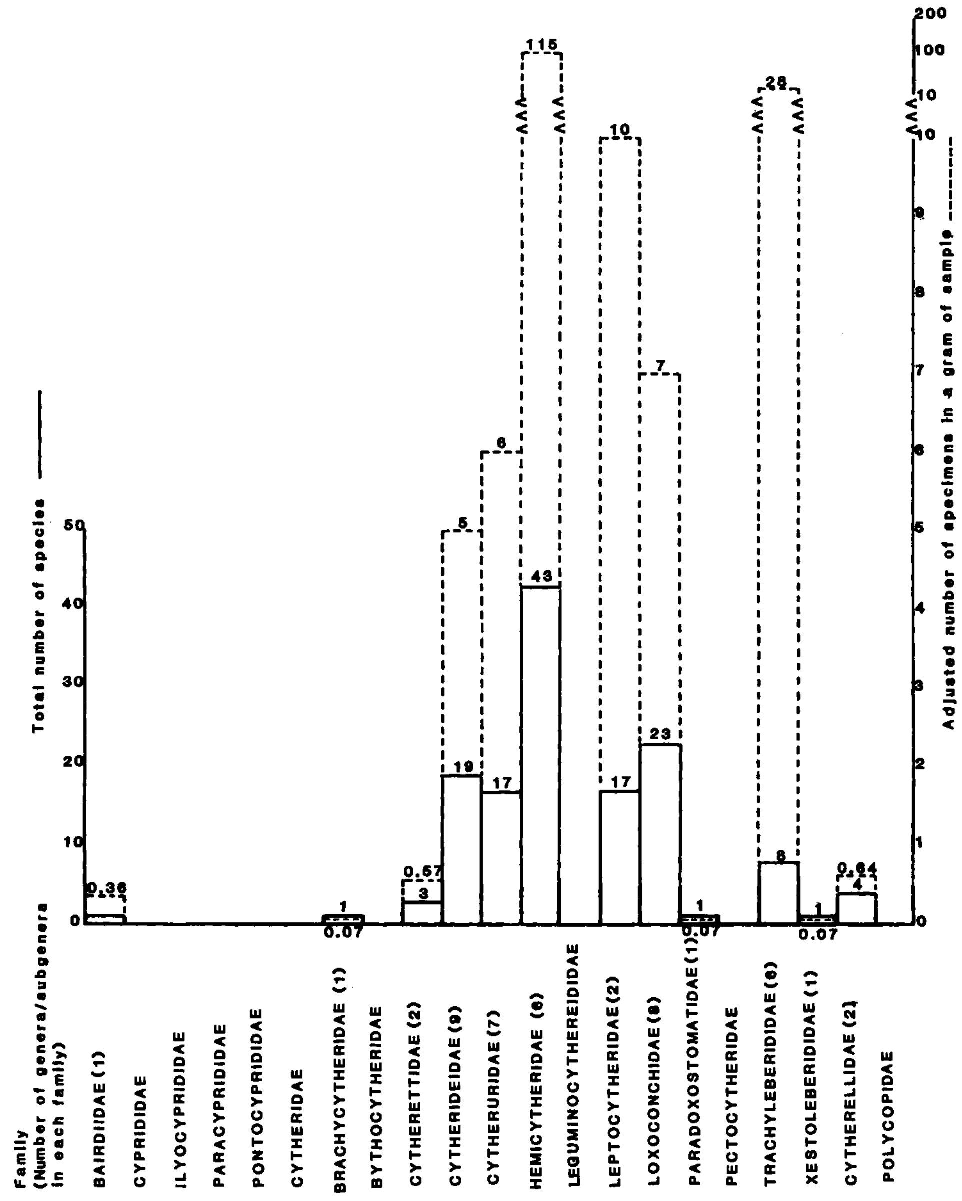
Total number of families = 10
Total number of genera/subgenera = 24
Total number of species/subspecies = 57
Total number of specimens = 269

15 families. Apart from the Hemicytheridae, with 90 specimens per gram of washed residue, incidence is generally low. The Hemicytheridae, with 37 species are by far the most diverse family followed by the Loxoconchidae (17 species), Cytherideidae (11 species), Cytherettidae (10 species and the Cytheruridae (9 species).



TEXT-FIG. 9—Total number of species and adjusted number of specimens in a gram of sample in each of the families occurring in the Angers Region calculated as a mean of the 10 samples which yielded Ostracoda.

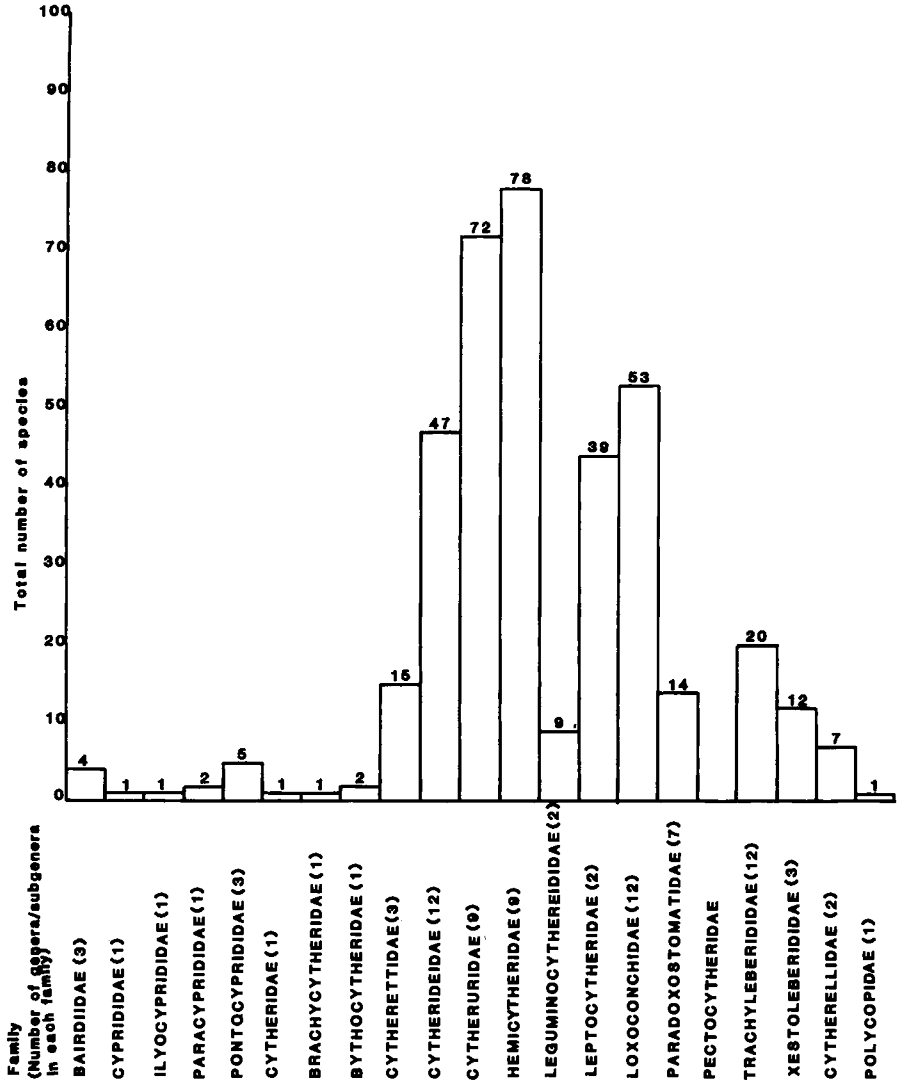
Total number of families = 15
Total number of genera/subgenera = 43
Total number of species/subspecies = 119
Total number of specimens = 1,881



TEXT-FIG. 10—Total number of species and adjusted number of specimens in a gram of sample in each of the families occurring in the Vendée Region calculated as a mean of the 28 samples which yielded Ostracoda.

Total number of families	=	12
Total number of genera/subgenera	=	46
Total number of species/subspecies	=	138
Total number of specimens	=	2,438

Text-fig. 10 shows that 138 species belonging to 12 families were recovered from the 28 samples studied in the Vendée. Given the relatively large number of samples, the largest from any of the French regions and 5 more than the productive samples from St. Erth, the diversity is relatively low (only within the context of this study, of course). The Hemicytheridae with 43



Text-fig. 11—Total number of species in each of the families occurring in North West France in all 58 of the samples which yielded Ostracoda.

Total number of families = 20
Total number of genera/subgenera = 86
Total number of species/subspecies = 384
Total number of specimens = 11,895

species, has more than twice the number of species of the second ranking family, the Loxoconchidae with 23. The third most diverse family is the Cytherideidae with the Cytheruridae and the Leptocytheridae joint fourth. Apart from the Hemicytheridae, with a mean adjusted figure of 115 specimens per gram of washed residue, the incidece is low. Diversity is closely related to incidence.

Text-fig. 11 is a composite histogram showing the distribution of all the 384 species by family, recovered from all the samples studied in North West France. It is not possible to give the mean incidence per gram because this data is not available for one of the French regions. The most diverse family is the Hemicytheridae with 78 species followed by the Cytheruridae (72 species), Loxoconchidae (53 species) and the Cytherideidae (47 species) respectively.

It is instructive to compare Text-fig. 11 with Text-fig. 4, which presents the same data with respect to the St. Erth fauna. The ten most diverse families in rank order for each fauna is given in Table 1.

Although 3 families (Loxoconchidae, Cytherideidae and Leptocytheridae) rank equally in the Cornish and French faunas and others such as the Trachyleberididae, Xestoleberididae and Cytheruridae are only displaced by one rank, other families rank very differently within the two faunas. For example, the Paradoxostomatidae decline from second ranking in species diversity at St. Erth to eighth in North West France and the Hemicytheridae which ranks first in the French fauna is only sixth at St. Erth. The Cytherettidae rank seventh in North West France and ninth at St. Erth. Many genera in this family are distinctly thermophilic and their enhanced importance in the French fauna is probably a significant indication of higher palaeotemperatures for the more southern region. The high diversity of the Paradoxostomatidae at St. Erth is probably indicative of the greater availability of phytal substrates there than in any of the French localities. The overwhelming dominance of the Cytheruridae at St. Erth (13% more diverse than the second ranking family) has no parallel in the French fauna in which the Hemicytheridae, the first ranking family, only exceeds the second family, the Cytheruridae, by 1.6%.

A COMPARISON OF THE DIVERSITY OF THE UPPER PLIOCENE OSTRACOD FAUNAS OF ST. ERTH AND NORTH WEST FRANCE WITH THAT OF OTHER FOSSIL AND RECENT OSTRACOD FAUNAS

In many cases it was difficult to make direct comparisons of the present faunas and those of other published or MS. accounts of ostracod faunas because many published works are concerned with only certain elements of fauna and in some papers, the reader is left to guess the number or size of the samples studied. Despite some anomalies, there has been a general increase in ostracod diversity since the Palaeozoic. Some Mezozoic faunas are very diverse, *e.g.*, Ware (1978 MS.) recovered 100 species from a 9 inch thick mammal bearing, marly clay in the Upper Bathonian of Oxfordshire, England. However, since Palaeozoic and Mesozoic Ostracoda differ from those of the post Cretaceous at the generic and to a certain extent familial level, and since the fauna of the present study is of late Neogene age, this analysis of selected faunas is confined to the Neogene to Recent interval.

MIOCENE

The Miocene Ostracoda of the Aquitaine Basin were described by Moyes (1965). He recorded 117 species belonging to 64 genera and 19 families. The precise number of samples studied by Moyes is not possible to determine from his paper, however, he appears to have examined at least one sample from 21 outcrop localities and 49 boreholes. This fauna has 450 species less than the number recovered in the present study, 29 less genera and 2 less families. When compared to the St. Erth fauna alone, the fauna described by Moyes has 261 less species and 13 less genera. The present fauna from North West France contains 267 more species and 22 more genera than the Miocene fauna of the Aquitaine Basin.

Another French fauna was described by Carbonnel (1969). The ostracods from this fauna were predominantly Miocene in age; but a few Pliocene species are also figured and described. The number of samples studied by Carbonnel is not stated. The fauna comprised 121 species, 56 genera and 18 families. This is 446 species less than that from the present study and 37 less genera. Compared solely with the St. Erth fauna, that described by Carbonnel comprises 257 less species and 21 less genera. Compared to the fauna of North West France, Carbonnel's fauna contains 263 less species and 30 less genera.

Whatley and Downing (1983) recorded 98 species belonging to 44 genera from a single large Miocene sample from South East Australia. Although this is a high number of species to be recovered from a single sample, it should be compared with 236 species from a single sample from St. Erth and 240 from one of the French samples of this study.

Whatley (1983), using data from a MS. in preparation by Harlow, records 238 species belonging to 62 genera from 48 × 50 c.c. Miocene D.S.D.P. samples from the South West Pacific. Although this represents very high diversity for a deep sea fauna, it must be remembered that Harlow's samples embrace an enormous area of the South West Pacific and encompass a latitudinal range of some 60°. Also, the number of species per sample in Harlow's study never exceeds 50.

PLIOCENE

The Coralline Crag of East Anglia is approximately contemporaneous (Upper Pliocene) with the fauna studied herein. Its fauna is strikingly less diverse, however, with only 62 species belonging to 42 genera and 17 families (Wilkinson, 1980). This represents 505 species less than recovered in the present study (316 less than St. Erth and 322 less than North West France) and 51 less genera (35 less than St. Erth and 44 less than North West France).

Carbonnel and Ballesio (1982) described a Pliocene fauna from South East France and recorded 90 marine species (52 lacustrine species are excluded from this analysis) belonging to 53 genera and 15 families. The number of samples studied is not given but they were collected from 28 different localities. It is difficult to understand why this fauna is so much less diverse than that of the present study.

A fauna of similarly low diversity is described from the late Pliocene of the Greek Island of Kos by Mostafawi (1981). He records only 89 species belonging to 42 genera and 17 families.

Whatley (1983) using data from Downing (MS. in preparation) records 200 species belonging to 50 genera from 61 Pliocene D.S.D.P. samples from the South West Pacific referred to above, this material covers a huge area and was sampled throughout the Pliocene rather than being confined to the late Pliocene as is the case with the present study.

QUATERNARY

The most diverse ostracod fauna of Quaternary age known to the authors is that documented by Whatley (1983) from 52 samples from 12 widely separated D.S.D.P. sites in the South West Pacific. This fauna, a composite of 2 Magister (Dainty, 1984, MS. and Smith, 1983, MS.) and one doctoral study in preparation (Ayress) comprises no less than 365 species. While this is 202 species less than that of the total for the present fauna, it is only 13 species less than the St. Erth fauna and 19 less than the fauna from North West France. By any standards it is a highly diverse fauna, which includes only those species autochthonous to the Quaternary deep sea environment of the area. No other deep sea fauna has yet been encountered which approaches this level of species diversity. Its generic diversity is, however, with 58 genera, considerably lower than the 93 genera encountered in the present study.

Whatley and Kaye (1971) described a fauna of Ipswichian age from Selsey, Sussex. Although from near the mouth of the Pleistocene Solent River, and therefore probably not fully marine, this fauna comprised 62 species belonging to 31 genera. Of the 5 samples Whatley and Kaye studied, 3 clearly represented low salinity palaeoenvironments.

RECENT

British Waters

Wall (1969, MS.) in a study of the Ostracoda of Cardigan Bay in the southern Irish Sea, encountered 71 species belonging to 33 genera and 11 families. His study was based on a total of approximately 30,000 specimens from 504 samples, of which 230 were areal sediment samples, 126 seasonally duplicated sediment samples and 148 weed samples.

Whittaker (1972, MS.) in a study of two essentially brackish water environments, Christchurch Harbour and The Fleet, together with marine samples from Weymouth Bay, lists only 60 species in 29 genera and 12 families.

Ralph (1983, MS.) encountered a much larger fauna from the western seaboard of Britain. However, his study embraced a much larger area including sediment samples from a wide area of the southern Irish Sea, West of the St. George's Channel, Caernarvon Bay and the Malin Sea, to the North of Ireland. He examined 393 samples of which 259 yielded Ostracoda. His approximately 15,800 specimens belonged to 171 species, 69 genera and 18 families. This is the most comprehensive account of British, Recent marine Ostracoda known to the author yet, despite its relatively high diversity, it falls short of that documented in the present study although it covers a similar areal extent.

North East Atlantic

Yassini (1969) in an ecological study of ostracods collected from the Arcachon Bay and Bay of Biscay from depths of 0–5,000 m described 106 species belonging to 62 genera. Although ecological data is provided for each of the species Yassini encountered, the exact number of samples that he analysed is unclear.

Ralph (1977, MS.) recovered 61 species (39 genera of 15 families) from 12 samples of the estuary and the adjacent continental shelf of the Rias of Pontevedra and Vigo (North West Spain). Ralph's study encompassed a depth range of from 8–83 fm.

Mediterranean

The diversity of three Recent Mediterrean faunas is analysed for comparison with the present study. Puri, Bonaduce and Gervasio (1969) studied 70 bottom samples on an East-West transverse from Port Said through the Nile Cone, the Herodotus Abyssal Plain, the Mediterranean Ridge and the Sicilian Basin to Gibraltar. From this transect of some 2,200 miles, these authors encountered 132 species belonging to 48 genera and 17 families. Considering the very considerable depth range sampled, the fauna recovered is of low diversity compared to the present study.

Bonaduce, Ciampo and Masoli (1975) examined 73 grab samples from a comprehensive range of depths in the Adriatic. They describe a very rich fauna of 246 species of 81 genera. Although more than 100 species less than either the St. Erth or the North West France fauna, it is, nonetheless, one of the highest diversity faunas yet described from an equivalent area in the Recent.

In the western Mediterranean, from a narrow continental shelf zone of the Bou-Ismail Bay area, west of Algiers, Yassini (1979b) from 49 bottom samples and 7,952 specimens, described 115 species belonging to 54 genera.

Space and time do not allow a more exhaustive treatment of other faunas here. However, even very rich tropical and equatorial faunas described from various parts of the world usually do not exceed 150–160 species. For example, Titterton (1984, MS.) in a study of 31 bottom sediment samples from Guadalcanal and 6 from Shortland Island in the Solomon Islands, recovered only 156 species of 55 genera.

Table 2 is designed to compare the distribution of species by family of the faunas of the two regions of the present study and 9 other Miocene to Recent faunas from Europe. Both actual numbers and percentages of the total faunas are given. This exercise has been undertaken to compare the distribution of species by families of the present study with that of other faunas in order to determine whether this will shed light on the reasons why the present fauna is so diverse.

TABLE 2—THE DISTRIBUTION OF SPECIES (ACTUAL NUMBER AND PERCENTAGE) BY FAMILY FOR THE PRESENT STUDY AND THE NINE COMPARATIVE FAUNAS.

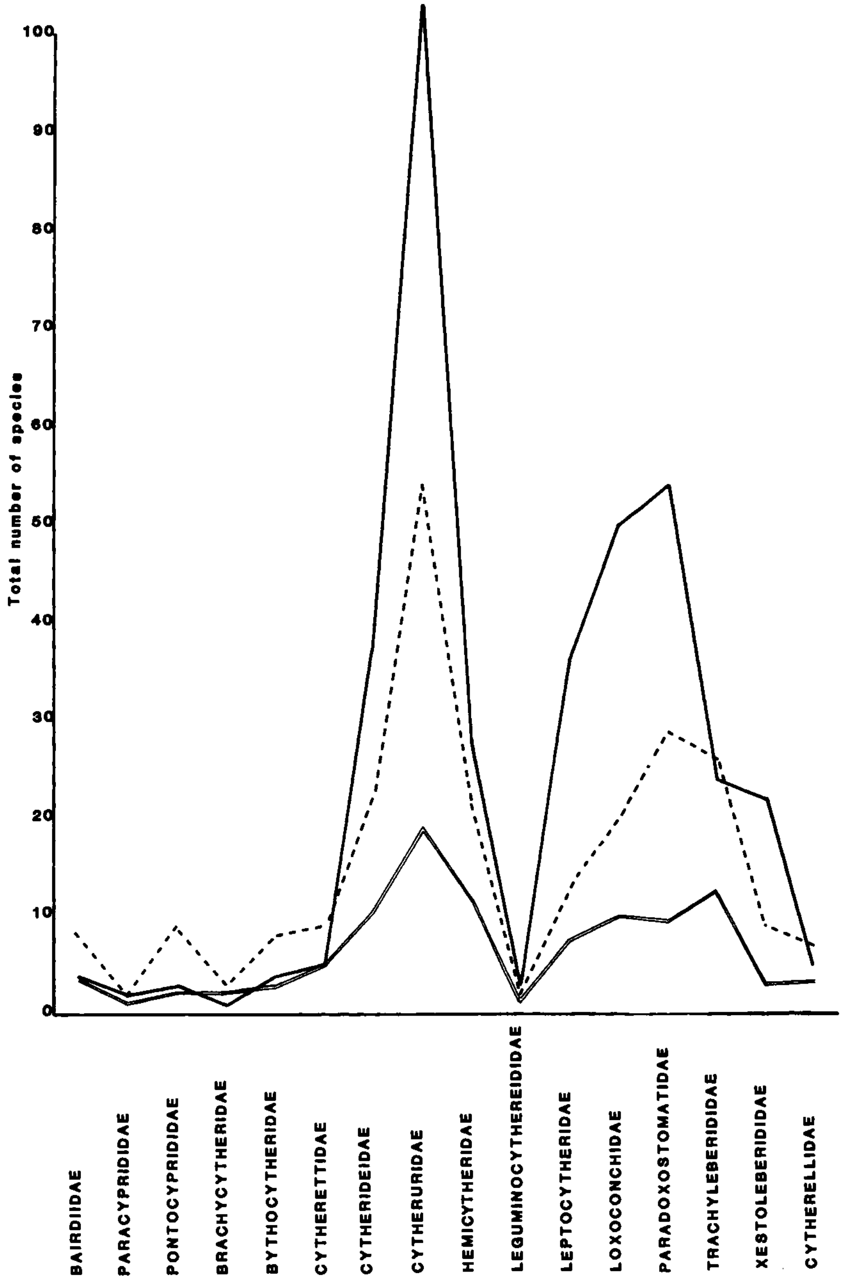
Family	Present study		Comparative faunas								
No. of species / % of total no. of species	St Erth	N.W. France	Recent Irish Sea Wall (1969 MS)	Recent English S. Coast Whittaker (1972 MS)	Recent Irish & Malin Seas Ralph (1983 MS)	Pliocene Coralline Crag Wilkinson (1980)	Neogene Rhône Valley Carbonnel (1969)	Miocene Aquitaine Basin Moyes (1965)	Pliocene S.E. France Carbonnel Ballesio (1982)	Recent Mediterranean Puri *et al.* (1969)	U. Pliocene Kos, Greece Mostafawi (1981)
BAIRDIIDAE	4 / 1.1	4 / 1.0			4 / 2.3	2 / 3.2	1 / 0.8	7 / 6.0	4 / 4.4	8 / 6.1	2 / 2.2
CYPRIDIDAE	1 / 0.3	1 / 0.3			1 / 0.6	1 / 1.6		1 / 0.9		2 / 1.5	2 / 2.2
ILYOCYPRIDIDAE		1 / 0.3						1 / 0.9			1 / 1.1
PARACYPRIDIDAE	2 / 0.5	2 / 0.5			1 / 0.6	1 / 1.6		2 / 1.7	1 / 1.1		1 / 1.1
PONTOCYPRIDIDAE	3 / 0.8	5 / 1.3	1 / 1.4	1 / 1.7	3 / 1.8	1 / 1.6	2 / 1.7	2 / 1.7	1 / 1.1	9 / 6.8	1 / 1.1
CYTHERIDAE		1 / 0.3	2 / 2.8	1 / 1.7	1 / 0.6		1 / 0.8	2 / 1.7		1 / 0.8	
BRACHYCYTHERIDAE	1 / 0.3	1 / 0.3	1 / 1.4		2 / 1.2	1 / 1.6		3 / 2.6	3 / 3.3	2 / 1.5	3 / 3.4
BYTHOCYTHERIDAE	4 / 1.1	2 / 0.5	4 / 5.6	1 / 1.7	8 / 4.7	1 / 1.6	2 / 1.7	1 / 0.9		4. / 3.0	
CYTHERETTIDAE	5 / 1.3	15 / 3.9				3 / 4.8	6 / 5.0	9 / 7.7			2 / 2.2
CYTHERIDEIDAE	37 / 9.8	47 / 12.2	6 / 8.4	3 / 5.0	17 / 9.9	8 / 13.0	22 / 18.2	16 / 13.4	12 / 13.3	5 / 3.8	4 / 4.5
CYTHERURIDAE	103 / 27.8	72 / 18.7	21 / 29.6	11 / 18.3	54 / 31.6	14 / 22.6	16 / 13.2	9 / 7.7	8 / 8.9	24 / 18.2	14 / 15.7
HEMICYTHERIDAE	28 / 7.4	78 / 20.3	4 / 5.6	5 / 8.3	11 / 6.4	7 / 11.3	20 / 16.5	17 / 14.5	22 / 24.4	6 / 4.5	13 / 14.6
LEGUMINOCYTHEREIDIDAE	3 / 0.8	9 / 2.3		1 / 1.7			2 / 1.7	2 / 1.7	1 / 1.1		1 / 1.1
LEPTOCYTHERIDAE	36 / 9.5	39 / 10.2	9 / 12.7	11 / 18.3	12 / 7.0	3 / 4.8	8 / 6.6	3 / 2.6	3 / 3.3	6 / 4.5	13 / 14.6
LOXOCONCHIDAE	50 / 13.2	53 / 14.6	10 / 14.0	8 / 13.3	15 / 8.8	5 / 8.1	20 / 16.5	7 / 6.0	9 / 10.0	9 / 6.8	8 / 9.0
PARADOXOSTOMATIDAE	54 / 14.2	14 / 3.6	10 / 14.0	14 / 23.3	29 / 17.0	1 / 1.6	3 / 2.5		1 / 1.1	15 / 11.4	3 / 3.4
PECTOCYTHERIDAE	1 / 0.3										
TRACHYLEBERIDIDAE	24 / 6.3	20 / 5.2	3 / 4.2	1 / 1.7	8 / 4.7	11 / 17.7	15 / 12.4	26 / 22.2	20 / 22.2	14 / 10.6	15 / 16.9
XESTOLEBERIDIDAE	17 / 4.5	12 / 3.1		3 / 5.0	2 / 1.2	1 / 1.6	no data	1 / 0.9	2 / 2.2	9 / 6.8	3 / 3.4
CYTHERELLIDAE	5 / 1.3	7 / 1.8			1 / 0.6	1 / 1.6	no data	7 / 6.0	2 / 2.2	5 / 3.8	3 / 3.4
POLYCOPIDAE		1 / 0.3								12 / 9.1	
SCHIZOCYTHERIDAE					1 / 0.6	1 / 1.6	2 / 1.7				
CYPRIDINIDAE					1 / 0.6						
INDET FAMILY							1 / 0.8				
SCHULERIDEIDAE								1 / 0.9			
PSAMMOCYTHERIDAE									1 / 1.1		
HALOCYPRIDIDAE										1 / 0·8	

TABLE 3—ST. ERTH: ABSOLUTE NUMBER AND PERCENTAGE OF SPECIES BY FAMILY COMPARED WITH THE 9 FAUNAS SHOWN IN TABLE 2 (minor families omitted).

	Total no.	%	Absolute number of species			Percentage		
Family	St. Erth		Comparative faunas: Maximum total number of species	Comparative faunas: Mean total number of species	St. Erth: Total number and its relationship to the mean total number of species of the comparative faunas	Comparative faunas: Maximum percentage of species per family	Comparative faunas: Mean percentage of species per family	St Erth: Percentage compared to that of the mean percentage of the comparative faunas
Bairdiidae	4	1.1	8	4.0	=	6.1	3.6	-2.5
Paracyprididae	2	0.5	2	1.2	+0.8	1.7	1.2	-0.7
Pontocyprididae	3	0.8	9	2.3	+0.7	6.8	2.1	-1.3
Brachycytheridae	1	0.3	3	2.1	-1.1	3.4	2.1	-1.8
Bythocytheridae	4	1.1	8	3.0	+1.3	5.6	2.7	-1.6
Cytherettidae	5	1.3	9	5.0	=	7.7	4.9	-3.6
Cytherideidae	37	9.8	22	10.3	+26.7	18.2	8.4	+1.4
Cytheruridae	103	27.2	54	19.0	+84.0	31.6	18.4	+8.7
Hemicytheridae	28	7.4	22	11.7	+16.3	24.4	11.8	-4.4
Leguminocythereididae	3	0.8	2	1.4	+1.6	1.7	1.5	-0.7
Leptocytheridae	36	9.5	13	7.5	+28.5	18.3	8.2	+1.3
Loxoconchidae	50	13.2	20	10.0	+40.0	16.5	10.0	+3.2
Paradoxostomatidae	54	14.2	29	9.5	+44.5	23.3	9.2	+5.0
Trachyleberididae	24	6.3	26	12.5	-6.2	22.2	12.5	-6.2
Xestoleberididae	17	4.5	9	3.0	+14.0	6.8	3.0	+1.5
Cytherellidae	5	1.3	7	3.2	+1.8	6.0	2.9	-1.6

Table 3 compares the total number of species and percentage of species per family at St. Erth with the maximum and mean total number of species and percentage of species per family of the 9 comparative faunas. Text-figs. 12 and 13 illustrate the same relationship between the St. Erth fauna and the 9 comparative faunas graphically, by total number of species and percentage of species per family respectively.

Of the 16 families at St. Erth considered in Table 3 and Text-fig. 12, the total number of species in 12 of them is higher than the mean figure for the comparative faunas. The number of the Cytheruridae at St. Erth is approximately double that of the maximum number of cytherurids among the 9 comparative faunas (54 species, Ralph, 1983, MS., Recent, western Britain). Also notably higher numbers of species than recorded in any of the comparative faunas are found at St. Erth in the Cytherideidae, Leptocytheridae, Loxoconchidae, Paradoxostomatidae and Xestoleberi-



TEXT-FIG. 12—St. Erth: Total number of species versus the 9 comparative faunas by families (minor families omitted).

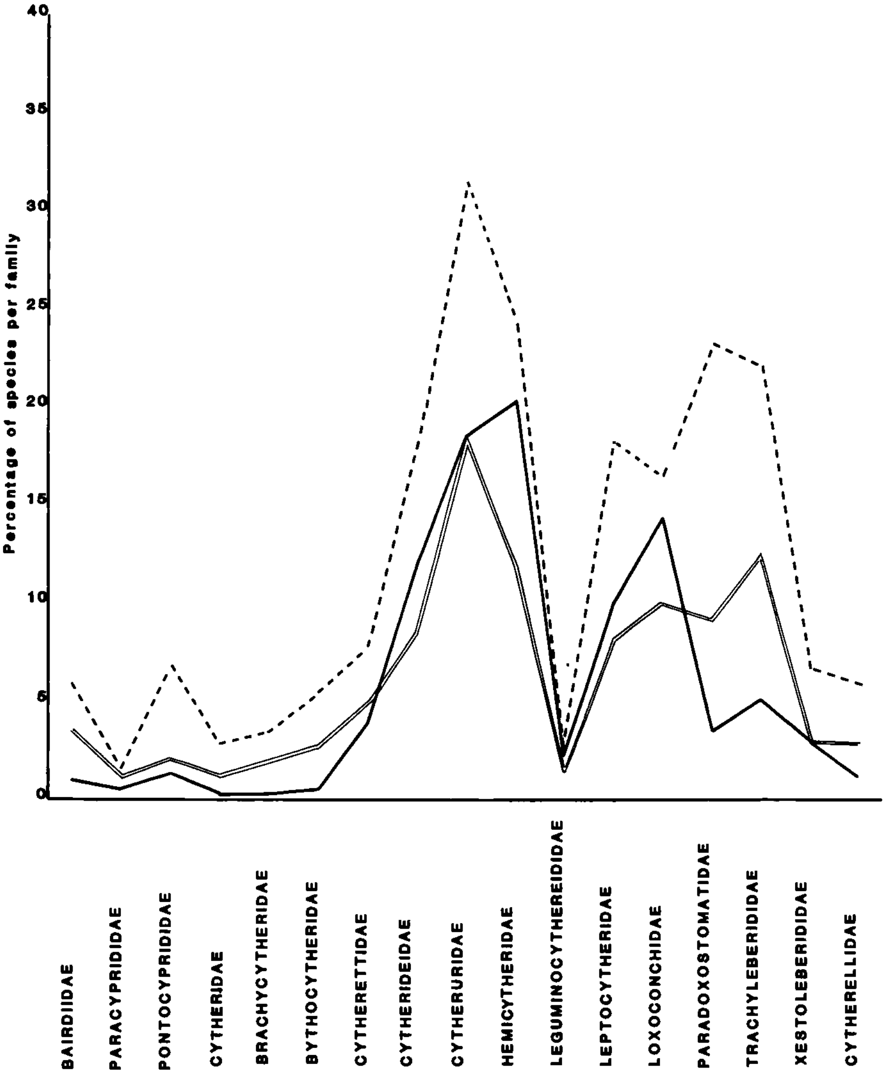
Key: ——— = St. Erth: Total number of species per family.

············ = Comparative faunas: Maximum value of species number per family.

*═══ = Comparative faunas: Mean number of species per family.

didae. It is important to note, however, in Text-fig. 12 that high species diversity in most families at St. Erth is mirrored by both the maximum and mean figures for the other faunas so that the peaks and troughs of the 3 lines drawn on the graph are approximately coincident.

Text-fig. 13 is revealing in that it demonstrates that while the St. Erth fauna is apparently unique in the very high species diversity exhibited by several families, when expressed in percentage of species per family, St. Erth is not unique at all. As Text-fig. 13 shows, with respect to all families, the maximum percentage of species recorded among the 9 comparative faunas always exceeds that



TEXT-FIG. 13—St. Erth: Percentage per family of the total number of species versus the 9 comparative faunas (minor families omitted).

Key: ——— = St. Erth: Percentage per family of the total number of species.

.... = Comparative faunas: Maximum percentage value of the total number of species per family.

═══ = Comparative faunas: Mean percentage of species per family.

Table 4—North West France: Absolute Number and Percentage of Species by Family Compared with the 9 Faunas shown in Table 2 (minor families omitted).

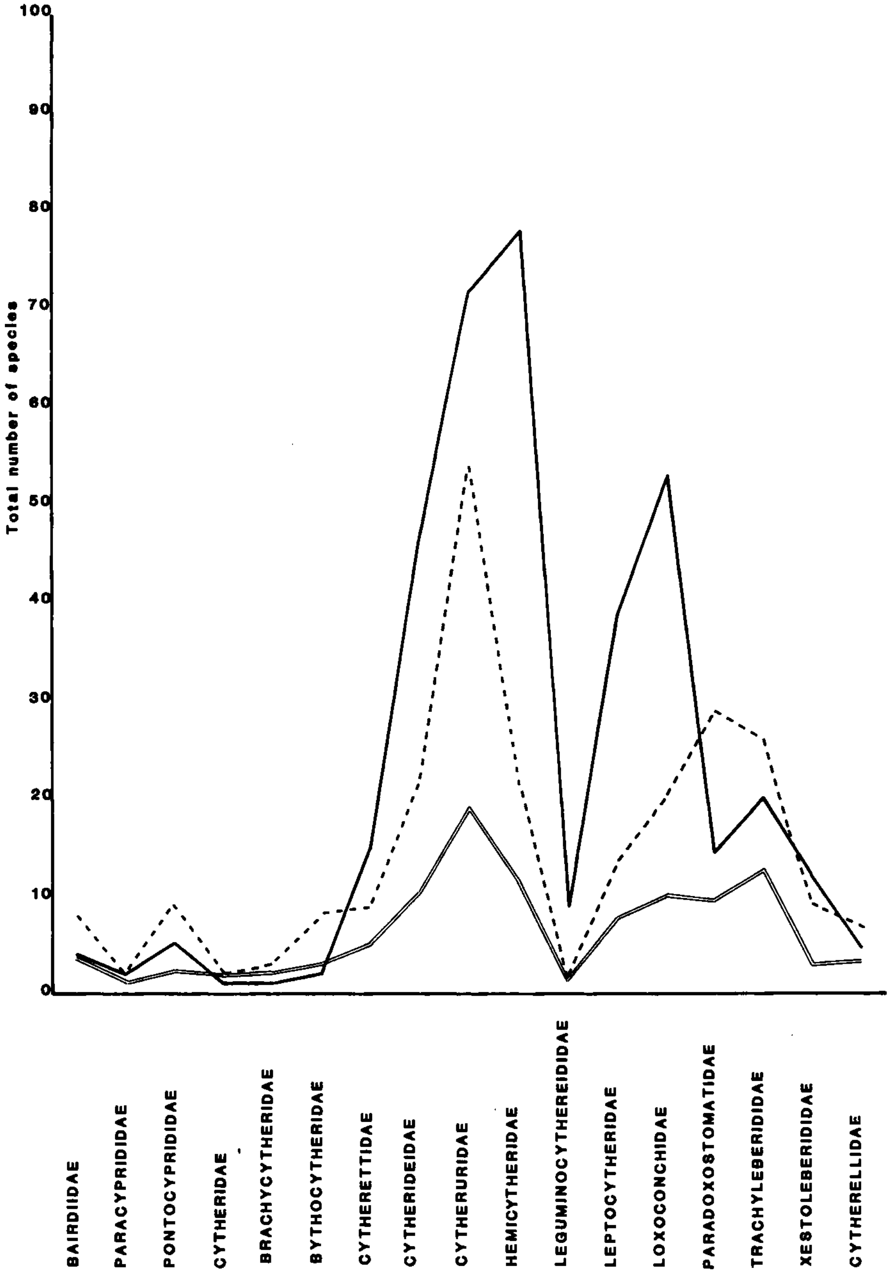
Family	Total no. %	Absolute number of species			Percentage		
	North West France	Comparative faunas: Maximum total number of species	Comparative faunas: Mean total number of species	North West France: Total number and its relationship to the mean total number of species of the comparative faunas	Comparative faunas: Maximum percentage of species per family	Comparative faunas: Mean percentage of species per family	North West France: Percentage compared to that of the mean percentage of the comparative faunas
Bairdiidae	4 1.0	8	3.7	+0.3	6.1	3.6	-2.6
Paracyprididae	2 0.5	2	1.2	+0.8	1.7	1.2	-2.6
Pontocyprididae	5 1.3	9	2.3	+2.7	6.8	2.1	-0.8
Cytheridae	1 0.3	2	1.3	-1.0	2.8	1.2	-0.9
Brachycytheridae	1 0.3	3	2.1	-1.1	3.4	2.1	-1.8
Bythocytheridae	2 0.5	8	3.0	-1.0	5.6	2.7	-2.2
Cytherettidae	15 3.9	9	5.0	+6.0	7.7	4.9	-1.0
Cytherideidae	47 12.2	22	10.3	+36.7	18.2	8.4	+3.8
Cytheruridae	72 18.7	54	19.0	+53.0	31.6	18.4	+0.3
Hemicytheridae	78 20.3	22	11.7	+66.3	24.4	11.8	+8.5
Leguminocythereididae	9 2.3	2	1.4	+7.6	1.7	1.5	+0.8
Leptocytheridae	39 10.2	13	7.5	+31.5	18.3	8.2	+2.0
Loxoconchidae	53 14.6	20	10.0	+43.0	16.5	10.0	+4.6
Paradoxostomatidae	14 3.6	29	9.5	+4.5	23.3	9.2	-5.6
Trachyleberididae	20 5.2	26	12.5	+7.5	22.2	12.5	-7.3
Xestoleberididae	12 3.1	9	3.0	+9.0	6.8	3.0	+0.1
Cytherellidae	5 1.3	7	3.2	+1.8	6.0	2.9	-1.6

of St. Erth. This is surprising, given the nature of the very high number of species in total numbers per family for the Cytheruridae, Leptocytheridae Loxoconchidae and Paradoxostomatidae as is shown in Text-fig. 13, at St. Erth. It does, however, confirm the overall diverse character of the St. Erth Ostracoda. Also important is the fact that the percentage of species at St. Erth only exceeds the mean percentage of the 9 comparative faunas the case of the Cytherideidae, Cytheruridae, Leptocytheridae, Loxoconchidae and Paradoxostomatidae.

Text-figs. 12 and 13 in conjunction also show that the St. Erth fauna is comparatively deficient in bairdiid, pontocypridid, brachycytherid, bythocytherid, cytherettid and cytherellid ostracods, although in all the faunas these families are relatively poorly represented.

Table 4 compares the total number of species and percentage of species in each family from

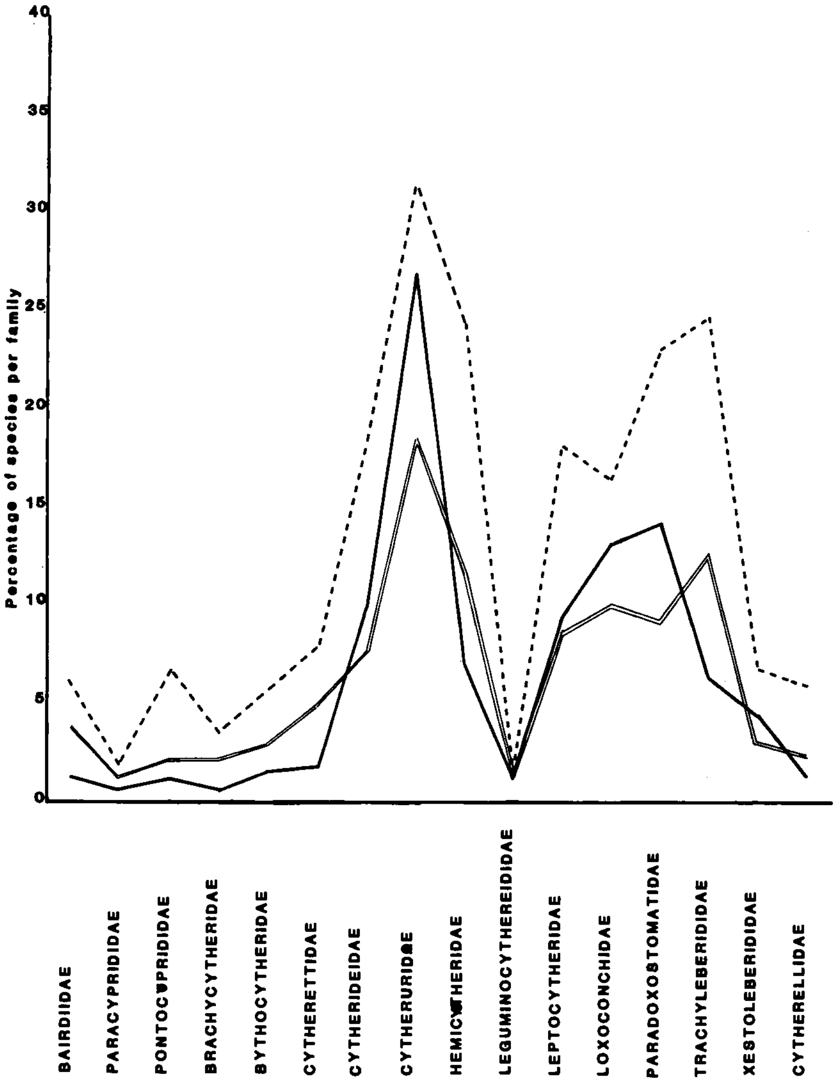
North West France with maximum and mean total number of species and percentage of species per family of the 9 comparative faunas. These data are plotted graphically with respect to total numbers and percentages of species in Text-figs. 14 and 15 respectively. As Text-fig. 14 shows



Text-fig. 14—North West France: Total number of species versus the 9 comparative faunas by families (minor families omitted).

Key: ——— = North West France: Total number of species per family.
.... = Comparative faunas: Maximum value of species number per family.
═══ = Comparative faunas: Mean number of species per family.

the high total of hemicytherid species in the Upper Pliocene of North West France contrasts not only with their relatively modest diversity at St. Erth, but also with that of the 9 comparative faunas. Although the Cytheruridae rank second in North West France, they nonetheless conspicuously exceed the maximum and mean figures for the comparative faunas. The Leptocytheridae and Loxoconchidae are also notable for their comparatively high number of species. The 5 families: Cytherideidae, Cytheruridae, Hemicytheridae, Leptocytheridae and Loxoconchidae are the families dominantly responsible for the high species diversity of the North West France fauna. Text-fig. 14 also shows other important distinctions between the French and Cornish



TEXT-FIG. 15—North West France: Percentage per family of the total number of species versus the 9 comparative faunas (minor families omitted).

Key: ——— = North West France: Percentage per family of the total number of species.

--------- = Comparative faunas: Maximum percentage value of the total number of species per family.

═══ = Comparative faunas: Mean percentage of species per family.

faunas. For example, the Cytherettidae are more prominent in the former and the Paradoxostomatidae much more in the latter.

Text-fig. 15 compares the percentage of species by family of the North West France fauna with that of the maximum and mean percentages of species per family for the 9 comparative faunas. As was the case with St. Erth, no family in North West France exceeds the maximum percentage of species for the comparative faunas, except the Leguminocythereididae and that by only 0.6%. In comparison with the mean percentage of species for the comparative faunas, only the Cytherideidae, Cytheruridae, Hemicytheridae, Leptocytheridae and Loxoconchidae exceed this percentage in the North West France fauna. The latter fauna is also shown to be comparatively deficient in species diversity particularly in the Bardiidae, Pontocyprididae, Brachycytheridae, Bythocytheridae, Cytherettidae, Trachyleberididae and Xestoleberididae.

Tables 3 and 4 and Text-figs. 12–15 demonstrate the families which have been responsible, both in Cornwall and North West France, for the uniquely high diversity of the Upper Pliocene Ostracoda from both regions. They also illustrate that, while the faunas are unique in high species totals for certain families, that it is these same families which contain, in almost all cases, the majority of species in the 9 comparative faunas. Although, therefore, the actual total of species in the present study is exceptionally high, the distribution of species among the families is unremarkable. The major exception to this is the Paradoxostomatidae whose high diversity at St. Erth is unusual despite a relatively high maximum total of 29 species recorded by Ralph (1983, MS.) from the Recent off western Britain. The mean figure for the Hemicytheridae in North West France is almost as worthy of comment. Text-figs. 13 and 15, reveal in percentage terms, however, that the distribution of species among the families at St. Erth and North West France is not unusual.

THE CAUSES OF THE HIGH DIVERSITY

In attempting to account for the abnormally high species diversity of Ostracoda in the Upper Pliocene deposits of St. Erth and North West France, one must consider a number of possibilities which would render this diversity apparent rather than real. If, for example, these faunas contained reworked material, this, together with the indigenous material could account for the enhanced diversity. Certainly among the Ostracoda from both regions are species which have only been previously recorded from the Miocene. However, there is no firm evidence to suggest that the faunas of either region represent anything other than Pliocene faunas. Also studies of the planktonic Foraminifera of St. Erth (Jenkins, 1982 and Jenkins, Whittaker and Carlton in press) have not yielded any contaminents. Similarly, Margerel (1968) did not find among the foraminiferal faunas of the same material studied by the present authors in North West France, any evidence of the presence of reworked earlier material. Reworked material is usually apparent by its abraded nature; such specimens are conspicuous by their absence in the present study. For the same objection outlined above, the faunas cannot be similar to those derived from condensed sequences.

To a certain extent, the taxonomic philosophy of a worker may influence the number of species recognized in any fauna. However, the writers are convinced that the high diversity of the faunas in question is not man-made and will soon demonstrate this by completing the publication of the species whose numbers are cited in this work. To date only 40 of these species have been formally described by the authors (Maybury and Whatley, 1980, 1983a, b, 1984 and Whatley and Maybury 1983a–c and 1984).

The faunas of both regions, but particularly that of St. Erth, contain numerous small, fragile specimens, particularly juveniles. Probably, therefore, in some measure, taphonomy is a major factor contributing to the high species diversity. Similar biocoenoses will result in quite distinct thanatocoenoses given differences in the physical, chemical and biological processes involved in their history of preservation. Is it possible that the Upper Pliocene Ostracoda of Cornwall and North West France owe their high diversity to some unique process of taphonomy? We are of the opinion that this may in part be responsible but that it could not be the sole reason. To opt for this solution would be to suggest that all other fossil ostracod faunas, had "lost" a not inconsiderable proportion of their species during their preservational history. There is certainly no evidence for this and the possibility is not supported by the careful studies of Recent Ostracoda cited earlier.

Ware and Whatley (1983) have shown how the size fractions of residue picked can radically influence the appearance of a fauna. Also, if one compares the studies carried out by workers in the Aberystwyth ostracod group on deep sea faunas, where the fine fraction is carefully picked, with such studies as those of some other authors who do not examine in detail the fine fraction (less than 60 mesh or 215 μm), the difference is remarkable. The result of the studies at Aberystwyth has been to increase the known diversity of some Tertiary deep sea intervals in the Indo-Pacific four or five fold by the simple expedient of considering the small species as well as the large. In the present study, the cut-off point for picking has been the 100 mesh number sieve fraction (150 μm) and of the British studies with which the present faunas have been compared have had the same cut-off point for picking. It is not possible to be certain that this has been the case with the continental studies quoted above.

If the high diversity of these faunas is not apparent but real, what combination of evolutionary and environmental conditions could have brought it about? The palaeotemperature of the Upper Pliocene sea in Cornwall and North West France was certainly warmer than that obtaining in the Western Approaches and the Bay of Biscay at the present day. Britain at that time was a peninsular appendage of Europe, probably washed on its western seaboard by a warm current from the South (Maybury and Whatley, 1980). In Maybury (1985, MS.) it is shown that the Upper Pliocene ostracod faunas of North West France and St. Erth have considerable affinities with contemporary and younger Mediterranean faunas. With, presumably, free access for migration from the South and given a warm sea, this alone could be argued to account in large measure for the enhanced diversity of the Ostracoda. However, as demonstrated above, none of the faunas of Upper Pliocene age, nor indeed Miocene or younger faunas, from the Mediterranean regions are as diverse as those of the present study. Also in Maybury (1985, MS.) evidence is presented of an admixture of southern, warm water species and northern colder water forms. If one imagines Cornwall and the northern part of North West France, as being an area near the limits of the ameliorating effect of a warm water current, allowing both thermophylic and cryophylic species to co-exist, then perhaps part of the enigma of the very high diversity of the St. Erth and Rennes faunas (Text-fig. 2) is resolved.

This hypothesis would be more readily acceptable, however, if more of the species were less restricted in their geographical distribution. In fact 294 species were found to be confined to 1 locality, 112 to 2, 77 to 3, 39 to 4, 24 to 5, 16 to 6 and only 4 species occurred at St. Erth and all 6 of the regions in North West France. The late Pliocene, Redonian transgression was not a major transgressive event and did not inundate but rather lapped around the Cornish and Armorican massifs and probably other elevated areas in North West France were also emergent. This is indicated by Pomerol (1982, fig. 6.6) and Maybury and Whatley (1980, fig. 1). During the Miocene most, if not all of this area was dry land. The Redonian transgression can be envisaged as gradually inundating this Miocene sculptured landscape and extending deep into the massifs along river courses. At its maximum, therefore, the Redonian shoreline was probably very irregular affording the possibility of effective isolation or partial isolation of benthonic communities. Although the time scale of events is geologically very short, not exceeding 2 MY, it was possibly long enough to allow some allopatric speciation to take place.

As is demonstrated in Maybury (1985, MS.) there is considerable evidence that the present faunas were of shallow, possibly littoral character. The high diversity of the Leptocytheridae throughout attests to this as does that of the Xestoleberididae and, at St. Erth the Paradoxostomatidae. Evidence also exists for the existence of lagoonal communities. (Pomerol, 1982 and Catt and Wier in Mitchell *et al.*, 1973).

In conclusion, the high diversity of the Upper Pliocene ostracod faunas of North West France and St. Erth is thought to be due to the fortunate combination of a number of factors. An area near to the limits of the ameliorating effects of a warm sea allowing of the admixture of thermophylic and cryophylic species. A strongly indented, immature coastline with spatial heterogeneity, in comparatively shallow water favouring diversity, providing a variety of new niches for occupation and also favouring allopatric speciation in isolated communites (Pianka, 1967, 1969).

Jenkins (verb. comm., 1983) has suggested, from studies of North Atlantic D.S.D.P. cores, that there was a late Pliocene warming period of short duration. Whatley (in prep.) has also suggested this possibility to account for the enhanced diversity of Pliocene Ostracoda in D.S.D.P. Leg 94 in the North Atlantic. This warming event, while evidently having little effect on the rather isolated faunas of the Coralline Crag, could have been a factor in the regions studied. The biological consequences of such a warming event are much more likely to be evident in an area such as Cornwall and North West France where, as suggested above, a warm sea is near the northern limits of its ameliorating effect. Such an event would have more influence here than in warmer regions to the South where its effects might not even be detectable.

Without doubt, however, and particularly with respect to St. Erth, the favourable taphonomic history of the fauna has preserved its uniquely high diversity. All the factors mentioned above would also lead to the very high incidence of specimens per unit weight in the deposits.

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DISCUSSION

Henning Uffenorde: Is there a similar high diversity in the foraminiferal fauna? Higher accumulation rates of diverse ostracod and relatively low diverse foraminiferal assemblages have been observed in the NW German Miocene (*e.g.*, in or just below the "*Ammonia baccarii* stratum", Hemmoor "stage"). It has been related there to a rapid decline in the environmental energy level (Uffenorde, 1981, in press).

Maybury: The foraminiferan faunas are diverse, although they do not attain such high levels of species diversity as do the Ostracoda. Margerel, for example, in Mitchell *et al.* (1973) lists 101 benthonic foraminiferan species from St. Erth: but this is 277 species less than the total number of ostracod species found at St. Erth. Similarly, the same author (1968) records 258 species (including varieties) from the Redonian deposits of North West France. This is 126 less than the total number of ostracod species occurring in the same area. That an inverse relationship exists between foraminiferan and ostracod species numbers in this instance must be viewed with care; for the numbers of foraminiferan species quoted above are unusually high for a littoral environment. Various localities, however, where this relationship obtains can be cited: for example, at L'Aigletière-la-Begassière in the Nantes region, Margerel (1972) recorded 94 foraminiferan species; but only 15 ostracod species occurred there and at Saint-Jean-la-Poterie in the Redon region Margerel (1968) recorded 23 foraminiferan species, whereas 61 ostracod species were recovered.

Palaeoenvironmental considerations (see Maybury and Whatley, 1980) do not rule out the possibility that high ostracod diversity is attributable, in part, to low environmental energy levels.

Wilkinson: Very often diversity and various statistical methods are related to relatively simple criteria e.g. salinity, water depth, temperature. But the problem is much more complex when such things as the trophic structure, food web, predation, environmental stability and heterogeneity is taken into account. The problem of your extremely high diversity will probably defy explanation.

Maybury: I agree.

Oligocene to Quaternary Ostracods of the Central Equatorial Pacific (Leg 85, DSDP-IPOD)

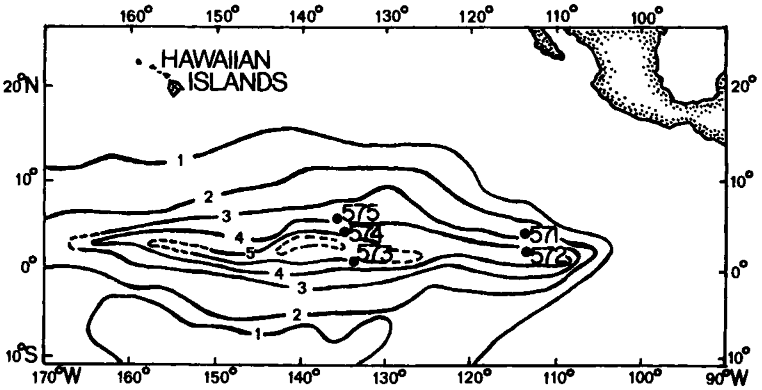
PAUL L. STEINECK, DAVID DEHLER, ERIC M. HOOSE AND DONALD MCCALLA
State University of New York, Purchase, USA

ABSTRACT

This study reports on the taxonomic, stratigraphical, biogeographical and palaeoceanographical significance of Oligocene to Quaternary ostracod faunas from the central equatorial Pacific (Leg 85, DSDP). A Lower Ecozone (Oligocene–lower Miocene) contains relatively diverse faunas characterised by the high frequencies of *Bradleya, Poseidonamicus, Henryhowella* and *Krithe.* Taxonomic affinity with coeval deep-sea faunas in the Caribbean is high. Low turnover rates suggest that stable oceanographical conditions were maintained by the circum-equatorial flow of warm, saline bottom-waters. The Upper Ecozone (middle Miocene–Quaternary) contains a lower subunit (middle–upper Miocene) in which local range terminations, speciation events and the immigration of new taxa are prevalent. A depauperate "psychrospheric" post-Miocene assemblage, dominated by *Bradleya, Krithe, Brachycythere* and *Thallasocythere,* was adapted to the corrosive bottom-waters present in equatorial regions during this interval. Stratigraphic trends in carbonate accumulation rate and ostracod number show an approximate, non-linear but generally positive correlation. This suggests that the availability of food has governed the density of the ostracod population in the Leg 85 area.

INTRODUCTION

The present report is a preliminary account of ostracods recovered from Oligocene to Pleistocene sediments cored during the operation of Leg 85 of the Deep Sea Drilling Project (DSDP) in the central equatorial Pacific (Mayer *et al.*, 1985; Text-fig. 1). Our objectives are three-fold. First, the taxonomy, stratigraphical succession and biogeographical affinities of the faunas recovered from Leg 85 will be summarised. Second, faunal data will be compared to the paleoceanographical history of the Pacific as reconstructed by Leg 85 scientists (Theyer *et al.*, 1985; Barron, 1985; Miller and Thomas, 1985) and others (Woodruff and Douglas, 1981; Kiegwin and Keller, 1984; Keller and Barron, 1983; Woodruff, 1985). Third, sites cored during Leg 85 occur in a north south transect (Text-fig. 1) located on oceanic crust which is drifting northwestward away from its point of origin at the East Pacific Rise. This drifting history has altered in a sequential and predictable fashion the proximity of these sites to a geographically-fixed equatorial zone of upwelling and fertile surface waters where primary productivity and the biomass of biomineralized plankton is among the highest in the modern oceans (Theyer *et al.*, 1985). Therefore, it is possible to use carbonate sedimentation rates to test the relationship of ostracod abundance to fluctuations in surface-water fertility.



TEXT-FIG. 1—Location map, sites 571 through 575, Leg 85 DSDP. Depth contours in kilometres. From Text-fig. 1 of Theyer *et al.*, (1985). Location and present depth of sites as follows: 575, 5°51'N, 135°02.16'W, 4536m; 674, 4°12.52'N, 133°18.57'W, 4555m; 573, 0°29.92'N, 133°18.57'W, 4309m; 572, 1°26.09'N, 113°50.52'W, 3893m.

THE FAUNA

General Comments

Analysis of over 55,025 cc aliquots from the core inventory of Leg 85 has revealed the presence of a biocoenose containing at least 47 species of ostracods (Table 1). The assemblages are sparse (0 to 35 specimens/sample) and low in diversity (maximum number of species/sample = 11). Approximately one-third of the samples processed were devoid of ostracods. Because of the limited recovery, our results most likely underestimate the diversity of past faunas in the central equatorial Pacific as well as the stratigraphical range of rare species. Two ecostratigraphic units have been defined on the basis of the vertical distribution of ostracod species. A Lower Ecozone (Oligocene–lower Miocene) is characterised by an internally uniform fauna. The Upper Ecozone (middle Miocene–Quaternary) contains a lower interval marked by a reduction in diversity, evolutionary changes in lineages of *Poseidonamicus, Bradleya* and *Abyssocythere* and by a transformation of the overall morphological aspect of the fauna.

Lower Ecozone (Oligocene to lower Miocene)

Faunas in this ecozone are relatively diverse (30–35 species per biostratigraphic zone; Text-fig. 2) and contain abundant representatives of *Poseidonamicus* and *Bradleya.* Taxa such as *Xestoleberis chamela, Eocytheropteron trinidadensis* and *Krithe kollmani* which originated in the Eocene of the Tethys and Caribbean, are present. Twenty-three species have been recorded in the lower Oligocene; an additional nine make their appearance in the upper Oligocene. Within the Oligocene to lower Miocene interval, there are no stratigraphical range terminations without replacement except for species with isolated occurrences (*e.g. Bythocypris* sp.). *Agrenocythere antiquata* evolved into *A. hazelae* in the late Oligocene as previously suggested by Benson (1972). Stability in the composition of the faunas and relative abundance of species in the Oligocene to lower Miocene of the central equatorial Pacific is one of the most noteworthy results of our investigation.

Upper Ecozone (middle Miocene–Quaternary)

A series of local extinctions, initial appearances and apparent speciation events which took

TABLE 1—STRATIGRAPHIC RANGES OF OSTRACOD SPECIES, LEG 85, DSDP-IPOD, EASTERN EQUATORIAL PACIFIC.

Name	Range in Pacific	Total Range
Abyssocythere australis Benson, 1971	Upper Miocene (N16) –Upper Pliocene (N19)	Upper Miocene–Recent
Abyssocythere japonica Benson, 1971	Upper Miocene (N17) –Quaternary (N23)	Pleistocene –Quaternary
Abyssocythere sp. 1	Upper Oligocene (P21) –Upper Miocene (N17)	
Abyssocythere trinidadensis (van den Bold, 1957)	Lower Oligocene (P19) –Upper Miocene (N17)	Late Cretaceous –Upper Miocene
Abyssocythereis sulcatoperferata (Brady, 1880)	Lower Oligocene (P19) –Quaternary (N23)	Same
Agrenocythere antiquata Benson, 1972	Lower Oligocene (P19) –Upper Oligocene (P21)	Middle Eocene –Upper Oligocene
Agrenocythere hazelae (van den Bold, 1946)	Upper Oligocene (P21) –Upper Miocene (N17)	Upper Oligocene –Recent
Ambocythere c.f. *A. caudata* van den Bold, 1965	Lower Oligocene (P20) –Upper Miocene (N17)	
Ambocythere challengeri Benson, 1983	Lower Miocene (N8) –Quaternary (N23)	Same
Argilloecia sp.	Lower Oligocene (P16) –Quaternary (N23)	
Bairdia oarion van den Bold, 1972	Lower Oligocene (P16) –Upper Miocene (N17)	Eocene–Upper Miocene
Bairdoppilata sp.	Lower Oligocene (P20) –Upper Miocene (N17)	
Brachycythere mucronalatum (Brady, 1880)	Lower Oligocene (P18) –Quaternary (N23)	Same
Bradleya dictyon (Brady, 1880)	Upper Miocene (M17) –Quaternary (N23)	Upper Miocene–Recent
Bradleya johnsoni Benson, 1983	Lower Oligocene (P19) –Upper Miocene (N17)	Lower Oligocene–Upper Miocene (Recent?)
Bradleya pygmaea Whatley, Harlow, Downing and Kesler, 1985	Pliocene (N19, N21)	Miocene–Quaternary
Bythocypris sp.	Lower Oligocene (P16)	
Eocytheropteron trinidadensis (van den Bold, 1960)	Upper Oligocene (P21) –Upper Pliocene (N19)	Middle Eocene –Upper Pliocene
Eucythere sp.	Lower Oligocene (P20) –Upper Miocene (N17)	
Henryhowella sp.	Lower Oligocene (P19) –Quaternary (N23)	
"Hyphalocythere" sp.	Lower Oligocene (P19) –Lower Miocene (N6)	
Krithe kollmani Pokorny, 1980	Lower Oligocene (P18, P19)	Upper Eocene –Lower Oligocene
Krithe morkoveni van den Bold, 1960	Lower Miocene (N6) –Quaternary (N23)	Same
Krithe reversa van den Bold, 1958	Middle Miocene (N9) –Quaternary (N23)	Same

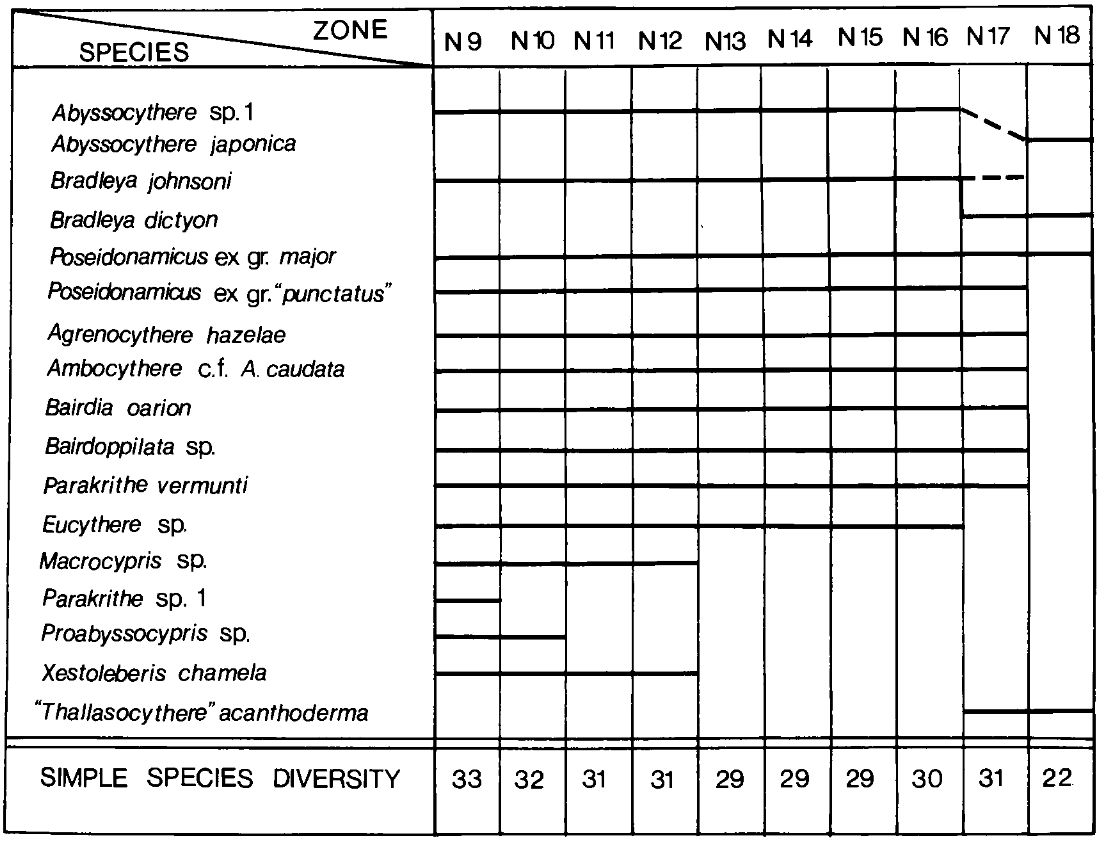
(*Continued*)

TABLE 1—*Continued.*

Name	Range in Pacific	Total Range
Krithe sp. 1	Lower Oligocene (P19) –Quaternary (N23)	
Krithe sp. 2	Lower Miocene (N5) –Quaternary (N22)	
Krithe sp. 3	Lower Oligocene (P19) –Quaternary (N23)	
Krithe sp. 4	Lower Oligocene (P18) –Quaternary (N23)	
Krithe sp. 5	Lower Miocene (N4) –Upper Pliocene (N21)	
Krithe sp. 7	Pliocene (N18–N21)	
Krithe vandenboldi Steineck, 1981	Lower Miocene (N5) –Upper Pliocene (N19)	Oligocene–Recent
Messinella guanajayensis van den Bold, 1969	Lower Oligocene (P19)	Middle Eocene –Lower Miocene
"Oxycythereis" sp.	Upper Oligocene (P21) –Quaternary (N23)	
Parakrithe sp. 1	Lower Oligocene (P19) –Middle Miocene (N9)	
Parakrithe vermunti van den Bold, 1946	Lower Oligocene (P19) –Upper Miocene (N17)	Same
Phacorhabdotus sp.	Lower Oligocene (P19) –Quaternary (N22)	
Poseidonamicus ex. gr. *major*	Lower Oligocene (P19) –Quaternary (N23)	Same
Poseidonamicus ex. gr. *punctatus*	Upper Oligocene (P21) –Upper Miocene (N17)	Upper Oligocene–Recent
Proabyssocypris sp.	Upper Oligocene (P21) –Middle Miocene (N10)	
Rockallia vscripta Whatley, Uffenorde, Harlow, Downing and Kesler, 1982	Lower Miocene (N5)	Lower Miocene –Quaternary
"Suhmicythere" suhmi (Brady, 1880)	Upper Oligocene (P21) –Upper Pliocene (N19)	Same
"Thallasocythere" acanthoderma (Brady, 1880)	Upper Miocene (N17) –Quaternary (N23)	Same
"Thallasocythere" bermudezi (van den Bold, 1960)	Lower Miocene (N5) –Middle Miocene (N10)	Upper Eocene –Middle Miocene
Trachyleberis sp.	Lower Oligocene (P20) –Quaternary (N22)	
Xestoleberis chamela van den Bold, 1960	Lower Oligocene (P20) –Middle Miocene (N12)	Middle Eocene –Middle Miocene

Sources for total ranges–van den Bold (1977, 1981), Benson (1971, 1972), Benson and Peypouquet (1983), Pokorný (1980), Steineck (1981), Whatley *et. al.* (1982, 1983). The N and P zones given in parentheses are the standard planktonic foraminiferal zones as defined and used by Leg 85 scientists. Their age assignments are followed throughout this paper.

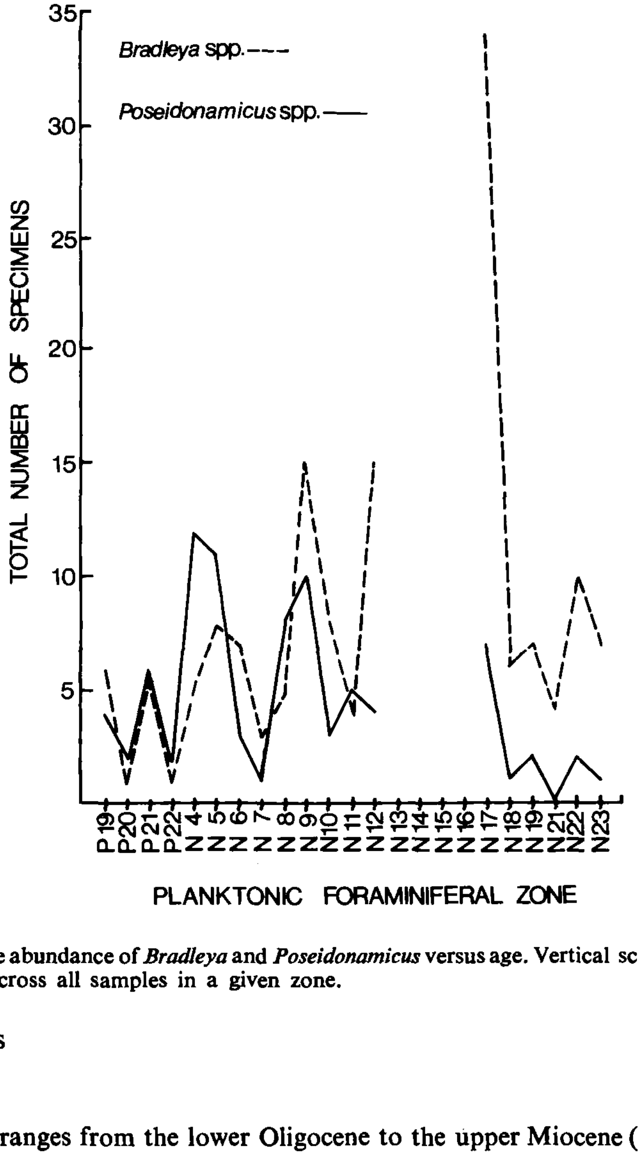
place in the middle to late Miocene dramaticaly transformed the nature of the ostracod faunas in Leg 85 cores. Fifteen species become locally extinct at this time; these terminations occur over an extended period of time (Text-fig. 2) but there is a concentration in upper Miocene sediments (N17). Coincident with the latter extinctions are two species-replacements that are parts of evolutionary lineages: *Bradleya johnsoni* –> *B. dictyon, Abyssocythere* sp. 1 –> *A. japonica.* Limited



Text-fig. 2—Stratigraphical range of selected species and simple species diversity per zone in the middle and upper Miocene. Planktonic foraminiferal zones taken from Mayer, Theyer and others (1985). Simple species diversity is the number of species summed across all samples in a zone.

data does not allow us to establish whether these speciation events took place locally or whether the replacements were related to the immigration of the descendant species. An important characteristic of Upper Ecozone assemblages is the rarity of *Poseidonamicus* relative to the occurrence of *Bradleya* (Text-fig. 3). Only 8 species survived the middle and upper-Miocene faunal event as recorded in the Leg 85 cores to be represented in Pliocene and younger sediments whose faunas are characterised by low species diversity (Text-fig. 2) and by the dominance of *Krithe* spp., *Bradleya dictyon, Brachycythere mucronalatum* and by *Thallasocythere acanthoderma.*

In addition to their distinctive taxonomic composition and population structure, faunas of the Upper Ecozone are recognizable by a shared morphological style. By the Pliocene, most of the quantitatively significant species possess a carapace morphology that conforms to the model elucidated by Benson (1977b, 1979) as diagnostic of ostracods inhabiting the deep-sea. The krithinids and *Brachycythere mucronalatum* increase in size; in some examples the length of the adult carapace exceeds 1400 µm. *Thallasocythere acanthoderma* and *Henryhowella* sp. bristle with a dense network of ominous-looking spines (Pl. 1, figs. 1–3, 10, Pl. 3, fig. 8). The reticular pattern of *Bradleya dictyon* is subdued and simplied compared to its progenitor *B. johnsoni* (compare Pl. 2, fig. 1 with figs. 2–4). These morphologies have the effect of reducing carapace mass relative to size and may confer a selective advantage, when cold, $CaCO_3$ undersaturated bottom-water is present, by minimizing the metabolic energy needed to secrete the shell following moulting.



Text-fig. 3—Relative abundance of *Bradleya* and *Poseidonamicus* versus age. Vertical scale is the number of specimens summed across all samples in a given zone.

Taxonomic Notes

Abyssocythere

A. trinidadensis ranges from the lower Oligocene to the upper Miocene (N17). This upper limit may represent a true extinction as other authors (van den Bold, 1977, fig. 7; Benson, 1971) noted the absence of this species from Pliocene sediments. This species dates back at least to the late

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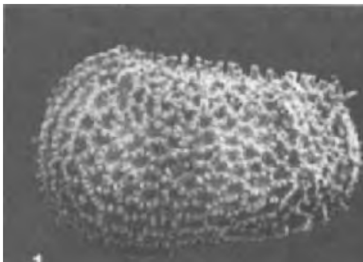
Plate 1—Figs. 1–3 *Henryhowella* sp. 1. 1) spinose form, adult left valve, 574A, 14–3, Middle Miocene (N2), ×96. 2) reticulate form, adult left valve, 572C, 3–1, Quaternary (N22), ×77. 3) long form, adult right valve, 572C, 4–6, Pliocene (N21), ×72. Fig. 4. *Thallasocythere bermudezi* (van den Bold). Subadult left valve, 574, 19–7, Middle Miocene (N10–N11), ×72. Figs. 5, 7. *Agrenocythere hazelae* (van den Bold). 5) adult right valve, 575, 7–1, Middle Miocene (N12), ×67. 7) detail of castrum, same specimen as 5, ×170. Fig. 6. *Phacorhabdotus* sp. Adult left valve, 575A, 19cc, Early Miocene (N5), ×112. Fig. 8. *Abyssocythereis sulcatoperforata* (Brady). Subadult left valve, 575, 8–2, Middle Miocene (N10), ×100. Fig. 9. *Brachycythere mucronalatum* (Brady). Adult left valve, 572c, 16–2, Upper Miocene (N17), ×64. Fig. 10. "*Thallasocythere*" *acanthoderma* (Brady). Adult right valve, 572c, 9–5, Pliocene (N19), ×87. Fig. 11. *Abyssocythere trinidadensis* (van den Bold). Adult left valve, 575, 9–3, Middle Miocene (N8), ×73. Fig. 12. *Ambocythere challengeri* Benson. Adult left valve, 572A, 9–6, Pliocene (N19), ×110.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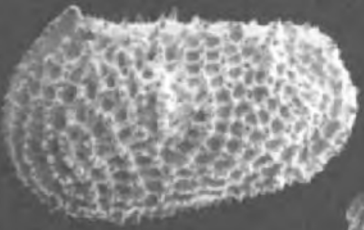
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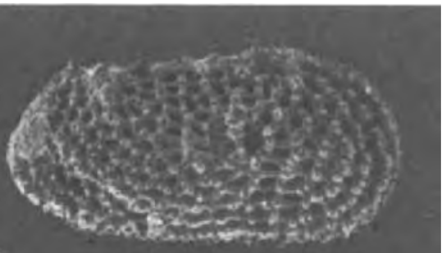
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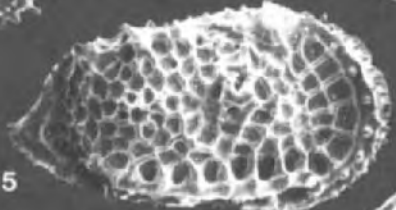
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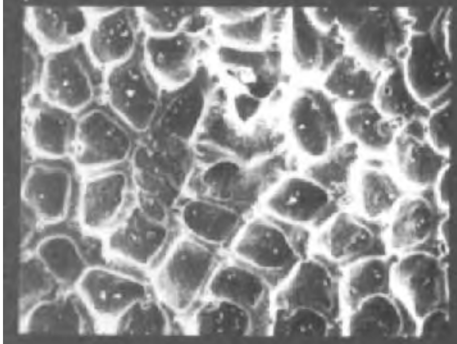

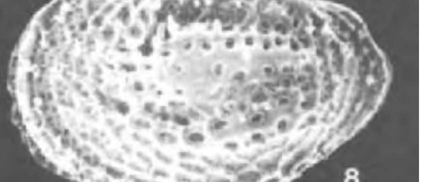
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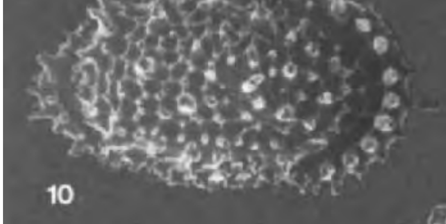
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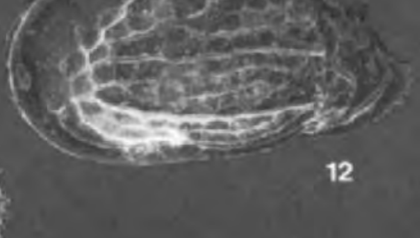
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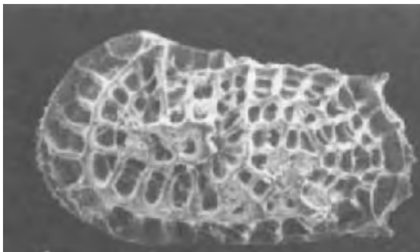
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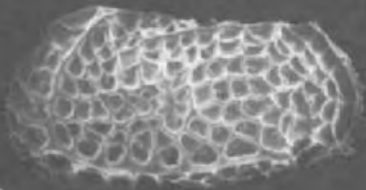
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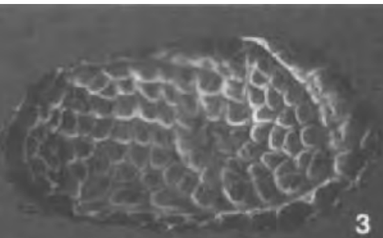
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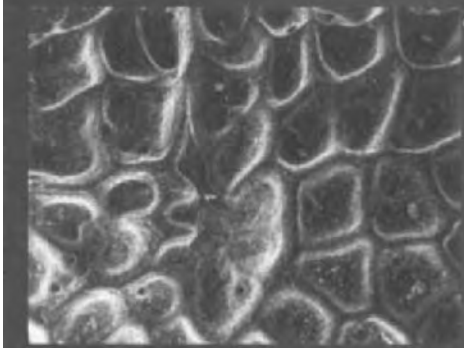
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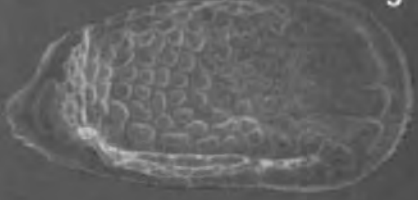
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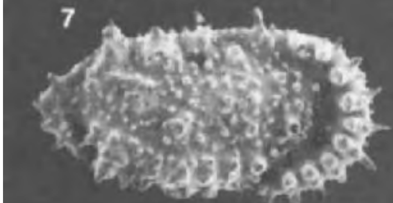
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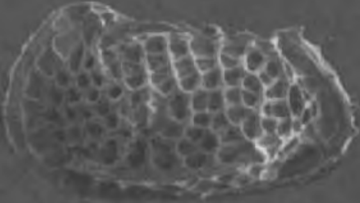
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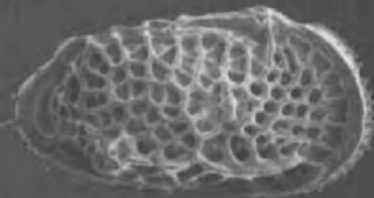
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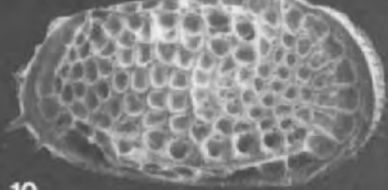
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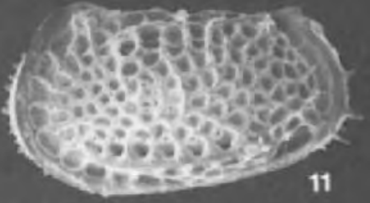
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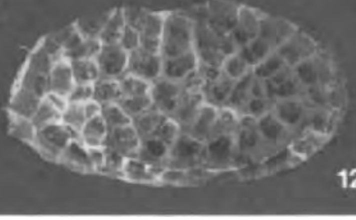
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Cretaceous (van den Bold, 1957) and had entered the abyss by the middle Eocene (Steineck *et al.*, 1984). The morphological stability displayed by this species over a period of 55 my is remarkable even for deep-sea ostracods (compare Pl. 1, fig. 11 with van den Bold, 1957, Pl. 3, fig. 1).

Abyssocythere sp. 1 first appeared in the upper Oligocene and persists upcore to the upper Miocene (N17) when it may have given rise to *A. japonica.* Both species are recognized by the elevated vertically-aligned muri which dominate the sculptural relief. *A.* sp. 1 is distinguished by a dome-shaped muscle scar node (absent in *A. japonica*) and by the extension of the anterior muri from the dorsum to the ventro-lateral complex (Pl. 3, fig. 5). In the descendant species, presumably homologous elements close ventrally to form U-shaped structures (Benson, 1971, fig. 11, Pl. 1. fig. 8).

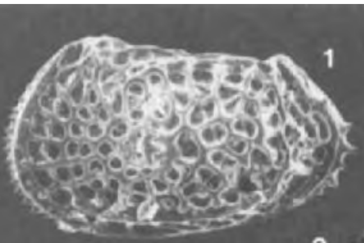
Bradleya

Bradleya johnsoni was first described from the Lower Miocene of the South Atlantic (Benson and Peypouquet, 1983, p. 811), but it had been previously recorded (as *B. dictyon*) in Oligo-Miocene faunas from the Caribbean (Steineck, 1981, Pl. 2, fig. 14; Steineck *et al.*, 1984, figs. 6i–k; van den Bold, 1981, Pl. 4, fig. 17). In the present study it occurs in Oligocene to upper Miocene sediments. *Bradleya johnsoni* is identified by a massive, primary reticulation composed of excavate muri, an elevated and robust bridge structure and subdued secondary muri which subdivide the primary fossae in the anterior, dorso-median and posterior regions (Pl. 2, fig. 1). It appears to have evolved into *B. dictyon* (sensu Benson and Peypouquet, 1983, Pl. 3, fig. 4) within zone N17 by development of a more open and irregular reticulum with less relief, (Pl. II, figs. 2–4). *Bradleya dictyon* of present usage may be conspecific with *B. lordhowensis* described by Whatley *et. al.* (1984) from the Pliocene of the S.W. Pacific. Benson (1972, Pl. 9, figs. 1–12) figured a recent or subfossil specimen that is close to *B. johnsoni* raising the possibility that this species is extant. Contrary to the assertions of Whatley *et. al.* (1984), the *B. dicyon* lineage has been present at abyssal depths in the Pacific since the earliest Oligocene.

Poseidonamicus

Two species complexes, differing in the pattern of anterior ornamentation, occur in Leg 85 material. The *P. major* complex (Oligocene-Quaternary), is identified by an anterior reticular field containing 1) a mural system which obliquely traverses the region between the muscle-scar node and the anterior margin and 2) large, oval to semi-circular fossae (Pl. 2, figs. 8–11, Pl. 3, figs. 1–3). Some specimens (Pl. 3, fig. 1) of *Poseidonamicus* ex. gr. *major* in the Lower Ecozone are similar to the form figured by Steineck *et. al.* (1984, figs. 7c–e), others may belong to *P. riograndensis* Benson, (Pl. II, figs. 8, 9) and a third group of individuals may belong to an undescribed species. Few Middle Miocene specimens were discovered. These are difficult to categorize because of the lack of well-preserved adults. Individuals found in the Upper Ecozone are considered to fall within the range of variation of *P. miocenicus* Benson (Pl. II, figs. 10, 11; see Benson and Peypouquet, 1983, Pl. 3, figs. 2, 3; Benson, 1983, fig. 1).

Plate 2—Fig. 1. *Bradleya johnsoni* Benson. Adult left valve, 572D, 33–5, Middle Miocene (N9), ×81. Figs. 2–4. *Bradleya dictyon* (Brady). 2) adult left valve, 572A, 2–1, Quaternary (N22), ×62. 3) adult right valve, 572A, 1–3, Quaternary (N23), ×70. 4) closeup of the central mural loop and posterior end of bridge, same specimen as 2, ×190. Fig. 5. *Poseidonamicus* ex. gr. *P. punctatus* Whatley, Harlow, Downing and Kesler. Adult right valve, 574A, 21–3, Middle Miocene (N9), ×103. Fig. 6. *Ambocythere* cf. *A. caudata* van den Bold. Subadult right valve, 573, 6–1, Pliocene (N21), ×101. Fig. 7. "*Hyphalocythere*" sp. Adult right valve, 574C, 6–2, Lower Miocene (N6), ×99. Figs. 8, 9. *Poseidonamicus* ex. gr. *P. major* (Brady). Form similar to *P. riograndensis* Benson. 8) adult left valve, 574A, 21–1, Lower Miocene (N6). 9) adult right valve, same sample as 8. Both ×88. Figs. 10, 11. *Poseidonanmicus* ex. gr. *P. major* Brady. Form similar to *P. miocenicus* Benson. 10) adult right valve, 572C, 13–2, Pliocene (N18). 11) adult left valve, same sample as 10. Both ×82. Fig. 12. *Bradleya pygmaea* Whatley, Harlow, Downing and Kesler. Adult right valve, 572C, 8–4, Pliocene (N19), ×80.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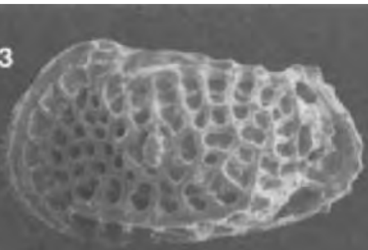
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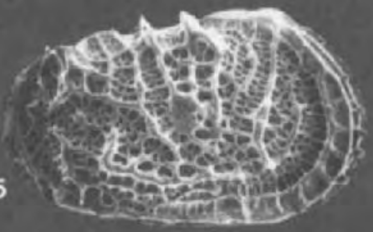
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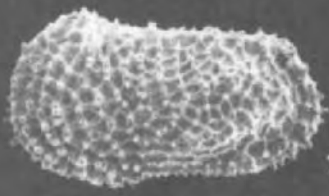
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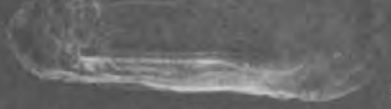
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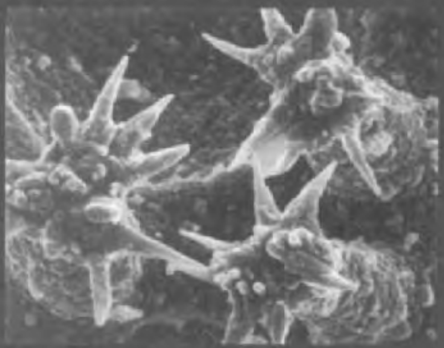
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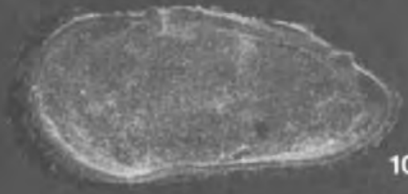
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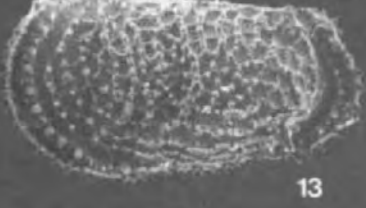
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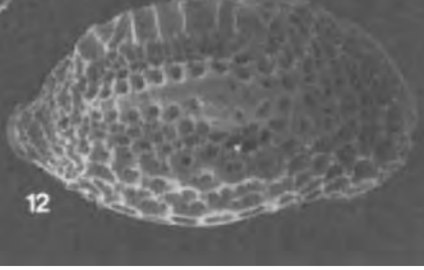
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The *Poseidonamicus punctatus* complex, including *P. anteropunctatus, P. punctatus,* and *P. praenudus* (Whatley *et. al.*, 1983), is distinguished by an array of fine to coarse anterior punctae. In many specimens, the punctae are set into a raised surface similar to the levatum of *Abyssocythere* (Pl. 2, fig. 5). Several subadult specimens from Miocene samples resemble *P. praenudus* (see Whatley *et al.*, 1983, fig. 2) in the near-total suppression of the reticulation but the chance of confusing this species with the moults of related forms is great. Most adult specimens (Pl. 2, fig. 5; Pl. 3, fig. 2) possess coarse anterior punctae and an orthogonal, posterior reticulum with broad non-excavate muri suggesting referral to *P. punctatus.* If lower Miocene specimens from the central equatorial Pacific are indeed correctly placed in *P. punctatus* (Pl. 3, fig. 2), then this species would predate *P. anteropunctatus,* its presumed ancestor in the phylogeny of Whatley *et al.* (1983, fig. 2).

Henryhowella

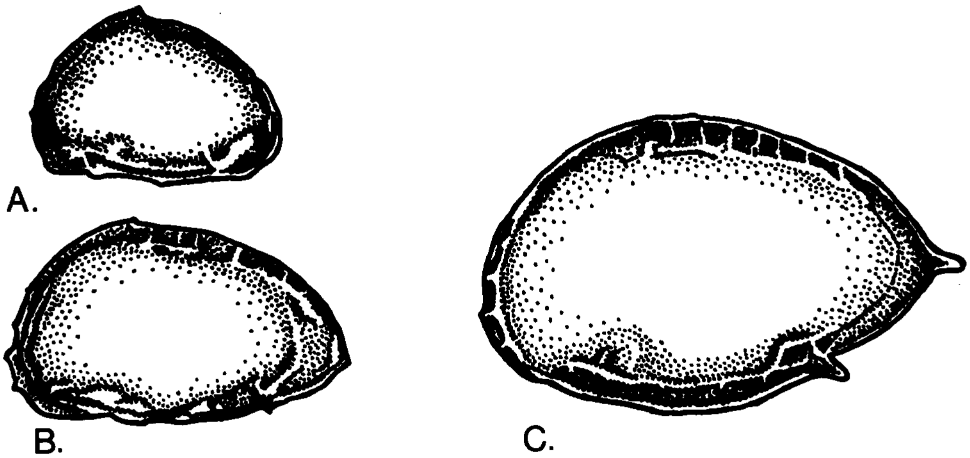
A significant bimodal variation in the size and shape of the carapace is present in assemblages of this genus in the Leg 85 cores. Both morphotypes are present at all stratigraphical levels and commonly co-occur in the same sample (see Pl. 1, figs. 1–3, Pl. 3, figs. 6, 7). Consistent morphological differences other than proportion are not evident. Perhaps, this is an example of extreme sexual dimorphism?

Henryhowellids in the Oligocene and lower Miocene typically possess a prominent muscle-scar node, posterior latitudinal ridges (or their remnants), and a hispid-reticular ornamentation (Pl. 3, figs. 6, 7). Those in the Upper Ecozone are larger, have longer and more delicate spines and lack the muscle-scar node and posterior ridges. Individuals with dominantly hispid or dominantly reticulate ornamentation can often be found in the same sample (Pl. 1, figs. 1–3). LeRoy and Levinson (1974, Pls. 10–12) illustrated similar variation in Recent populations of *Henryhowella* from the Gulf of Mexico. In Upper Miocene to Quaternary specimens, the reticular pattern is similar to that in deep-sea species referred to *Echinocythereis;* elongate morphs of this age may be conspecific with *E. circumdentata* (Brady) (Brady, 1880, p. 180, Pl. 26 figs 2a–c; Puri and Hulings, 1976, p. 269, Pl. 17, figs. 3–6). However, in those specimens where the adductor scars are visible, the intact, U-shaped frontal-scar is diagnostic for *Henryhowella* (M. Kontrovitz, pers. comm., 1985). Until the morphological lability of Pacific populations of *Henryhowella* can be partitioned into evolutionary or ecophenotypic components, the material at hand is retained in a single taxon left in open nomenclature.

Brachycythere

Brachycythere mucronalatum (Pl. 1, fig. 9) is a long-ranging and morphologically-stable species. It was first described by Brady (1880, p. 140–141, Pl. 33, Figs. 8a–d) from a number of locations in the North and South Atlantic and eastern Pacific. Puri and Hulings (1976, p. 307, Pl. 22, figs.

PLATE 3—Figs. 1, 3. *Poseidonamicus* ex. gr. *P. major* (Brady). 1) adult left valve, 575A, 12–2, Lower Miocene (N5), ×84. 3) adult left valve, 572D, 32–2, Middle Miocene (N9), ×90. Fig. 2. *Poseidonamicus* ex. gr. *P. punctatus* Whatley, Harlow, Downing and Kesler. Adult right valve, 575A, 12–2, Lower Miocene (N5), ×101. Fig. 4. *Messinella guanajayensis* van den Bold. Adult right valve, 574C, 33–1, Lower Oligocene (P19), ×160. Fig. 5. *Abyssocythere* sp. 1. Adult right valve, 573–12cc, Upper Miocene (N17), ×103. Figs. 6–8. *Henryhowella* sp. 6) short form with node, adult left valve. 575A, 33–1, Lower Miocene (N4), ×84. 7) long form, adult left valve, 573B, 19–1, Lower Miocene (N4), ×101. 8) detail of spine terminations, dorsal margin of adult right valve, 574A, 14–3, Middle Miocene (N12), ×1190. Figs. 9,10. *Phacorhabdotus* sp. 9) adult right valve, 575A, 19cc, Lower Miocene (N5), ×110. 10) interior of subadult (?) right valve, 573B, 5CC, Middle Miocene (N13/N14), ×110. Fig. 11. *Eocytheropteron trinidadensis* (van den Bold). Interior view and hinge, adult right valve, 572D, 15–1, Middle Miocene (N13), ×117. Fig. 12. *Abyssocythereis sulcatoperforata* (Brady). Adult right valve, 572C, 6–5, Upper Pliocene (N19), ×70. Fig. 13. *Oxycythereis* sp. Subadult left valve, 573B, 18–2, Lower Miocene (N4), ×94.



Text-fig. 4—Suggested ontogenetic development in *Brachycythere mucronalatum*. A, early instar (573B, 30–2, Upper Oligocene), 900 μm long × 600 μm high. B, late instar (575A, 12–1, Lower Miocene), 1100 × 750 μm. C, adult (573, 2–2, Quaternary), 1250 × 1000 μm. Note the proportional decrease in length and development of smoothlyarched dorsal margin with maturation.

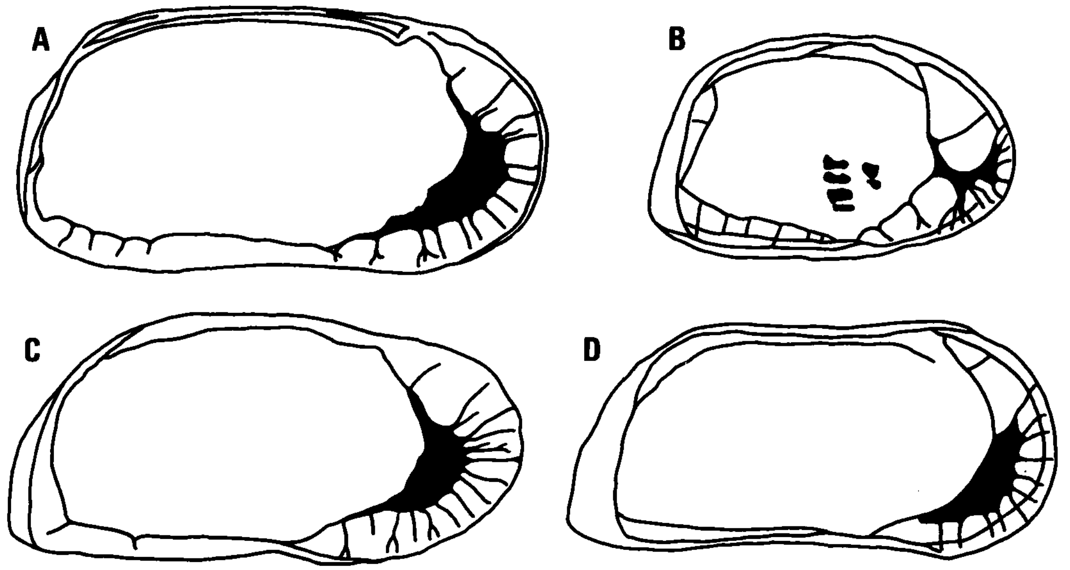
14–18) commented that their lectoholotype lacks the broadly-arched dorsum discussed and illustrated by Brady. Text-figure 4 suggests that they selected a subadult.

Krithe

Two taxonomic philosophies have been applied to deep-sea representatives of this genus. The first (van den Bold, 1977, 1981; Pokorný, 1980) defines narrowly circumscribed species on the basis of traditional internal and external carapace features. The other, (Kaesler and Lohmann, 1972; Peypouquet, 1979; Benson and Peypoquet, 1983) emphasizes the environmental plasticity of the krithinid carapace under the influence of environmental parameters. In Peypouquet's (1979) taxonomy, a few, highly-variable species are differentiated by the number and length of pore canals in the dorsal third of the anterior vestibule; ecomorphotypes of these species vary in length (up to 250%), shape, vestibular size and shape and valve overlap. Different species can approach each other in overall appearance so completely as to be virtually indistinguishable (Benson and Peypouquet, 1983, Pl. 5, figs. 5, 7). Such extreme variation has not been demonstrated in other euhaline, podocopid ostracods. Although often criticized by others (Pokorný, 1980; Whatley, 1983; Steineck *et. al.*, 1984), this system has given rise to palaeoenvironmental intepretations consistent with sedimentological and geochemical data (Ducasse and Peypouquet, 1978, 1979; Benson and Peypoquet, 1983).

Attempts to develop a taxonomy of Leg 85 krithinids began with the establishment of two labile species: *Krithe* C (= *K. vandenboldi* and related forms) and *K.* D (= *K. morkhoveni*) of Peypouquet (1979) (Text-fig. 5). However, a consistent ecomorphotypic stratigraphy related to interpretable environmental change could not be demonstrated. Subsequently, a more conservative taxonomy based on limited intraspecific variation was adopted (Table 1).

Discrimination of species of *Krithe* remains a formidable undertaking regardless of the taxonomic approach used. In Leg 85 material, a middle Miocene to Quaternary population with reverse overlap closely resembles *K. reversa* (van den Bold, 1958; Pl. fig. 5; Text-fig. 5B). In the Caribbean where it is widespread, *K. reversa* has same stratigraphical range as in the central equatorial Pacific (van den Bold, 1977, fig. 5). In the Pacific, *K.* 3 is identical to *K. reversa* except for normal valve overlap (Text-fig. 5C) and slightly smaller size. *Krithe* sp. 3 first appeared in the lower



TEXT-FIG. 5—Outline sketches of the internal characteristics of species of *Krithe*. A. *Krithe* sp. 3, adult left valve (normal overlap), length=900 μm. B. *K.* sp. 1, adult left valve, D-type of Peypouquet (1979), length=1100 μm. C. *K. reversa*, adult left valve (reverse overlap), length = 1000 μm. D. *K.* sp. 6, adult left valve, C-type of Peypouquet (1979), length=900 μm. A and C from 575, 9–4, Middle Miocene (N9). B and D from 574, 21cc, Middle Miocene (N9).

TABLE 2—SPECIES PRESENT IN THE OLIGOCENE OF EASTERN EQUATORIAL PACIFIC (LEG 85, DSDP) AND THE CODRINGTON COLLEGE MEMBER (OLIGOCENE), OCEANIC FM., BARBADOS.

Abyssocythere trinidadensis (*A.* sp.)
Agrenocythere antiquata
Bairdia oarion (*B. cespedecensis*)
Bairdoppilata sp. (*B. cassida*)
Bradleya johnsoni (*B. dictyon*)
Eocytheropteron trinidadensis
Eucythere sp.
Henryhowella sp. (*H.* aff. *H. asperrima*)
Messinella quanajayensis[1]
Oxycythereis sp.
Poseidonamicus ex. gr. *major*
Trachyleberis sp.
Xestoleberis chamela

Names in parentheses are those given in Steineck *et al* (1984, fig. 7). 1, first record of genus outside of Caribbean.

Oligocene and is present with *K. reversa* in middle Miocene to Quaternary samples. Does this represent a single and long-ranging species accompanied by a discrete dimorph in the latter part of its range? Alternatively, are these separate species which diverged in the middle Miocene?

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Steineck *et. al.* (1984, p. 1469–1495) enumerated the taxonomic affinities of Palaeogene deep-sea ostracod faunas in the Caribbean and eastern Meditteranean. This consanquinity can now be extended to the eastern equatorial Pacific. Twenty-two well-characterised and consistently occurring species have been recognised in the Lower Ecozone (excluding the krithinids which present special comparitive problems). Of these, 13 occur in the Oligocene Oceanic Fm. of Barbados (Table 2). Three additional Leg 85 forms (*Ambocythere* cf. *A. caudata, Phacorhabdotus* sp., *Proabyssocypris* sp.) are very similar to congeners in the Oceanic.

Steineck *et al.* (1984) speculated that Palaeogene deep-sea ostracods achieved cosmopolitan distributions via active dispersal across the circum-equatorial Tethys Ocean abetted by the dominantly latitudinal circulation of deep-water of that period. This circulation could have easily extended a "Caribbean fauna" westward into the Pacific through the broad and deep "Bolivar Trough" (Durham, 1985) which allowed full interchange of faunas and water-masses between the Pacific and Caribbean. Similar palaeodepths (2.5 to 3.0 km) for the Oceanic Formation (benthic microfossils—Saunders *et al.*, 1984; Wood *et al.*, 1985; Steineck *et al.*, 1984) and for Oligocene crust in the Leg 85 area (age-depth subsidence—Theyer *et al.*, 1985) enhance the plausibility of active dispersal across regions of uniform environmental conditions established by the routes of thermohaline currents.

Recent interpretations of the origin and displacement of Caribbean crust present an alternative explanation for the faunal similarities between the Pacific and Caribbean (Sykes *et al.*, 1982; Durham, 1985). Forty million years ago the Caribbean Plate was in the eastern Pacific. It has subsequently moved east-northeastward 1400 miles to its present (and relatively fixed) geographical co-ordinates. The Caribbean deep-sea fauna may have originated in the Pacific, colonised the "Caribbean" Plate and then was carried eastward by the movement of crustal blocks. Additional biogeographical data are needed to bring this problem into clearer focus; tectonic transport and active current-oriented dispersal may not be mutually exclusive hypotheses. Some species present in the Oligocene of the central equatorial Pacific (*e.g. Abyssocythere trinidadensis*) first appeared in Cretaceous sediments deposited on the northeastern slope of continental South America (van den Bold, 1957). For these species, at least, active dispersal westward is required.

PALAEOCEANOGRAPHIC IMPLICATIONS

The Oligocene to lower Miocene ostracod faunas of the central equatorial Pacific (this report) and the Caribbean (van den Bold, 1977, 1981; Steineck, 1981; Steineck *et. al.*, 1984) are here combined into a single biogeographical/tectonic/palaeoceanographical province. These assemblages are recognized by 1) low rates of faunal turnover, 2) relatively high species diversity, 3) "archaic" faunal elements derived from the Cretaceous and Eocene, and 4) taxonomic affinities to the faunas of the Tethyan region. Oxygen-istope data for this interval (as interpreted by Matthews and Poore, 1980 and Poore and Matthews, 1984a, b) reflect the continuing presence of warm (10–12 °C) bottom-waters in many areas of the World Ocean. The areal extent of upper Palaeogene and lower Miocene sedimentary hiatuses (Keller and Barron, 1983) indicate the unimpeded flow of deep-water from the Atlantic to the Pacific. These data can be explained by invoking the existence of a stable oceanographical regime dominated by the circum-equatorial flow of warm, saline bottom-waters (WSBW of Brass *et. al.*, 1982) during the period of time represented by the Lower Ecozone. Such circulation derives its energy, excess density and volume by the reflux of salty brines from epeiric seas situated in the belts of Hadley Cell-aridity between 10 and 30° N and S latitude.

Land ice had accumulated on the Antarctic continent by the middle Eocene (Leckie and Webb, 1983). Major glacial advances at 36, 32–29 and 26–17 Ma (Leckie and Webb, 1983; Kiegwin and Keller, 1984; Miller and Thomas, 1985) may have lowered sea-surface temperatures around the coastline of Antarctica sufficiently to initiate the production of cold sinkwater. The lack of correlative low-latitude microfaunal responses to these events (Woodruff and Douglas, 1981; Woodruff, 1985) suggests that the northward advection of this water-mass either was intercepted by topographic barriers (Rio Grande Rise, a constricted and still-shallow Drake Passage) or lacked the buoyancy flux (Hay, 1983, p. 16–18) necessary to displace thermospheric waters from the base of the water-column in equatorial regions. Eocene-Oligocene changes in the ostracod fauna of the south Atlantic (Benson, 1975, 1977) may be due to the proximity of this area to the Ross Sea, a likely source for cold bottom-waters in the Palaeogene.

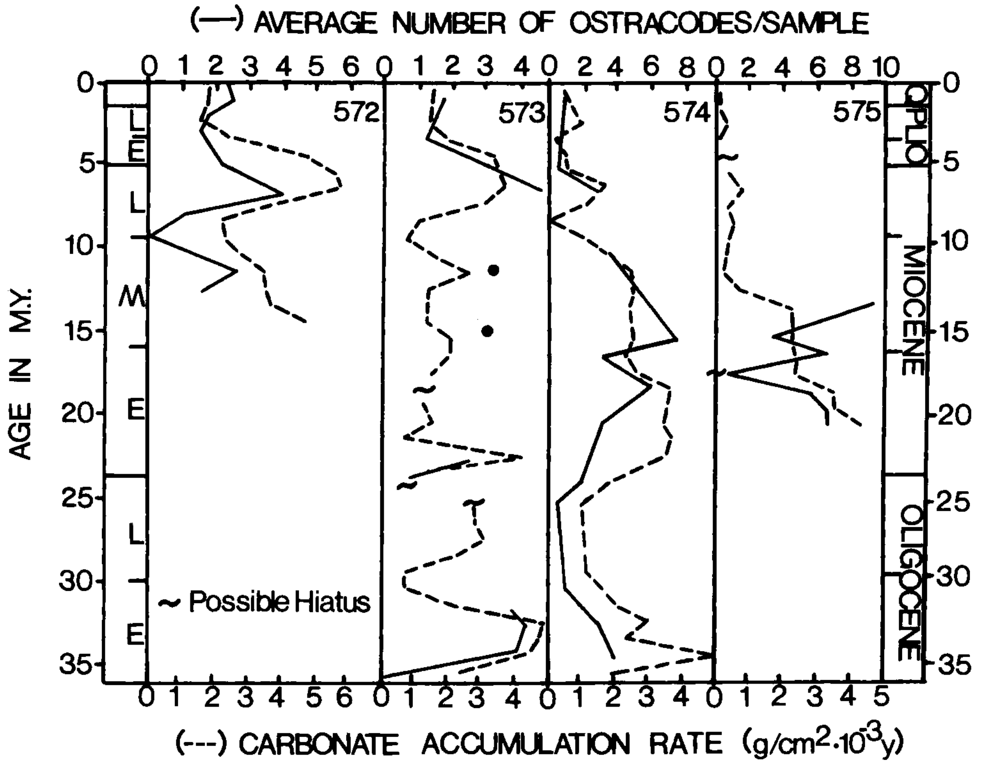
Thus, two contrasting types of negatively buoyant water-masses are inferred to have been present in the deep circulation of the Palaeogene World Ocean. The dominance of one or the other at a given place and time was determined by their rates of production, comparitive densities and by the influence of topographical features on their path of flow. In conclusion, we recognize that other interpretations of the oxygen-isotopic and faunal records discussed here are equally plausible (*e.g.* Shackleton *et al.*, 1984).

During the late early and middle Miocene (16–12 Ma), Pacific-wide changes in hydrography, patterns of sediment accumulation, surface-water productivity and carbonate dissolution had profound and irreversible effects on the distribution and taxonomic composition of major microfossil groups and on their preservation in the sedimentary record (Woodruff and Douglas, 1981; Barron, 1985; Woodruff, 1985). Yet, for all their scope and magnitude, middle Miocene oceanographic events had little influence on the ostracod record of the central equatorial Pacific as it is presently known. Only two faunal responses have been identified in samples of this age: 1) the extinction of typically Palaeogene species; and 2) a reversal in the relative frequencies of *Bradleya* and *Poseidonamicus* (Text-figs. 2, 3). This apparently diffuse and extended pattern of accommodation to major oceanographical changes may become sharper and more sudden when the taxonomic affinities and evolutionary trends of lower and middle Miocene populations of *Krithe, Bradleya* and *Poseidonamicus* in this region of the Pacific are better understood.

A marked faunal turnover in zone N17 (9–5 Ma) created the distinctive *Krithe-Bradleya-Bracycythere* faunas present in Pliocene to Quaternary sediments of the central equatorial Pacific. This assemblage took form in synchrony with the onset of a hydrological regime in the Leg 85 region favouring the accumulation of biogenic silica, the production of large quantities of organic carbon, and the intense dissolution of calcite (Barron, 1985; Theyer *et al.*, 1985).

Our belief that this correlation is not fortuitous is based on the study of Bremer and Lohman (1982) who demonstrated that the relative saturation of bottom-water with respect to calcite controls the distribution of benthonic-foraminiferal assemblages in the South Atlantic. We have tentatively concluded that the lengthening duration and growing intensity of dissolution episodes during the late Miocene and Pliocene were primarily responsible for the ostracod faunal changes that occurred in the Leg 85 region.

Ostracod species which occur in Pliocene to Quaternary sediments of the central equatorial Pacific are not restricted to benthonic settings in contact with corrosive bottom-waters. In fact, many occur in association with the high-pH, Norwegian Sea Overflow Water, west of Iceland (van den Bold, 1965), on the continental-rise east of Newfoundland (Benson *et al.*, 1983) and in the south Atlantic (Benson and Peypouquet, 1983). Rather, it seems that only these forms are capable of successful growth and reproduction when undersaturated bottom-water is present. As this situation became increasingly prevalent at abyssal depths in the Pacific, other species either became extinct or were restricted to intermediate water-masses in a fashion similar to the late Miocene upslope migration of the *Astrononion-Uvigerina-Melonis* benthonic foraminiferal fauna in the western Pacific (Woodruff and Douglas, 1981).



Text-fig. 6—Ostracod abundance versus carbonate accumulation rate. Ostracod abundance plotted as the average number of specimens per sample per biostratigraphical zone; note the variation in scale across the top margin. Blackened circles represent isolated recovery in an otherwise unfossiliferous interval. Carbonate accumulation rate is the sedimentation rate corrected for compaction. This data taken from Theyer *et.al.* (1985, fig. 6).

Palaeofertility and Ostracod Abundance

Does the density of ostracod populations in the deep-sea vary with the availability of food? Benthonic organisms in the abyssal and hadal zones depend on organic particles transported from terrestrial, shallow-marine and planktonic communities for food. In general, the rate of supply of this material plays an important role in determining the biomass that can be supported at a given site on the sea-floor (Thiell, 1977; Wolff, 1977). In the open ocean, the most important and predictable source of organic particles is the rain of dead plankton and faecal pellets from surface-waters; the flux is controlled primarily by primary productivity which in turn, is tied closely to the amount of dissolved nutrients in the euphotic zone. In the central equatorial Pacific, sediments are predominantly composed of the skeletons of planktonic organisms. Temporal and spatial variations in the primary productivity of surface waters have modulated the rate at which these particles accumulated at Leg 85 sites over the past 40 MY except for those periods when carbonate dissolution took place either in the water column or on the seabottom (Theyer *et al.*, 1985).

The following hypothesis is proposed: increased quantities of organic debris reaching the sea-floor correlate with growth in the size of the ostracod population. It is tested by a comparison of trends in ostracod abundance and carbonate accumulation rate (CAR) in Leg 85 sediments

TABLE 3—A TEST OF THE HYPOTHESIS THAT CHANGES IN PRIMARY PRODUCTIVITY AND OSTRACOD ABUNDANCE ARE POSITIVELY CORRELATED. SUMMARY OF POSSIBLE OUTCOMES.

DATA TRACKING	CARBONATE DISSOLUTION	OUTCOME	EXAMPLE
A, Ostracod number covaries with carbonate accumulated rate	NO	A1 Hypothesis accepted	site 574, Oligocene
	YES	A2 Covariance reflects dissolution	site 573, Pliocene–Quaternary
B, Ostracod number varies independently of carbonate accumulation rate	NO	B1 Hypothesis rejected	site 573, late Oligocene
	YES	B2 No conclusion drawn; may indicate differential dissolution	site 574, Pliocene–Quaternary

(Text-fig. 6). Carbonate accumulation rate is inferred to track the fertility of surface-waters, euphotic biomass and the flux of organic debris to the sea floor.

The size of the living ostracod population over time is estimated by a crude density statistic—mean number of valves and carapaces per sample per biostratigraphical zone. Sparse faunas preclude a more ambitious statistical treatment; variance about the mean/zone is likely to be high. The plot of CAR over time in the Leg 85 core inventory is taken from Theyer *et. al.* (1985, fig. 6). These authors and other Leg 85 scientists (*e.g.* Barron, 1985) have discussed the processes which control this and other aspects of sedimentation rate in the region under study. Table 3 outlines the outcomes possible from the test undertaken here.

Oligocene sediments were cored at sites 573 and 574. At site 574, the tracking of CAR by ostracod number is good except in the early Oligocene when a peak CAR is not fully reflected in ostracod number. However, this peak in CAR is accompanied by a maximum ostracod number at 573. Outcome A1 is indicated. The absence of ostracods in upper Oligocene samples of site 573 requires outcome B1.

At site 575, high CAR between 20 and 13 Ma is matched by the greatest ostracod abundances recorded in Leg 85 sediments. Tracking is poor as ostracod number exhibits greater variability than CAR. The absence of ostracods at 16.5 Ma corresponds to a hiatus or an interval of carbonate dissolution. Outcome A1 is suggested. Upcore, % carbonate is low due to dissolution; this interval has not been sampled for ostracods. At site, 574, maximum CAR occurred at 16–17 Ma and remained high until 10 Ma. Ostracod number correlates well with CAR throughout this interval (Outcome A1). The remainder of the core is characterised by carbonate dissolution and low numbers of ostracods; outcomes A2 or B2 are equally likely.

Sites 572 and 573 are situated at about the same latitude and experienced a similar Neogene sedimentation history. Accumulation rates at site 572 are consistently higher, however, by virtue of its easterly location adjacent to an intense zone of upwelling associated with the Equatorial Current. Ostracod number closely tracks the Late Miocene increase and subsequent decline in CAR in both cores. However, the Late Miocene CAR at site 572 is a regional maximum; ostracod number is high but exceeded by values at site 575. Outcome A1 is indicated. Only 12 samples from the early, middle and early late Miocene of site 573 were available for analysis. Ten were barren; the two fossiliferous samples have relatively abundant ostracod faunas which correspond to peaks on the CAR curve.

This section has examined the covariance of ostracod abundance and food resources using a simplified model relating primary productivity to sedimentation rate. Qualitative assessment of the tracking between ostracod abundance and CAR curves reveals an approximate, non-linear but generally positive correlation in those samples where ostracods are present and carbonate dissolution is minimal. Taken at face value, this result suggests that food supply has governed the density of ostracod populations in the central equatorial Pacific.

Whether this correlation arises from cause-and-effect, random variation or the effects of other factors remains to be seen. Future studies of this sort should include, 1) statistical analysis of more abundant faunas, 2) a better understanding of the trophic dynamics and microenvironmental preferences of ostracods in the deep-sea, and 3) a more realistic assessment of the fate of organic matter on the sea-bed, including the role of mixing in partitioning organic matter between surface and subsurface sediments. Such studies may permit the use of trends in ostracod-abundance as a tracer of changes in the fertility of surface-waters in ancient oceans. Perhaps, more information then is commonly supposed is encoded in the fossil record of deep-sea ostracods.

DISCUSSION

Whatley (1983) and Whatley *et al.* (1983) disagreed with the commonly held view that the deep-sea was initially colonised by ostracods seeking a refuge from the intense competition for eco-space taking place in shallow-water environments as new and more highly-adapted forms evolved and diversified. As an alternative to the "active migration" process, they noted that the subsidence of oceanic plateaus, aseismic ridges and microcontinental fragments can transfer shallow-water faunas involuntarily to oceanic depths. In those cases where the rate of submergence was gradual, some taxa might be able to adapt successfully to the new environmental conditions. As examples, Whatley *et. al.* (1983, figs. 2, 3) cited the history of *Bradleya* and *Poseidonamicus*. Their data indicated that Palaeogene species were endemic to the S.W. Pacific and restricted to bathyal depths. Populations of both genera were subsequently introduced into the deep-sea when the Lord Howe Rise, a large oceanic plateau located to the east of Australia, subsided to abyssal depths in the early Miocene. However, both genera are now known from lower Oligocene sediments in the central equatorial Pacific (Table 1), in the Oceanic Formation of Barbados (Steineck *et. al.*, 1984) and the southern Indian Ocean (Benson, 1983). Thus, they were present in oceanic settings 18 MY earlier than the subsidence history of the Lord Howe Rise would allow. Most ostracod genera known to have occurred in Palaeogene oceans are of Palaeozoic or Mesozoic origin and had entered the deep-sea by the middle Eocene (van den Bold, 1957, 1960; Esker, 1968, Porkornỳ, 1975, 1981; Benson, 1977; Steineck *et al.*, 1984). The problem of when, where and why this fauna colonised the deep-sea requires much further study. Both the "active migration" and "involuntary transfer" processes are attractive but largely unsubstantiated possibilities.

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DISCUSSION

Cronin: With reference to the tectonics of the Caribbean, do you feel the Pacific ostracods were moved gradually on the moving plate or that the rock units (or "terrains") containing fossil ostracods were moved after deposition and lithification?

De Deckker: I assume that it is included in your paper but could you define the difference between carbonate accumulation rate versus carbonate sedimentation rate?

Steineck: Carbonate accumulation rate is the $CaCO_3$ sedimentation rate corrected for compaction. Thus Oligocene chalks and their sedimentation rates can be compared directly with Miocene oozes which are unlithified and uncompacted.

Hazel: I am curious as to why you refer that winged smooth species to *Brachycythere.* I have not seen true *Brachycythere* above the lower Eocene. If it is a *Brachycythere.* the muscle scars will be distinctive (*e.g.*, see Hazel and Paulsen, 1964).

Henning Uffenorde: Do you use the invalid genus "*Thalassocythere*" sensu Benson (1977) or are you going to describe it in your paper?

Palaeobiogeography and Palaeoecology of the Tertiary Ostracods of Northwestern India with Palaeooceanographic Remarks

PRATAP SINGH
Oil and Natural Gas Commission, Dehra Dun, India

ABSTRACT

Marine strata ranging in age from Eocene to Miocene are well represented in northwestern India constituting a part of the Bombay Offshore, Cambay, Saurashtra, Kutch, and Rajasthan basins and have yielded a fairly rich assemblage of ostracods. The ostracod assemblages suggest that the basins mentioned above were in existence during Eocene, Early Oligocene, and Early Miocene times and all received their sediments from the same Tethys Sea.

An attempt is made to show the palaeobiogeography of the important species of ostracods and to discuss their palaeoecology with the help of other associated microfauna. The distribution of the Tethys sea during Early Eocene, Middle Eocene, Late Eocene, Early Oligocene, and Early Miocene times in northwestern India is shown.

A substantial amount of significant data on the ostracod and foraminiferal content of the marine fossiliferous Tertiary sequence developed in the Bombay Offshore, Cambay, Saurashtra, Kutch, and Rajasthan basins of the northwestern India (Text-figs. 1–5) has been published and tempted the writer to utilize the published data in determining the palaeobiogeography and palaeoecology of the Tertiary ostracods of these basins and to reconstruct the palaeoshore lines of the Tethys Sea that occupied these basins in the Tertiary period.

Because of limited space, the geology, stratigraphy and ostracod assemblages of these basins are not discussed individually. Only the important references are given for general information, and details can be ascertained from these.

GEOLOGY AND STRATIGRAPHY

Geology and stratigraphy have been dealt with by a considerable number of authors and the principal references in connection with the various basins are given below. Sahay (1978), Rao and Talukdar (1960), Mohan *et al.* (1982), and Mitra *et al.* (1983) worked out the geology and stratigraphy of the Bombay Offshore Basin.

Mathur and Kohli (1963), Mathur *et al.* (1968), Raju (1968, 1979), Chandra and Chowdhary (1969), Rao (1969), Sudhakar and Basu (1973), and Raju and Srinivasan (1983) contributed to the geology and stratigraphy of the Cambay Basin.

Fedden (1884), Mohan and Chatterji (1956), and Biswas and Deshpande (1983) studied the geology and stratigraphy of the Saurashtra Basin.

Wynne (1872) was the first to describe the geology of Kutch. Biswas (1965) for the first time proposed a chronostratigraphic classification of the Tertiary sequence of the Kutch Basin. This was followed by Biswas and Deshpande (1970, 1983), Biswas and Raju (1973), and Singh and Singh (1981) who all made useful contributions on the geology and stratigraphy of the Kutch Basin.

The geology and stratigraphy of the Rajasthan Basin have been described by Oldham (1886), La Touche (1902), Singh (1951, 1952, 1953, 1971), Khosla (1967, 1971, 1973), Pareek (1981), Datta (1983), and Singh (1984).

OSTRACOD ASSEMBLAGES

i. *Bombay Offshore Basin.* Guha (1974, 1975, 1978b) studied in detail the Eocene, Oligocene, and Miocene ostracods of this basin.
ii. *Cambay Basin.* Bhatia and Mandwal (1960) described the Early Miocene ostracods of this basin. Guha (1965, 1967a, 1971, 1974, 1978a), Biswas and Guha (1970), and Guha and Rao (1977) reported a fairly rich assemblage of Ostracoda from the Eocene, Oligocene, and Early Miocene strata of the Camby Basin.
iii. *Saurashtra Basin.* Guha (1967b), Khosla (1978), and Khosla and Pant (1978) listed a fairly rich assemblage of ostracods from the Early Miocene starta.
iv. *Kutch Basin.* The Palaeogene and Neogene ostracods have been studied by Tewari and Tandon, (1960), Lubimova *et al.* (1960), Guha (1961, 1968), Tewari and Bhargava (1968), Guha and Rao (1977), Khosla and Pant (1981), and Pant and Khosla (1982).
v. *Rajasthan Basin.* Singh and Misra (1968), and Khosla (1967, 1968, 1972, 1973) described the Early and Middle Eocene ostracods of this basin.

PALAEOBIOGEOGRAPHY

The distribution of the important and common species of ostracoda in the Bombay Offshore, Cambay, Saurashtra, Kutch, and Rajasthan basins during Eocene, Early Oligocene, and Early Miocene times has been shown in Text-figs. 1–5. The common distribution of these ostracod species suggest that transgression resulted in these basins being occupied by the Tethyan Sea in Early Eocene, Middle Eocene, Late Eocene, Early Oligocene, and Early Miocene times.

PALAEOECOLOGY

General Data Review

An attempt has been made to determine a general palaeoecology of the ostracod assemblages that were thriving in the northwestern basins of India during the Early Eocene, Middle Eocene, Late Eocene, Early Oligocene, and Early Miocene times. The writer has also taken into account the associated foraminiferids for achieving the above objective. Because of limited space, it is not possible to review the many palaeontological studies carried out on Ostracoda over the last twenty years. It is assumed that readers will be fairly familiar with this work. However, since they will probably be less familiar with the significance of the Foraminifera, a brief résumé of the palaeoecological implications of relevant taxa is given below. Foraminiferids are well known from work in northwestern India and attention has been focussed mainly on the larger foraminiferids. From the voluminous literature it is only possible to abstract some representative conclusions.

For example, Hottinger (1960) concluded that alveolinids could apparently live on a shallow sea bottom with a poor supply of detritus. No alveolinids have so far been recorded from brackish sediments and all recent species of the family Alveolinidae have been reported from marine waters of normal salinity.

Luterbacher (1970) recorded the foraminiferal genera *Alveolina* (now known as *Fasciolites*) from lagoon deposit, and *Operculina, Assilina,* and *Nummulites* from lagoon, muddy beach, lagoon-bay deposits, bay skeletal, protected platform limestone, *Turritella* shales, *Pattalophyllia* shales and *Nummulites* shales (probable water depth 0–30 metres). The genus *Discocyclina* is distributed in *Nummulites* bar deposits, *Turritella* shales, *Pattalophyllia* shales and *Nummulites globulus* shales deposited at a probable water depth of 5 and 30 metres.

Murray (1973) pointed out that the genus *Sorites* prefers salinities of more than 37‰, temperature 18°–26° C and inhabits lagoon and near shore environments. The genera *Ammonia* (15°–30° C, 0–50 m), *Archaias, Elphidium* (keeled 35–50‰, 15° C, 0–50 m; unkeeled 0–70‰, 1–30° C, 0–50 m) and *Operculina* inhabit an inner shelf environment.

Gammers (1978) considered that the foraminiferal genus *Discocyclina* lived in deeper water than *Nummulites* and generally thrived in moderately deep shelf waters (*ca.* 15–50 m).

PALAEOECOLOGICAL INTERPRETATIONS

Early Eocene ostracod Assemblage

The Early Eocene strata of the Cambay Basin include Cambay black shales and argillites in areas south of the Narmada river (Chandra and Chowdhary, 1969; Sudhakar and Basu, 1973; Pandey and Dwarikanath, 1977). The smaller foraminiferids are rare in the Cambay black shales. The ostracods are represented by *Alocopocythere lunejensis, Anticythereis memorans, Ovocythereidea cambayensis, Paracypris jhingrani, P. lakiensis,* and *Schizocythere* cf. *S. levinsoni* (Guha, 1974). The poor faunal contents, pyrite, and plant remains suggest that the Cambay black shales were deposited in a very shallow marine, reducing, environment. According to Sudhakar and Basu (1973), the Cambay black shales were deposited in lagoons and paludal swamps.

The Early Eocene strata of the Kutch Basin consist of the gypseous shales in the lower part and calcareous shales and limestone in the upper part (Biswas and Raju, 1973; Raju, 1974; Singh and Singh, 1981; Biswas and Deshpande, 1983). Singh and Singh (1981) recognised the following biostratigraphic zones in the ascending order: i. Barren zone, ii. *Discocyclina* Acme-zone, iii. Barren interzone I, iv. *Nummulites globulus* Acme-zone, v. Barren interzone II, and vi. *Nummulites* (*Assilina spinosa* Acme-zone. The ostracods are fairly well distributed in the *Nummulites globulus* Acme-zone and *Nummulites* (*Assilina*) *spinosa* Acme-zone. The important ostracod genera, indicating a shallow marine environment, are *Aglaiocypris, Bairdoppilata, Cytherella, Cytherelloidea, Cytheropteron, Occultocythereis, Paracythereidea, Semicytherura,* and *Xestoleberis* (Lubimova *et al.*, 1960; Guha, 1974; Khosla and Pant, 1981; Pant and Khosla, 1982). The associated larger foraminiferids are *Lockhartia* sp., *Nummulites burdigalensis* de la Harpe, *N. globulus* Leymerie, *N.* (*Assilina*) *daviesi* Cizancourt, and *N.* (*A.*) *spinosa* Davies (Singh and Singh, 1981). It may be safely concluded from the above data that the recorded ostracod assemblage inhabited a lagoonal environment. This contention is further supported by the presence of gypsum, absence of planktonic foraminiferids, and rarely distributed stunted calcareous nannoplankton.

The Early Eocene strata of the Rajasthan Basin are represented by the fuller's earth, marlstone, calcareous shales, and limestones in the lower part and limestones are interbedded with shales in the upper part and have yielded a fairly rich assemblage of ostracods and foraminferids (Singh and

Misra, 1968; Singh, 1971; Khosla, 1971, 1972, 1973). The important ostracod genera, suggesting a shallow marine environment, are *Bairdia, Bairdoppilata, Cytherella, Cytherelloidea, Cytherura, Hermanites, Neocyprideis, Occultocythereis, Quadracythere, Semicytherura, Trachylebereis,* and *Xestoleberis.* The ostracod genera, occurring at all depths of marine water, are *Buntonia, Cytheropteron, Echinocythereis, Eucythere. Paracypris* and *Bythocypris* which generally occur in a somewhat deeper water environment, are also present. The associated foraminiferal genera are *Assilina, Nummulites,* and *Operculina* and mollusc shells also occur. The above fauna indicates a shallow, warm (temperature more than 10° C), inner shelf environment.

Middle Eocene Ostracod Assemblage

The Middle Eocene strata of the Tarapur Sub-basin, Cambay Basin, and Kutch Basin are generally represented by limestones and shales containing a fairly rich assemblage of ostracoda and foraminiferids. The larger foraminiferids are represented by the genera *Assilina, Discocyclina, Fasciolites, Halkyardia, Lockhartia,* and *Nummulites* (Singh, 1951, 1952, 1953; Tewari, 1952; Sen Gupta, 1959, 1964; Raju *et al.*, 1970; Khosla, 1973; Tandon, 1976; Pandey and Dwarikanath, 1977; Pandey and Guha, 1979; Kumar, 1979; Jauhari and Vimal, 1978) and the planktonic foraminiferal genera are *Indicola, Dentoglobigerina, Globigeropsis, Globigerinoides, Globorotalia* (*Acarinina*), *G.* (*Morozovella*), *G.* (*Turborotalia*), *G.* (*Truncorotaloides*), *Muricoglobigerina* and *Subbotina* (Samanta, 1970; Mohan and Soodan, 1970; Singh, 1971; Jauhari, 1974; Pandey and Guha, 1979). The important associated ostracod genera which indicate a shallow, marine environment are *Bairdia, Bairdoppilata, Cytherella, Cytherelloidea, Cytheromorpha, Cytheropteron, Cytherura, Hemicythere, Hermanites, Kingmaina, Neocyprideis, Occultocythereis, Paijenborchella, Paracythereidea, Quadracythere, Schizocythere, Trachyleberis, Uroleberis,* and *Xestoleberis* (Tewari and Tandon, 1960; Lubimova *et al.*, 1960; Guha, 1965, 1968, 1974, 1978a; Singh and Misra, 1968; Khosla, 1968, 1972, 1973; Biswas and Guha, 1970; Khosla and Pant, 1981; Pant and Khosla, 1982). In general this diverse microfaunal assemblage suggests that a warm inner shelf environment having a water depth of more than five metres and a temperature probably more than 10° C prevailed during Middle Eocene time in all the basins mentioned above.

Late Eocene Ostracod Assemblage

The Late Eocene strata of the Tarapur Sub-basin and the Cambay Basin are composed of limestones, calcareous shales and shales. The ostracods and foraminiferids are very well represented. The larger foraminiferal genera include *Assilina, Asterocyclina, Discocyclina, Nummulites,* and *Pellatispira* (Raju *et al.*, 1970; Pandey and Guha, 1979; Kumar, 1979). The important associated ostracod genera are *Bairdia, Bairdoppilata, Cytherella, Cytherelloidea, Cytherura, Hermanites, Hemicythere, Paijenborchella, Quadracythere, Schizocythere, Uroleberis,* and *Xestoleberis* (Guha, 1971, 1974, 1978b). These microfaunal assemblages indicate a warm, inner shelf environment again with a water depth of more than five metres and a temperature more than 10° C.

Early Oligocene Ostracod Assemblage

Fossiliferous limestones interbedded with shales constitute the Early Oligocene strata of the Bombay Offshore Basin. In the Cambay Basin they are represented by grey, sandy shales and argillaceous sandstone (Chandra and Chowdhary, 1969). The Early Oligocene strata of the Kutch Basin are represented by banded marlites, impure limestones with glauconite pellets and claystones (Biswas and Deshpande, 1983). Generally the Oligocene strata are found to contain a fairly rich assemblage of foraminiferids and ostracods.

The important ostracod genera of the Bombay High Sub-basin are *Aurila, Bairdia, Bythocypris, Cytherella, Cytherelloidea, Echinocythereis, Hemicythere, Loxoconcha, Loxoconchella, Miocypri-*

deis, Neomonoceratina, Occultocythereis, Paracypris, Propontocypris, Uroleberis, and *Xestoleberis* (Guha, 1974, 1975). The associated foraminiferal genera are *Archaias, Grzybowskia, Heterostegina, Nephrolepidina, Nummulities, Operculina,* and *Pararotalia* (Panddy and Guha, 1979). The significant ostracod genera of the Tarapur Sub-basin are *Bairdia, Bradleya, Clithrocythereidea, Cytherella, Neocyprideis, Trachyleberis,* and *Uroleberis* (Guha, 1978b). The associated foraminiferal genera are *Cassigerinella, Chiloguembelina, Globigerina, Heterostegina, Lepidocyclina, Nummulites, Pararotalia,* and *Uvigerina* (Pandey and Guha, 1979). In the Cambay Basin important ostracod genera include *Bairdoppilata, Cyprideis, Cytherella, Cytherelloides, Cytheropteron,* and *Occultocythereis* (Guha, 1965, 1967a, 1974). The associated foraminiferal genera are *Cassigerinella, Nummulites, Pararotalia, Pseudohastigerina,* and *Rotalia* (Raju *et al.*, 1970; Datta and Bhatia, 1972; Kumar, 1979). The important ostracod genera of the Kutch Basin are *Bairdoppilata, Clethrocythereis, Cytherelloidea, Hornibrookella, Leguminocythereis, Loxoconcha, Miocyprideis, Neomonoceratina, Neonesidea, Paracypris, Paracythereidea, Pokornyella, Trachyleberis, Uroleberis,* and *Xestoleberis* (Lubimova *et al.*, 1960; Khosla and Pant, 1981). Associated with them are the foraminiferal genera *Asterigerina, Nummulites, Operculina* and *Lepidocyclina* (Biswas and Deshpande, 1983). The ecological interpretation of this microfaunal data suggests that the ostracod and foraminiferal communities were inhabiting a warm inner shelf environment in all these basins.

Early Miocene Ostracod Assemblage

The Early Miocene strata of the Bombay Offshore Basin, Cambay Basin, Saurashtra Basin, and Kutch Basin are generally represented by limestones and calcareous shales containing ostracods and foraminiferids in abundance. In addition to these microfossils, they are also rich in lamellibranchs, gastropods, and echinoid shells.

The important ostracod genera of the Bombay High Sub-basin are *Aurila, Bradleya, Clethrocythereis, Cytherella, Cytherelloidea, Echinocythereis, Hemicythere, Loxoconcha, Neomonoceratina, Paijenborchella, Triebelina,* and *Uroleberis* (Guha, 1974, 1975). The associated foraminiferal genera are *Ammonia, Archaias, Elphidium, Miogypsinoides, Nephrolepidina, Nummulites, Operculina, Sorites,* and *Turborotalia* (Pandey and Guha, 1979). In the Cambay Basin significant ostracod genera are *Actinocythereis, Aurila, Bairdia, Bradleya, Cytherelloidea, Cytheromorpha, Hermanites, Krithe, Leguminocythereis, Loxoconcha, Miocyprideis, Neomonoceratina,* and *Paracypris* (Bhatia and Mandwal, 1960; Guha, 1978a). Associated with them are the foraminiferal genera *Ammonia, Austrotrillina, Cassigerinella, Lepidocyclina* (*Nephrolepidina*), and *Miogypsina* (Datta and Bhatia, 1972, 1977). A more or less similar ostracod assemblage has been recorded from the Tarapur Subbasin, Saurashtra Basin, and Kutch Basin (Tewari and Tandon, 1960; Lubimova *et al.*, 1960; Guha 1961, 1967b, 1978; Khosla, 1978; Khosla and Pant, 1978). The important ostracod genera of these basins are *Aglaiocypris, Actinocythereis, Aurila, Bairdoppilata, Buntonia, Caudites, Clethrocythereis, Cyprideis, Cytherella, Cytherelloidea, Cytheretta, Cytheropteron, Cytherura, Echinocythereis, Hemicythere, Hemicyprideis, Hermanites, Leguminocythereis, Leptocythere, Loxoconcha, Macrocypris, Miocyprideis, Neomonoceratina, Neonesidea, Occultocythereis, Paijenborchella* (*Eupaijenborchella*), *Paracypris, Paracytheridea, Pokornyella, Propontocypris, Quadracythere, Trachyleberis, Triebelina,* and *Xestoleberis.* The associated foraminiferal genera are *Ammonia, Archaias, Austrotrillina, Borelis, Elphidium, Miogypsina, Operculina, Lepidocyclina* (*Nephrolepidina*), *Sorites,* and *Taberina* Chatterji, 1961; Mohan and Singh, 1975; Jauhari, 1981). From this one may conclude that again a warm, inner shelf environment prevailed in all these basins during Early Miocene time.

PALAEOOCEANOGRAPHIC REMARKS

Singh (1952), Raju *et al.* (1970), Datta and Bhatia (1972), Sudhakar and Basu (1973), Pandey and Dwarikanath (1977), Mathur and Chowdhary (1977), Kumar (1979), Rao and Talukdar (1980) and Mohan *et al.* (1982) carried out palaeooceanographic studies on the Tertiary strata of the Bombay Offshore, Cambay and Rajasthan basins.

The major orogenic movements were initiated in the Himalayan region just after the collison of the Indian plate with the Eurasian plate probably in Late Cretaceous time (Singh, 1980a). The transgressions or regressions of the Tethyan Sea during Early Eocene, Middle Eocene, Late Eocene, Early Oligocene, and Early Miocene times in the northwestern India may be attributed to the repeated tectonic disturbances in the Himalayan region in the Tertiary period (Singh, 1980b)

Tethys transgressed the northwestern part of the Rajasthan and Kutch basins from Pakistan and the Cambay Basin through the gulf of Cambay during Early Eocene time. At this time, the Bombay High and Saurashtra regions were positive areas (Text-fig. 1). The Rajasthan Basin was deeper towards Pakistan and gradually shallowed towards the Indian side. The deep marine foraminiferal facies has been recorded in the subsurface Early Eocene strata lying between Ghotaru and Bandah regions (Singh, 1984). The Birmania—Barmer—Nagar Parker High (Das Gupta and Chandra, 1978) prevented the transgression of Tethys into the interior parts of the Rajasthan region during Early Eocene time.

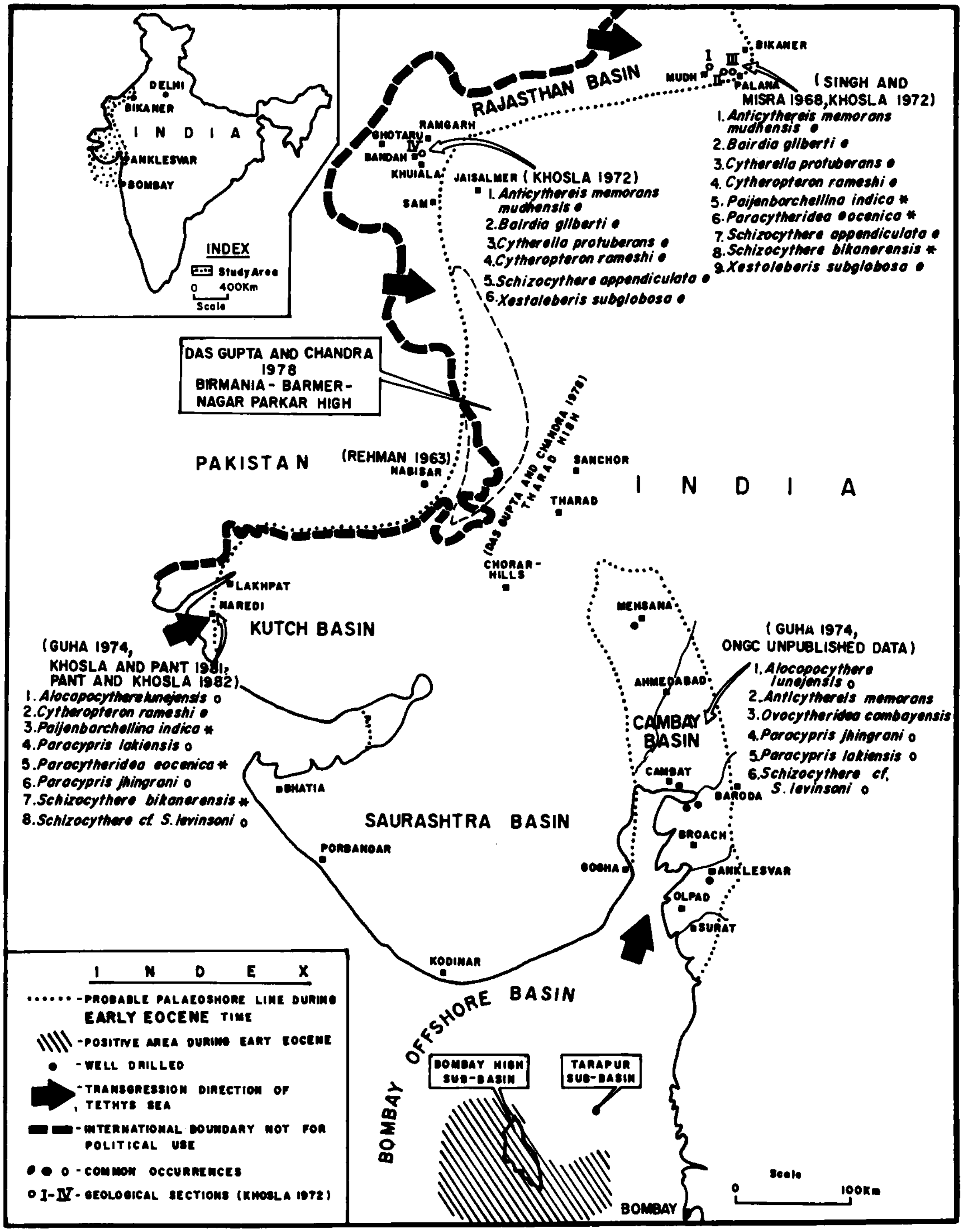
The Middle Eocene witnessed a major orogenic movement in the Himalayan region as a result of that the Tethyan Sea transgressed across the northwestern part of Kutch and deep into the Cambay region forming an epicontinental sea. The Bombay High and Saurashtra regions were the positive areas at this time (Text-fig. 2). Due to the presence of the Tharad High (Das Gupta and Chandra, 1978), there was no sea connection between the Rajasthan Basin and the Cambay Basin through the Kutch region (Text-fig. 2).

The Late Eocene saw the withdrawal of the sea from the Rajasthan and Kutch basins probably due to some major orogenic movement that took place in the Himalayan region. The Bombay High and Saurashtra regions were positive areas at this time. In the Cambay Basin, Tethys showed a slight regression from the northern parts of the Tharad and Chorar Hills (Text-fig. 3). The ostracod and foraminiferal assemblages suggest that the sea was not deep in the Cambay and Tarapur regions.

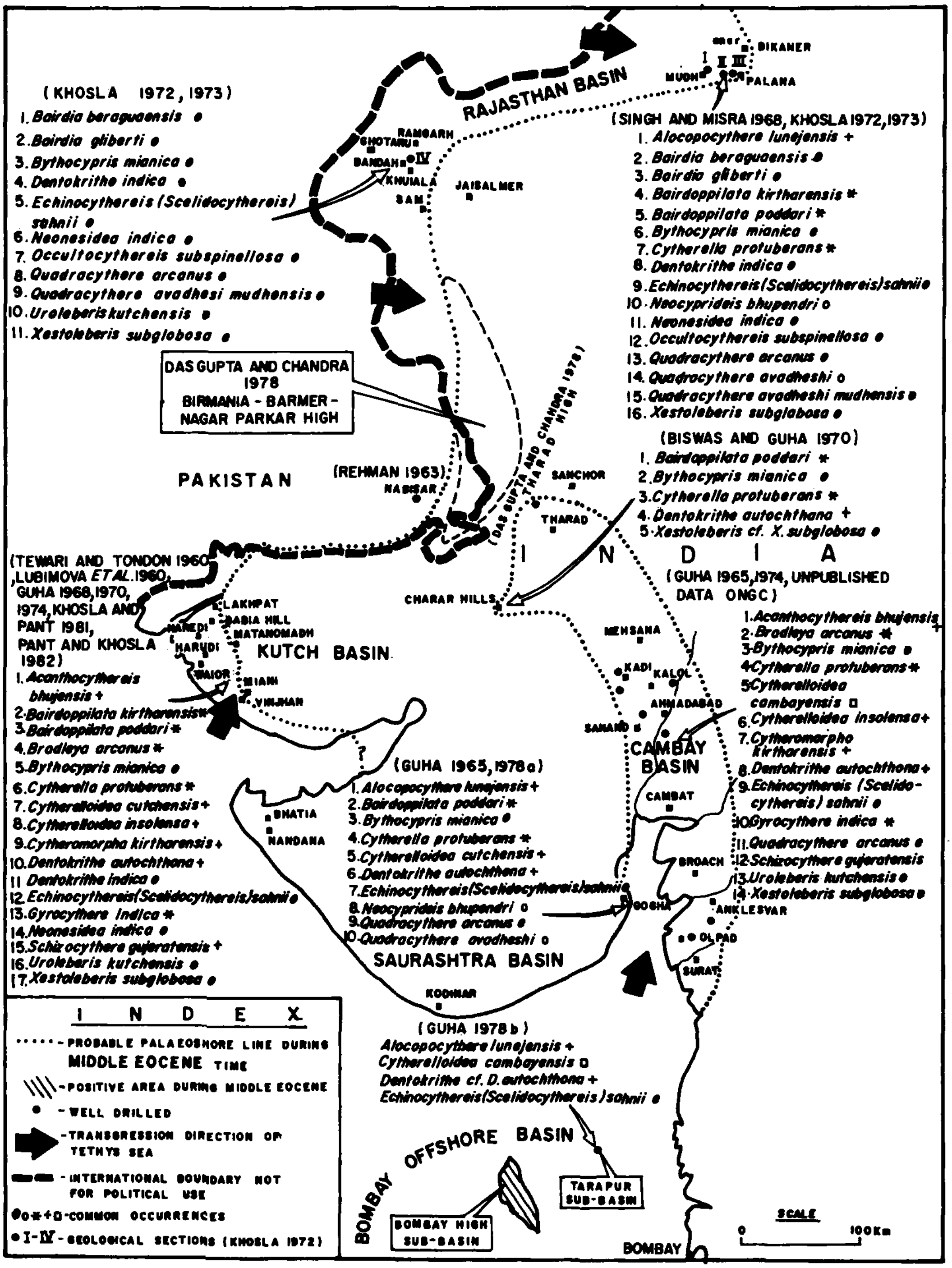
Another readjustment in the distribution of Tethys took place during Early Oligocene time, again probably caused by orogenic movements in the Himalayan region. The sea advanced into the Kutch region and occupied only the peripheral part of the Kutch mainland. At the same time, it withdrew from the Tharad region to the Mehsana area in the Cambay Basin because of some of orogenic movement that affected the northern part of the Cambay Basin. The coastal part of Bombay High island got submerged; the Saurashtra region remained as a positive area. Only a warm shallow marine depositional environment prevailed (Text-fig. 4).

The Himalayan region saw more major tectonic activity during Early Miocene time resulting in a major transgression of Tethys into the Kutch and Saurashtra regions (Text-fig. 5). However, the sea withdrew from the Mehsana area to the north of the Kalol region in the Cambay Basin. Bombay High island was completely submerged.

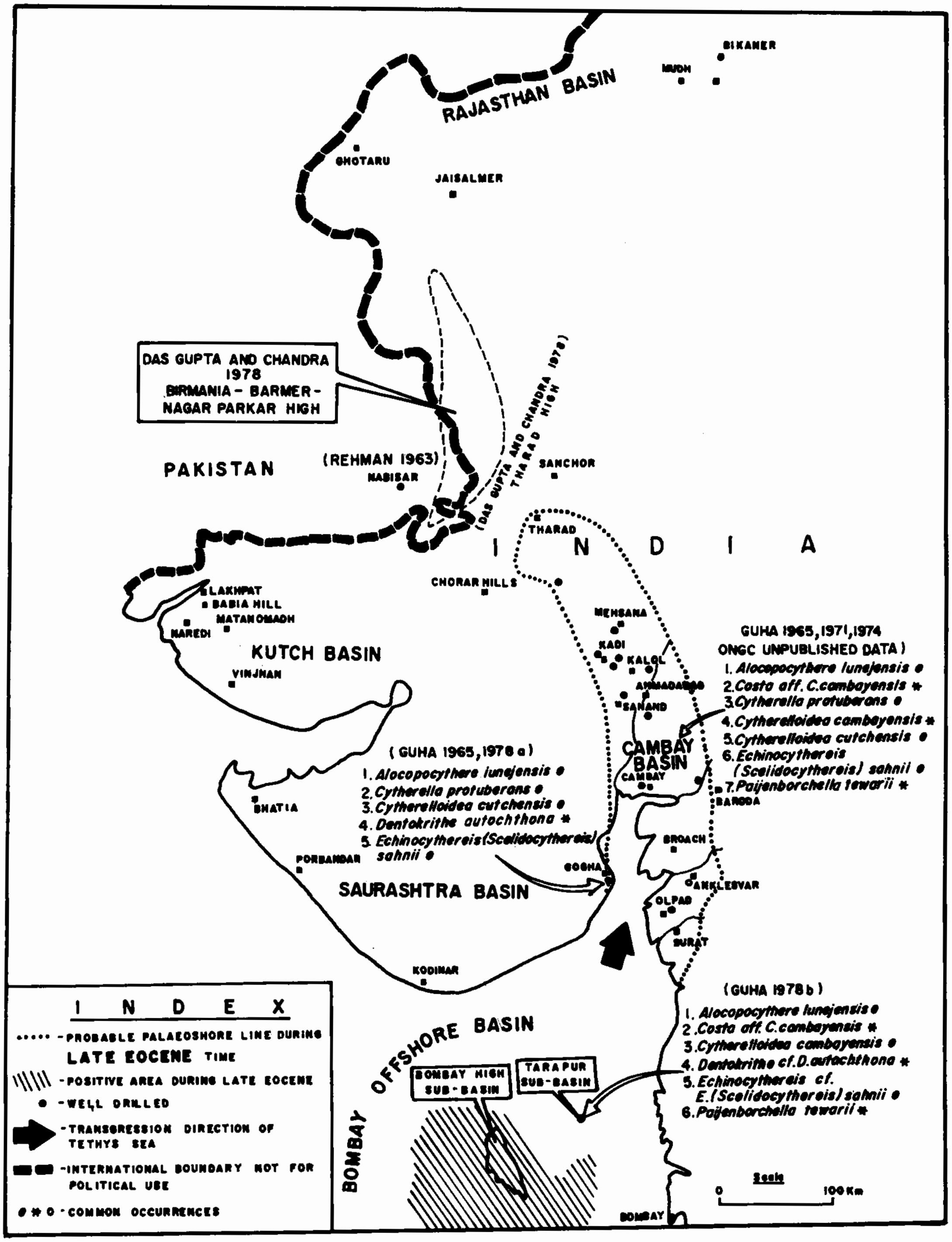
In summary the data show that all the basins mentioned above were in existence during Eocene, Early Oligocene, and Early Miocene times and that all received their sediments from the same Tethys Sea.



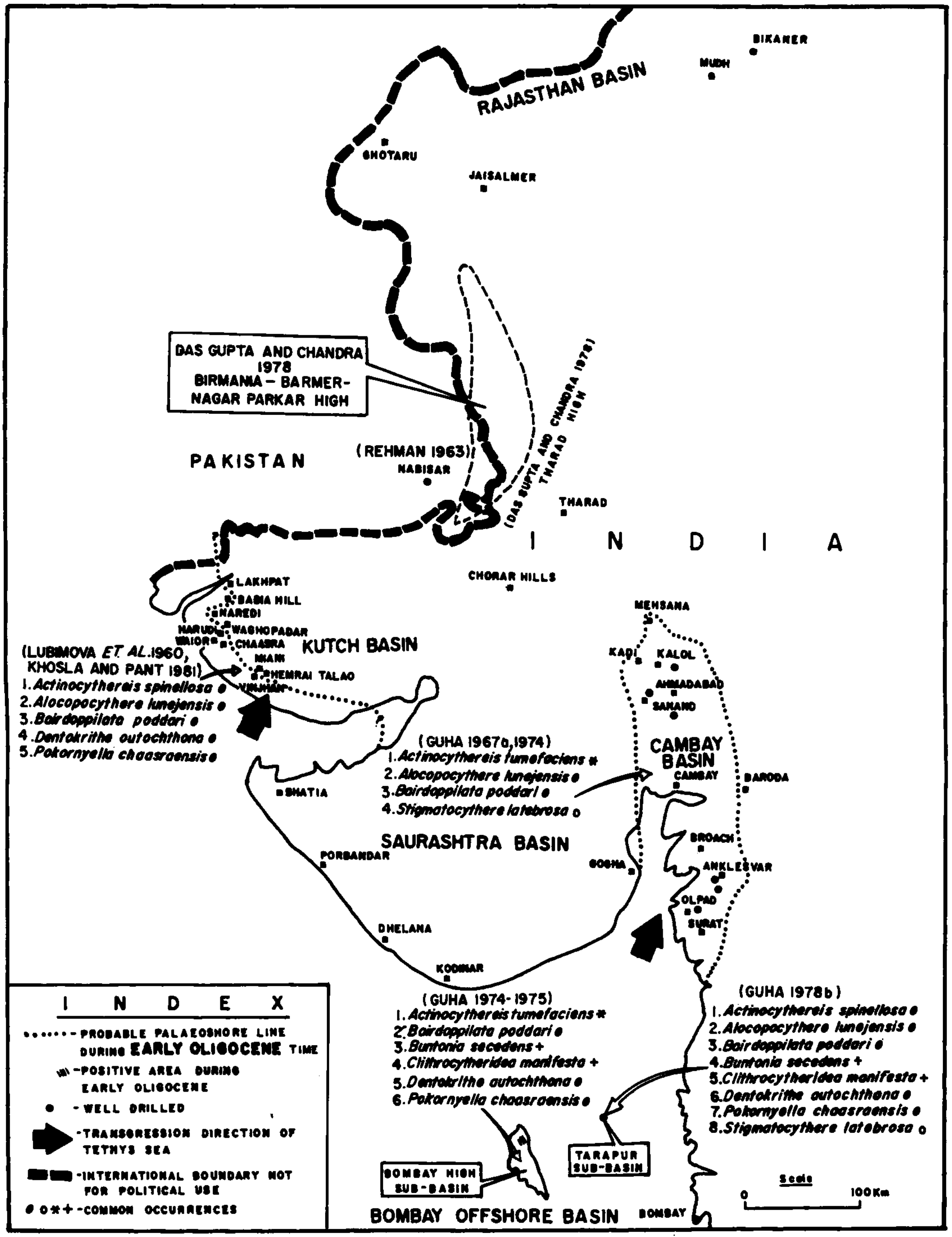
TEXT-FIG. 1—Showing the distribution of important species of ostracods in the northwestern basins of India and palaeoshore line during Early Eocene time.



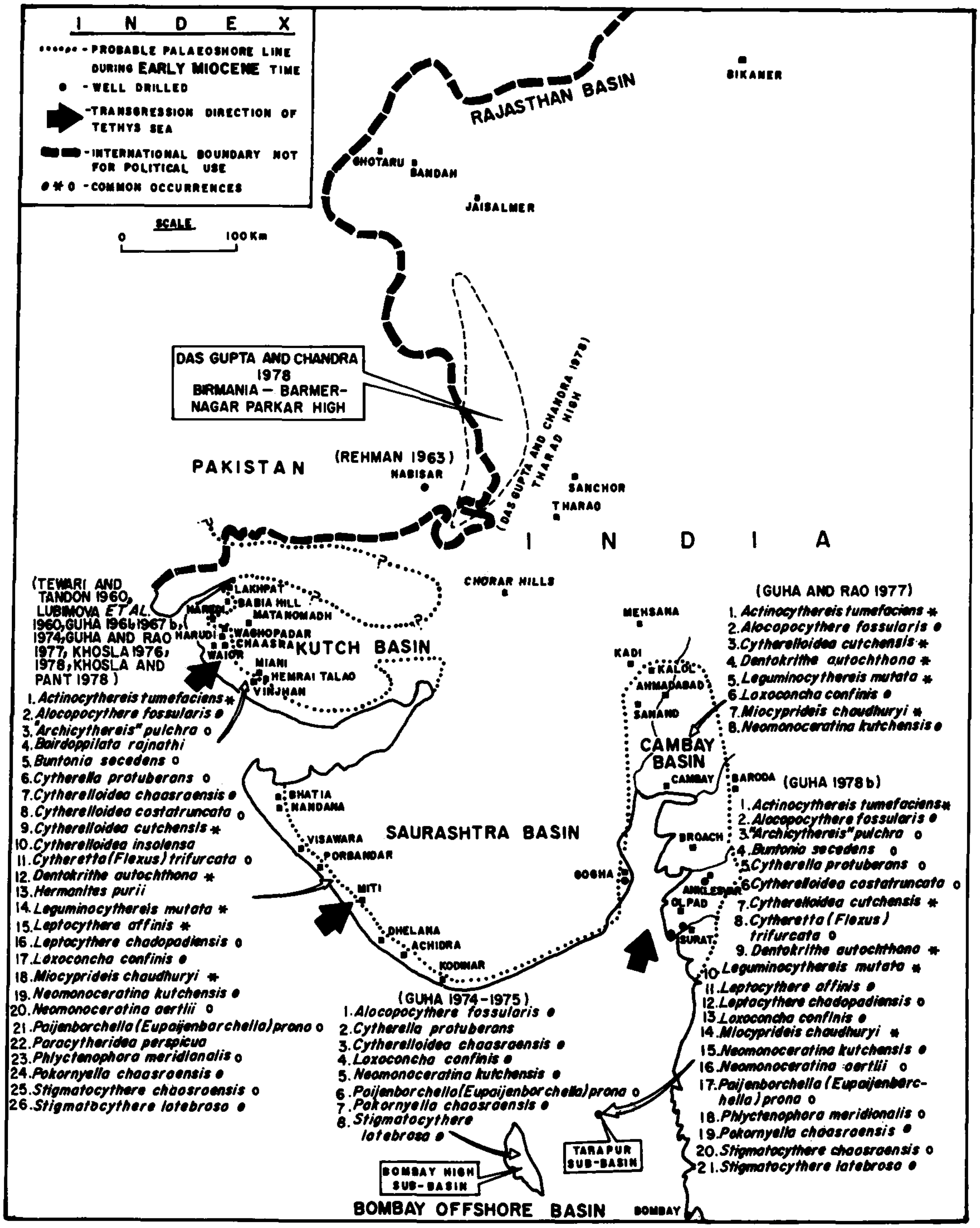
TEXT-FIG. 2—Showing the distribution of important species of ostracods in the northwestern basins of India and palaeoshore line during Middle Eocene time.



TEXT-FIG. 5—Showing the distribution of important species of ostracods in the northwestern basins of India and palaeoshore line during Early Miocene time.



TEXT-FIG. 4—Showing the distribution of important species of Ostracoda in the northwestern basins of India and palaeoshore line during Early Oligocene time.



TEXT-FIG. 3—Showing the distribution of important species of ostracods in the northwestern basins of India and palaeoshore line during Late Eocene time.
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CHECK LIST OF OSTRACOD SPECIES MENTIONED IN TEXT-FIGURES 1–5

1. ACANTHOCYTHEREIS BHUJENSIS (Tewari and Tandon, 1960)
   Trachyleberis? *bhujensis* TEWARI and TANDON, 1960, p. 155, Text-figs. 6, 3a–b.
   Acanthocythereis bhujensis (Tewari and Tandon). PANT AND KHOSLA, 1982, p. 512.
2. ACTINOCYTHEREIS SPINELLOSA (Lubimova and Guha, 1960)
   Cythereis spinellosa Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 31–32, Pl. II, fig. 10.
   Trachyleberis spinellosa (Lubimova and Guha). GUHA *et al.*, 1965, p. 13, Pl. III, fig. 15: GUHA, 1974, p. 163–165.
   Actinocythereis spinellosa (Lubimova and Guha). KHOSLA AND PANT 1981, p. 161–162, Pl. 1, fig. 7.
3. ACTINOCYTHEREIS TUMEFACIENS (Lubimova and Guha, 1960)
   Trachyleberis tumefacentis Lubimova and Guha in LUBIMOVA, GUHA AND MOHAN, 1960, p. 36–37, Pl. III, fig. 4.
   Actinocythereis tumefacentis (Lubimova and Guha). GUHA, 1961, p. 4, figs. 7, 11, 16.
   Actinocythereis tumefaciens (Lubimova and Guha). KHOSIA, 1978, p. 266, Pl. 4, fig. 1.
4. ALOCOPOCYTHERE FOSSULARIS (Lubimova and Guha, 1960)
   Trachyleberis fossularis Lubimeva and Guha, in Lubimova, Guha and Mohan, 1960, p. 40–41, Pl. III, fig. 7.
   Echinocythereis fossularis (Lubimova and Guha). GUHA, 1961. p. 4, figs. 5, 9; GUHA *et al.*, 1965, p. 13, Pl. III, fig. 12.
   Quadracythere fossularis (Lubimova and Guha). GUHA, 1968b, p. 215–216, Pl. II, fig. 20.
   Alocopocythere fossularis (Lubimova and Guha). KHOSLA, 1978, p. 226–227, Pl. 4, fig. 2.
5. ALOCOPOCYTHERE LUNEJENSIS (Guha, 1967)
   Leguminocythereis lunejensis Guha, 1967, p. 21, Pl. I, figs. 3, 6, 8.
   Alocopocythere lunejensis (Guha). KHOSLA AND PANT, 1981, p. 175.
6. ANTICYTHEREIS MEMORANS (Lubimova and Guha, 1960)
   Trachyleberis memorans Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 38–39, Pl. III, fig. 5.
   Anticythereis memorans (Lubimova and Guha). KHOSLA, 1972, p. 487, Pl. 2, fig. 5, Pl. 4, fig. 4.
7. ANTICYTHEREIS MEMORANS MUDHENSIS Khosla, 1972
   Anticythereis memorans mudhensis KHOSLA, 1972, p. 487, Pl. 2, figs. 5, 6, Pl. 4, fig. 5, Pl. 5, fig. 4.
8. "ARCHICYTHEREIS PULCHRA" (Lubimova and Guha, 1960)
   Cythereis pulcheris Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 35–36, Pl. II, figs. 3a, b.
   "*Archicythereis*" *pulchra* (Lubimova and Guha). KHOSLA, 1978, p. 267, Pl. 4, fig. 6, Pl. 6, fig. 13.
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   Bairdia beraguaensis Singh and Tewari, in TEWARI AND SINGH, 1966, p. 119–170, Pl. 1, figs. 4a–d.
10. BAIRDIA GLIBERTI (Keij, 1957)
    Bairdoppilata gliberti KEIJ, 1957, p. 53–54, Pl. 1, figs. 18–21.
    Bairdia gliberti (Keji), KHOSLA, 1972, p. 483, Pl. 1, fig. 9.
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    Bairdia? *kirtharensis* TEWARI and TANDON, 1960, p. 149–150, Text-fig. 1, figs. 4a, b.
    Bairdoppilata kirtharensis (Tewari and Tandon). PANT AND KHOSLA, 1982, p. 512.
12. BAIRDOPPILATA PODDARI Lubimova and Mohan, 1960
    Bairdoppilata poddari Lubimova and Mohan, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 21–22, Pl. II, figs. 1a, b; GUHA, 1967, p. 17–18, Pl. 1, fig. 1.
    Bairdia poddari (Lubimova and Mohan). KHOSIA, 1972, p. 484, Pl. I, fig. 12; Guha, 1974, p. 160.
13. BAIRDOPPILATA RAJNATHI Tewari and Tandon, 1960
    Bairdoppilata rajnathi TEWARI AND TANDON, 1960, p. 150, Text-fig. 1, figs. 5a, b.
14. BRADLEYA ARCANUS (Lubimova and Guha, 1960)
    Cythereis arcanus Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 33, Pl. III, figs. 1a, b.
    Quadracythere arcanus (Lubimova and Guha). GUHA, 1968, p. 91, Pl. I, fig. 24.
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    Cytheretta secedens Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 44, 45, Pl. 4, figs. 2a, b.
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    Bythocypris mianica TEWARI AND TANDON, 1960, p. 150, 151, text-fig. 2, figs. 1a, b.
17. CLITHROCYTHERIDEA MANIFESTA Lubimova and Guha, 1960
    Clythrocytheridea manifesta Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 29, 30, Pl. II, figs. 8a, b.
    Clithrocytheridea manifesta Lubimova and Guha. GUHA, 1974, 1975, p. 13, 14.
18. COSTA AFF. COSTA CAMBAYENSIS Guha, 1967
    Costa cambayensis GUHA, 1971, p. 20, Pl. I, figs. 2, 4, 9, 12, 16.
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    Cytherella protuberantis Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 17, 18, Pl. I, fig. 3.
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    Cytherelloidea cambayensis GUHA, 1965, p. 145, 146, Pl. XI, figs. 6, 8, text-fig. 2.
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    Cytherelloidea chaasraensis GUHA, 1961, p. 2, Text-fig. 1.
22. CYTHERELLOIDEA COSTATRUNCATA Lubimova and Guha, 1960
    Cytherelloidea costatruncata Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 20, 21, Pl. I, fig. 7.
23. CYTHERELLOIDEA CUTCHENSIS Lubimova and Guha, 1960
    Cytherelloidea cutchensis Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 18, 19, Pl. I, figs. 5a, b.
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    Cytherelloidea insolensa Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 19, 20, Pl. I, figs. 6a, b.
25. CYTHERETTA (FLEXUS) TRIFURCATA Lubimova and Guha, 1960
    Cytheretta trifurcata Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 45, 46, Pl. IV, fig. 3.
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26. CYTHEROPTERON RAMESHI (Singh and Misra, 1968)
    Cytherura rameshi SINGH AND MISRA, 1968, p. 31, 32, Pl. 5, figs. 4–6.
    Semicytherura rameshi (Singh and Misra). KHOSLA, 1972, p. 495. Pl. 3, fig. 11.
    Cytheropteron rameshi (Singh and Misra). PANT AND KHOSLA, 1982, p. 512.
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    Cytheromorpha kirtharensis GUHA, 1968, p. 84, 85, 87, Pl. I, figs. 5, 7, 19.
28. DENTOKRITHE AUTOCHTHONA (Lubimova and Guha, 1960)
    Krithe autochthona Lubimova and Guha, in LUBIMOVA GUHA AND MOHAN, 1960, p. 25, 26, Pl. II, fig. 4.
    Dentokrithe autochthona (Lubimova and Guha). KHOSLA AND PANT, 1981, p. 174, 175.
29. DENTOKRITHE INDICA (Tewari and Tandon, 1960)
    Krithe indica TEWARI AND TANDON, 1960, p. 152, 153, Text-fig. 2, figs. 5a, b.
30. ECHINOCYTHEREIS (SCELIDOCYTHEREIS) SAHNII (Tewari and Tandon)
    Hemicythere sahnii TEWARI AND TANDON, 1960, p. 157, Text-fig. 4, figs. 1a–d.
    Echinocythereis (Scelidocythereis) sahnii (Tewari and Tandon). KHOSLA AND PANT, 1981, p. 173, 176, 178.
31. GYROCYTHERE INDICA (Tewari and Tandon, 1960)
    Hermania indica TEWARI AND TANDON, 1960, p. 158, Text-fig. 4, figs. 3a–c.
    Gyrocythere indica (Tewari and Tandon). PANT AND KHOSLA, 1982, p. 512.
32. HERMANITES PURII Tewari and Tandon, 1960
    Hermania purii TEWARI AND TANDON, 1960, p. 158, 159, Text-fig. 5, figs. 1a, b.
33. LEGUMINOCYTHEREIS MUTATA (Lubimova and Guha, 1960)
    Trachyleberis mutata Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 41, 42, Pl. III, figs. 8, 9.
    Leguminocythereis mutata (Lubimova and Guha). GUHA, 1961, p. 2, 3, fig. 17.

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   Leptocythere chadopadiensis Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 27, 28, Pl. II, figs. 6a, b.
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   Cytheroteron confinis Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 52–54, Pl. IV, fig. 10.
   Loxoconcha confinis (Lubimova and Guha). GUHA, 1974, p. 171.
36. MIOCYPRIDEIS CHAUDHURYI (Lubimova and Guha, 1960)
   Cyprideis chaudhuryi Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 30, 31, Pl. II, fig. 9.
   Miocyprideis chaudhuryi (Lubimova and Guha). GUHA, 1961, p. 2, Text-figs. 3, 19.
37. NEOCYPRIDEIS BHUPENDRI (Singh and Misra, 1968)
   Shulredia bhupendri SINGH AND MISRA, 1968, p. 32, Pl. 8, figs. 7–9.
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   Neomonoveragina kutchensis GUHA, 1961, p. 3, figs. 12, 14, 18.
39. NEOMONOCERATINA OERTLII Guha, 1967
   Neomonoceratina oertlii GUHA, 1967, p. 35, 36, Text-fig. 1.
40. OCCULTOCYTHEREIS SUBSPINELLOSA Khosla, 1972
   Occultocythereis subspinellosa KHOSLA, 1972, p. 491, Pl. 2, figs. 21, 22, Pl. 4, fig. 11, Pl. 5, fig. 8.
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   Ovocythereidea cambayensis GUHA, 1974, p. 167, 168, Pl. I, figs. 7, 13, Pl. II, figs. 1, 16, 22.
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   Paijenborchella tewarii GUHA, 1971, p. 18, 19, Pl. I, figs. 1, 5, 15, 17.
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   Paijenborchella (*Eupaijenborchella*) *prona* Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 43, 44, Pl. IV, figs. 1a, b.
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   Paijenborchella (*Eupaijenborchella*) *indica* KHOSLA, 1972, p. 494, Pl. 3, figs. 14, 15, Pl. 5, fig. 11.
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   Paracypris jhingrani Singh and Tewari, in TEWARI AND SINGH, 1966, p. 112, Pl. 2, figs. 5a, b; GUHA, 1974, p. 161, 162, Pl. II, fig. 14.
46. PARACYPRIS LAKIENSIS Guha, 1974
   Paracypris lakiensis GUHA, 1974, p. 161, Pl. I, figs. 1, 2, 6.
47. PARACYTHEREIDEA EOCENICA Khosla, 1972
   Paracythereidea eocenica KHOASLA, 1972, p. 493, Pl. 3, figs. 9, 10, Pl. 4, fig. 17, Pl. 5, fig. 10.
48. PARACYTHEREIDEA PERSPICUA Lubimova and Guha, 1960
   Paracythereidea perspicua Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 50, 51, Pl. 4, figs. 8a, b.
49. PHLYCTENOPHORA MERIDIONALIS (Lubimova and Mohan, 1960)
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50. POKORNYELLA CHAASRAENSIS (Lubimova and Guha, 1960)
   Trachylebereis chaasraensis Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 39, 40, Pl. III, figs. 6a, b.
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   Cythereis avadhesi SINGH AND MISRA, 1968, p. 35, Pl. 10, figs. 6–8.
52. QUADRACYTHERE AVADHESHI MUDHENSIS Khosla, 1972
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53. SCHIZOCYTHERE APPENDICULATA Tribel, 1950
   Schizocythere appendiculata TRIEBEL, 1950, p. 324, Pl. 3, figs. 23–27; KHOSLA, 1972, p. 486, 487, Pl. 2, fig. 1.

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Schizocythere? *levinsoni* RAJAGOPALAN, 1962, p. 67, Pl. IV, figs. 16–19.
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Occultocythereis chaasraensis GUHA, 1961, p. 4, 5, figs. 8, 10, 13.
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58. STIGMATOCYTHERE LATEBROSA (Lubimova and Guha, 1960)
Cythereis latebrosa Lubimova and Guha, in LUBIMOVA, GUHA AND MOHAN, 1960, p. 24–35, Pl. III, fig. 2.
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Uroleberis kutchensis GUHA, 1968, p. 88, Pl. I, figs. 1, 2, 4, 8.
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DISCUSSION

Neale: Dr. Singh's paper showed that *Schizocythere* disappeared from the area after the late Eocene regression. On the other hand, *Alocopocythere* (also a useful stratigraphical index) appeared to continue unaffected. Could Dr. Singh make any suggestion for what appears to be a very different response to this regression?

Singh: In my paper, I have mentioned only those species which are common in the northwestern basins of India. I cannot say with confidence that the genus *Schizocythere* disappeared from the area after the Late Eocene regression. Only future detailed work can throw some light on the disappearance of the genus *Schizocythere*. The genus *Alocopocythere* has been reported from the Early Eocene to Early Miocene strata of India. Therefore, it may perhaps be concluded that the genus *Alocopocythere* was more resistent to the fluctuations of the palaeoenvironments of the Tertiary period in India.

One Hundred Million Years of Predation on Ostracods: The Fossil Record in Texas

ROSALIE F. MADDOCKS
University of Houston, Texas, U.S.A.

ABSTRACT

Cretaceous, Paleogene, and Holocene ostracod assemblages of Texas were systematically surveyed for evidences of predation. Twenty kinds of predation scars include drillholes of naticid and other gastropods, digestive-solution holes, and holes made by unknown animals. Ostracods may provide an important food source for juvenile naticids. Abundance, large size, and smooth carapace favour predation. The earliest naticid drillholes occur in the Cenomanian, although other gastropod holes occur earlier (Albian). Dramatic increases in naticid predation occurred in the Late Campanian and at the Cretaceous-Tertiary boundary, producing high adult mortality rates during the early Cenozoic. Holocene assemblages show somewhat lower predation rates, for which taphonomic, environmental, or evolutionary factors may be responsible. These recorded fluctuations in predation intensity have potential paleoecological, biostratigraphical, and evolutionary applications. Naticid and other gastropod drillholes are most abundant in shallow marine environments, while abundance of solution features characterises upper and midbay facies in coastal estuaries and lagoons. Some evolutionary trends in Cenozoic ostracods may have resulted from increased predation.

INTRODUCTION

Drillholes made by carnivorous gastropods are familiar features on modern and fossil ostracod shells. Snails of the families Naticidae and Muricidae produce a circular, bevelled hole that is readily identifiable. These holes allow us to study predation on Ostracoda in communities of the geologic past.

This report surveys the frequencies of gastropod drillholes in ostracod assemblages from the Lower Cretaceous (Albian) to the Holocene in Texas. Because Kornicker and Sohn (1971) warned that solution holes in carapaces eaten by fish may be mistaken for gastropod drillholes, specimens showing 'possible solution features or other marks of predation were also sought out. The data compiled below may help us to understand the factors that control predation on ostracod species. The intensity of this predation has varied through time, and its stratigraphical record may have paleoecological or biostratigraphical applications.

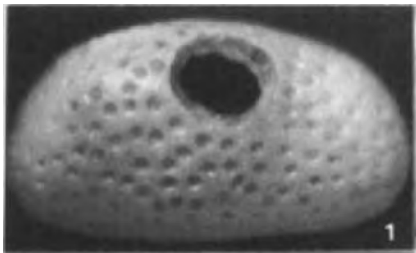
The boring mechanisms and behaviour of modern gastropods and the morphological characterisics of the resulting holes have been reviewed by Carriker (1961), Carriker and Yochelson (1968), and Taylor *et al.* (1980) (see also references cited in those papers). The drilling habit is variously thought to have evolved first in the Late Triassic (Fürsich and Jablonski, 1984), Albian (Taylor *et al.*, 1980), or Cenomanian (Fisher, 1964; Sohl, 1969), although the Naticidae and Muricidae themselves date from the Early Jurassic and Albian, respectively. Several palaeobiologists have analysed drillhole frequencies in Cenozoic mollusc assemblages, attempting to reconstruct the modes and rate of co-evolution of this predator-prey system (Kitchell, 1982). None of these investigations has included Ostracoda.

Reyment (1963, 1966, 1967) reported that modern drilling gastropods on the Niger Delta prefer molluscs (pelecypods, gastropods, scaphopods), but that where molluscs are less abundant, the juvenile gastropods readily attack either adult or juvenile ostracods. He suggested that large species with smooth carapaces, pelecypod-like shape, and infaunal habit may be more vulnerable to attack. Paleocene ostracod assemblages of Nigeria, he also reported, have abundant drillholes, perhaps because pelecypods are not common in these rocks.

The material for this study was provided by faunal assemblages already in the micropalaeontology collections of the University of Houston. Stratigraphical units not included are non-marine in outcrop or have few ostracods. Many of these assemblages were originally collected during preparation of the excursion guidebook for the Eighth International Symposium on Ostracoda (Maddocks, 1982), in which full stratigraphical documentation and species lists were given for these localities (Maddocks and Ross, 1982). The faunal assemblages corresponding to the publications by Garbett and Maddocks (1979), Moysey and Maddocks (1982), Ross and Maddocks (1983), Chimene and Maddocks (1984), and Maddocks (1985) were also included, as well as other unpublished recent and fossil samples. The contributions of many former students, especially Alta Cate, J. B. Chimene II, Peggy Cole, Elizabeth Garbett, Jo Ann Locklin, David G. Moysey, and James E. Ross are gratefully acknowledged, as well as the verifications of certain species identifications by Joseph E. Hazel, Alvin Phillips, and W. A. van den Bold. In total, the material encompasses over 400 slides, 80,000 specimens, and 425 species, covering more than 100 million years of history.

The counts of **specimens** include both adults and juveniles, single valves and whole carapaces, and identifiable fragments that are large enough that at least part of any naticid hole would have been retained. The counts of **individuals** signify the minimum number of adult animals represented, calculated as the number of adult whole carapaces plus the number of adult right valves or left valves, whichever was greater (ignoring juveniles, the less numerous valve, and most fragments). **Mortality** is calculated as percentage of total adult individuals bearing drillholes or other presumably fatal predation scars. (For assemblages in which left and right valves have been counted, this calculation is based on a conservative estimate of the number of individuals as half the number of specimens. Species of *Cytherella* were not counted separately, although most samples contain two to four species. Tables 1–12 summarize the stratigraphical distribution of evidence for predation,

PLATE 1—Fig. 1. Phenon N. *Peratocytheridea bradyi* (Stephenson, 1938), RV, Holocene, West Bay, UH2578, ×80. Fig. 2. Phenon R. *Cytherella* sp., RV anterior margin, Navarro Group, UH 4729, ×80. Fig. 3. Phenon Q. "*Cythereis* sp. C" of Moysey and Maddocks, 1982, RV anterior margin, Walnut Formation, UH1473, ×80. Fig. 4. Phenon D. *Trachyleberis elmana* (Stadnichenko, 1927), LV, Cook Mountain Formation, UH5337, ×80. Fig. 5. Phenon L. *Asciocythere rotunda* (Vanderpool, 1928), RV, Glen Rose, UH5035, ×125. Fig. 6. Phenon D. *Actinocythereis davidwhitei* (Stadnichenko, 1927), LV anterior margin, Cook Mountain Formation, UH 5333, ×90. Fig. 7. Phenon A. *Pterygocythereis* sp., LV, Holocene, Gulf of Mexico, UH4125, ×45. Fig. 8. Phenon K. *Clithrocytheridea subpyriformis* (Sutton and Williams, 1939), RV, Cook Mountain Formation, UH5337, ×70. Fig. 9. Phenon O. *Brachycythere rhomboidalis* (Berry, 1925), LV dorsal margin, Navarro, UH5034, ×70. Fig. 10. Phenon M. "*Cythere ornata*" of Vanderpool, 1928, LV, Glen Rose, UH5072, ×80. Fig. 11. Phenon N. *Cythereis paupera* Jones and Hinde, 1889, LV, Del Rio, UH4901, ×80. Fig. 12. Phenon G. *Henryhowella orelliana* (Sutton and Williams, 1939), RV, Cook Mountain Formation, UH4313, ×80. Fig. 13. Phenon U. *Brachycythere crenulata* Crane, 1965, LV, Dessau Formation, UH5327, ×80. Fig. 14. Phenon S. *Haplocytheridea globosa* (Alexander, 1929), RV, Navarro Group, UH5359, ×80. Fig. 15. Phenon S. *Brachycythere ovata* (Berry, 1925), LV, Navarro, UH4732, ×60.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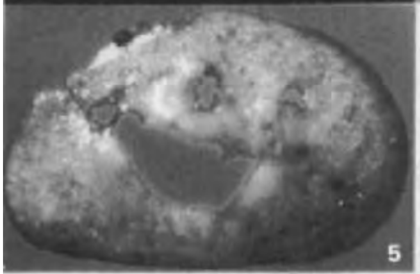
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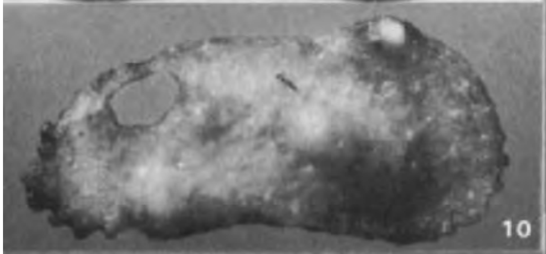
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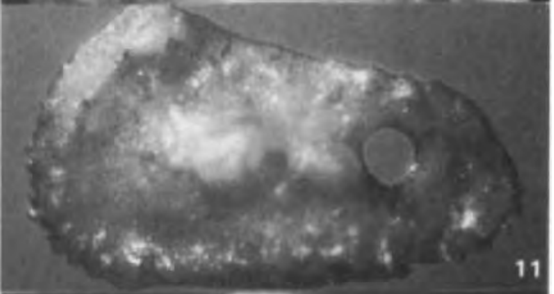
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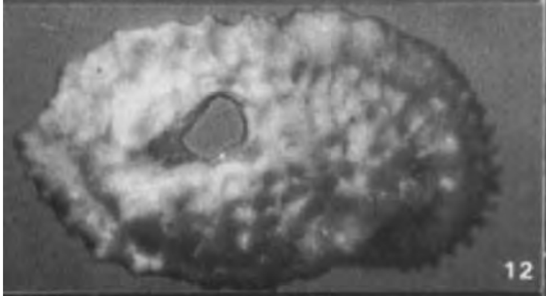
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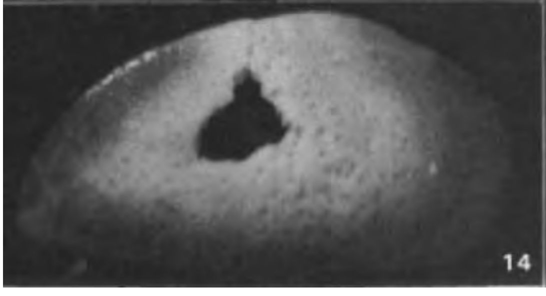
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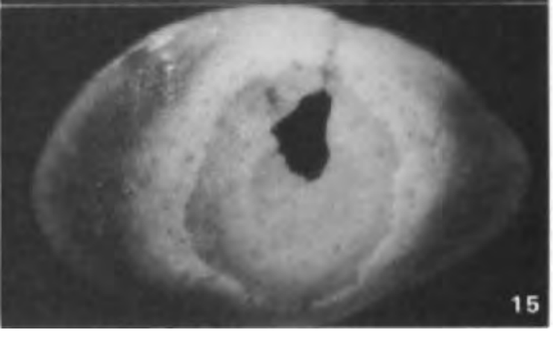
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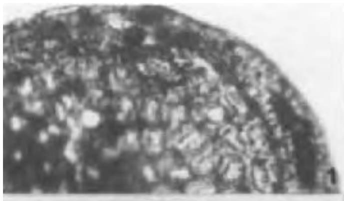
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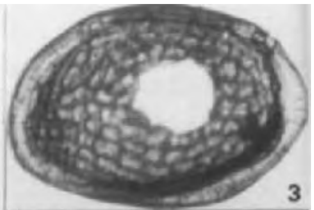
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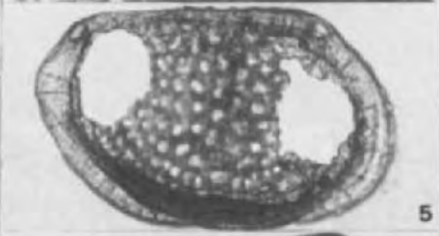
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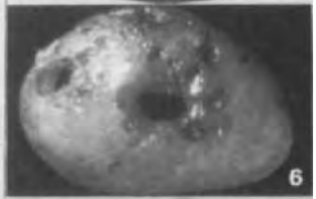
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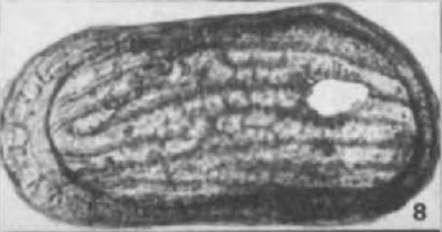
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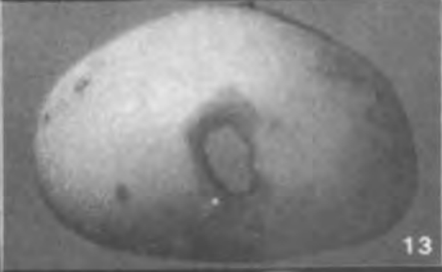
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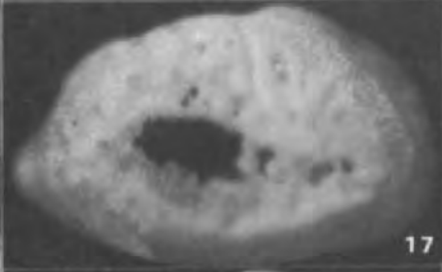
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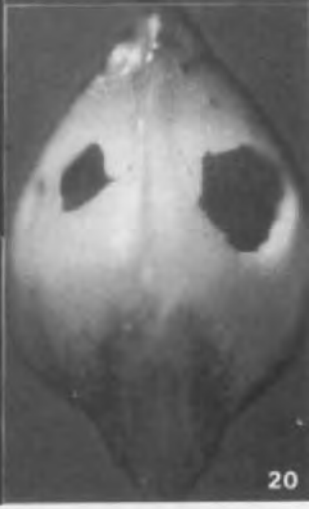
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together with the total numbers of localities, assemblages, specimens, individuals, and species examined and names of species.

PREDATION ICHNOPHENA

Carriker and Yochelson (1968) reviewed the distinct drilling methods used by modern naticids and muricids, illustrating the diagnostic morphological criteria by which the resulting holes may be identified. Many authors have stated that the two kinds of holes are easy to distinguish, and some molluscan studies have tallied them separately with considerable success. However, in small, thin-shelled, ridged, or reticulate mollusc shells, naticid and muricid drillholes are less distinct, and the prescribed taxonomic criteria for distinguishing them do not apply easily to Ostracoda.

On the other hand, within any given stratigraphical interval it proved relatively easy to recognize arbitrary ichnophena (Greek, *ichnos*=track or trace, plus *phainein*=to show; for groups of morphologically similar trace fossils), according to such parameters as size, shape, taper, and roughness of edges. Twenty ichnophena were arbitrarily defined (designated A-U), some of which may represent transitional or aberrant examples of others. Recognition of some of these ichnophena is subjective, because their appearance varies with size, thickness, and ornament of the ostracod shell. For the most part in this data set, these phena are consistently recognized and distinguished from each other within any one stratigraphical interval but less so vertically. Representative examples are illustrated in Plates 1 and 2.

A: Very small, acute-conical to cylindrical holes with circular to oval circumference, wall planar and smooth.

B: Small, approximately parabolic holes with near-circular to oval to irregularly oblong circumference, edges slightly irregular or jagged; wall gently to steeply sloping, uneven to nearly smooth, not planar.

C: Small to medium-sized holes with steep sides and smoothly curved edges, outline rounded-triangular to ovate to subquadrate.

D: Small to medium-sized cylindrical holes with circular to ovoid outlines and vertical to steeply sloping, smooth walls; may have flat to parabolic inner floors with tiny circular inner hole.

E: Small to medium-sized to large, oblong holes with sharp, more or less jagged edges and variable shape; not accompanied by cracks, enlarged normal pore-canals, abrasion, or frosting.

F: Irregular holes of all kinds, often accompanied by cracks, that could have resulted from ordinary

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PLATE 2—Fig. 1. Phenon P. *Malzella* sp., RV anterodorsal margin, Holocene, Gulf of Mexico, UH4125, ×60. Fig. 2. Phenon C. *Phacorhabdotus formosus* (Alexander, 1934), LV dorsal margin, Midway, UH4885, ×120. Fig. 3. Phenon E. *Loxoconcha* aff. *L. moralesi* Kontrovitz, 1978, LV, Holocene, Gulf of Mexico, UH4120, ×80. Fig. 4. Phenon D. *Krithe* sp., RV, Holocene, Gulf of Mexico, UH4125, ×75. Fig. 5. Phenon J. *Loxoconcha claibornensis* Murray, 1938, RV, Cook Mountain Formation, UH5333, ×120. Fig. 6. Phena A and I. *Haplocytheridea nanifaba* Crane, 1965, LV, Burditt Formation, UH4829, ×80. Fig. 7. Phenon A. *Cytherelloidea crafti* (Sexton, 1951), RV, Bergstrom Formation, UH4868, ×100. Fig. 8. Phenon E. *Megacythere repexa* Garbett and Maddocks, 1979, LV, Holocene, West Bay, UH2622, ×140. Fig. 9. Phenon L. *Asciocythere rotunda* (Vanderpool, 1928), RV, Glen Rose, UH5036, ×70. Fig. 10. Phenon B. *Cytherella* sp., LV, Navarro Group, UH4639, ×80. Fig. 11. Phenon L. *Buntonia alabamensis* (Howe and Pyeatt, 1934), LV, Stone City Formation, UH1931, ×80. Fig. 12. Phenon B. *Cytherella* sp., LV, Midway, UH4049, ×80. Fig. 13. Phenon I. *Asciocythere goodlandensis* (Alexander, 1929), LV, Walnut Formation, UH1437, ×125. Fig. 14. Phenon S. *Brachycythere plena* Alexander, 1934, dorsal view of whole carapace, Midway Group, UH4051, ×60. Fig. 15. Phenon R. *Cytheropteron fossatum* Skinner, 1956, LV, Bergstrom Formation, UH4802, ×80. Fig. 16. Phenon T. *Cytherelloidea* sp., LV, Del Rio Formation, UH4854, ×90. Fig. 17. Phenon H. *Perissocytheridea brachyforma* Swain, 1955, RV, Holocene, West Bay, UH2856, ×140. Fig. 18. Phenon S. *Antibythocypris macropora* (Alexander, 1929), LV, Navarro, UH4788, ×80. Fig. 19. Phenon S. *Haplocytheridea* aff. *H. everetti* (Berry, 1925), RV, Navarro Group, UH5357, ×80. Fig. 20. Phenon S. *Brachycythere ledaforma* (Israelsky, 1929), dorsal view of whole carapace, Navarro Group, UH4786, ×80.

post-mortem breakage rather than predation or solution; not further discussed in this report.

G: Medium-sized, irregular holes with oblong, polygonal, or irregular outlines and uneven wall; edges fairly smooth; surrounding area may be unevenly abraded or sloping.

H: Small to medium-sized holes of variable outline with smoothly curving to slightly irregular to more or less jagged, sharp edges; neighbouring region scraped, frosted, abraded, crumbling, or flaking, usually white.

I: Small to medium-sized holes with very irregular to jagged edges; outer edge chipped, gouged, or unevenly excavated and abraded; walls sloping gently to steeply, uneven.

J: Medium-sized to large, oblong holes in thin, transparent shells; edges sharp, smoothly curved to slightly jagged.

K: Small holes with polygonal outlines, keyhole-shaped, trefoil-shaped, L-shaped, rhombic, or quadrate; walls vertical to steeply sloping.

L: Lacy clusters of small to medium-sized to large solution(?) holes with irregular outlines and jagged edges, walls vertical to unevenly sloping; outer edge may be more or less abraded or gouged or dissolved; some may be located at normal pore-canals.

M: Medium-sized to large, oval to oblong holes with smoothly curving to slightly irregular edges, walls vertical to steeply sloping, smooth but not planar.

N: Large, parabolic holes with round to oval circumference; walls countersunk and smoothly beveled, planar; obviously naticid.

O: Small to medium-sized, rounded-triangular to ovoid holes with vertical walls and smooth edges.

P: Small holes, the shape of and occupying just one fossa of the reticulate ornament.

Q: Very tiny holes with rounded to irregular to scalloped margins, vertical but uneven walls, outer margin not chipped or abraded.

R: Small to medium-sized, L-shaped to triangular to rhombic or rectangular holes with slightly irregular to jagged edges; outer edge not chipped, gouged, or abraded; walls vertical; some may appear to be two or more holes joined.

S: Large, saddle-shaped, solution holes. Early stages have a large, circular to oblong hole symmetrically located dorsolaterally on each valve of the carapace. In later stages a crack connects the two holes across the dorsum, which then is enlarged by further solution to form a broad channel. The adjacent lateral surface is opaque, frosted, roughened, flaking, or crumbling. Many examples consist of disarticulated or still-articulated U-shaped valves retaining only the free margin plus a narrow band of adjacent shell. Assemblages in which such specimens are common usually also have abundant tiny shards showing the final fragmentation of these weakened shells.

T: Small, rounded-triangular to angulate-triangular to crescentic holes with smooth edges, usually two convex edges and one concave edge; outer edge not frosted, abraded, chipped, or gouged.

U: Elongate to equidimensional grooves, gouges, and shallow pits, usually not penetrating shell; edges and walls very irregular; mostly affecting just one side of carapace.

X: Triangular to polygonal, straight-edged holes in smooth, thin shells; molds of pyrite crystals in partly pyritized shells; not caused by predation, not discussed further in this report.

The tunnels of boring algae and fungi were also recognized but not considered further, because these are parasitic or post-mortem rather than predatory in nature.

INTERPRETATION OF ICHNOPHENA

The 20 ichnophena recognized may be grouped into 4 intergradational categories according to their inferred origins:

Naticid drillholes: Phenon N. They are best expressed in smooth, robust shells, and early examples are less perfectly drilled than younger ones.

Gastropod drillholes: Phena A–D, M, O. Some may be naticid holes in thin or ornamented shells; others may have been drilled by muricids, other gastropods, or perhaps by octopus or turbellarians.

Holes made by unknown, less patient predators: Phena E, G, I–K, P–R, T, U. They appear to have been ripped, gouged, punctured, or dug out rater than drilled.

Solution holes: Phena H, L, S. Some closely resemble the digestive-solution holes illustrated by Kornicker and Sohn (1971), while others show enlarged normal pore-canals and characteristic frosting. Because overall preservation in these assemblages is good to excellent, only a few specimens of a few species in each assemblage show these holes, and the position of the holes corresponds to the location of soft parts, they are here attributed to digestion rather than to sedimentary or diagenetic alteration. Solution features also occasionally accompany other phena.

STRATIGRAPHIC OCCURRENCE OF ICHNOPHENA

Glen Rose Formation (Lower Albian)

Three phena of predation scars were seen (Table 1). Preservation in these assemblages ranges from poor to fair, and some shells are recrystallized and bear calcite overgrowths. Because only a few specimens of a few species in each assemblage show solution holes (I), the latter are tentatively interpreted as predation rather than diagenetic alteration. One good gastropod drillhole (M) was seen. Estimated mortality due to predation was very low, about one percent.

Walnut Formation (Middle Albian)

Specimens of 12 species bear predation scars belonging to 3 phena (Table 2). Many, but not all, of the remaining species are quite rare. Phenon I occurs in 5 of the 6 facies and in all 3 members, while M and Q occur only in Facies III and IV of the Bee Cave Member, which also have the richest ostracod and larger invertebrate faunas. Estimated mortality due to predation was low, about 3 percent.

Del Rio Formation (Cenomanian)

Five phena were recognized, including a good naticid drillhole (N) (Table 3). Estimated mortality due to predation was very low, about one percent.

Austin and Lower Taylor Groups (Lower Campanian)

These date are for cytheraceans only. Table 4 shows the occurrence of the nine phena recognized. Likelihood of predation (or of preservation of evidence for predation) appears to have been controlled by abundance, size, and smoothness of carapace, in declining order of importance. Naticid drillholes (N) become increasingly common and of better morphologic quality up the section. Only four phena are present in all three formations. There is no significant change in predation intensity either just above or just below the minor unconformities that mark the formation boundaries. Estimated mortality due to predation was low, about 2 percent.

Middle and Upper Taylor Group (Middle and Upper Campanian)

Specimens of *Cytherella* dominate these faunas but are under-represented on the picked slides. Although the 13 species bearing 9 ichnophena account for only 53 percent of the fauna (exclusive of *Cytherella*), most of the remaining species are quite small and thin-shelled, suggesting that predation is less intense or less easily detected on such species (Table 5). Predation intensity was very low during deposition of the Pecan Gap Formation and increased only slightly for most of the Bergstrom (estimated mortality about one percent). At the highest locality (Cottonwood Creek near Kimbro), stratigraphically just below the unconformable Taylor-Navarro contact, it increased dramatically (estimated mortality about 6 percent). While many Taylor species do not continue into the Navarro, there is insufficient information about the Mollusca to determine whether the increased predation on ostracods resulted from extinction of other prey taxa, evolution of new predator taxa, or unusual environmental conditions.

Navarro Group (Maastrichtian)

These localities include three classic Cretaceous-Tertiary boundary exposures (Maddocks, 1985). In three of them mortality due to predation was moderate (4–8 percent). At the Littig Quarry, however, the faunas are very nearshore in aspect, dominated by species of *Haplocytheridea.* The exceptionally high predation rate there (16 percent adult mortality) may result either from greater abundance of predators in nearshore communities or from greater vulnerability to predation of Cytherideidae. There are no significant stratigraphical trends in predation intensity, except at the Cretaceous-Tertiary boundary itself. This supports the abrupt nature of the boundary inferred from other evidence.

Midway Group (Danian)

The assemblages examined (Table 7) come from three classic Cretaceous-Tertiary contact exposures plus additional, younger exposures. At the Brazos River in southern Falls County (now considered to be a continuous section), a 3 m transitional interval, bounded by very minor scoured or burrowed surfaces, separates undoubted Navarro (Maastrichtian) below from Midway (Danian) above. Within this transitional interval, the sparse ostracod assemblages are dominated by Cretaceous species near the base, by Paleocene species near the top, and have mixed species associations in the middle. Maddocks (1985) reported the first appearances of the diagnostic Paleocene species *Bairdoppilata suborbiculata* and *Brachycythere plena* at 20 and 70 cm above the base of this interval. Predation was quite intense in this interval (adult mortality 8 percent, mostly by naticid drilling). Because the assemblages are small and most specimens fragmentary, no reliable stratigraphical trends in predation intensity can be detected within this interval, except that the extreme abundance of fragments suggests that these data probably underestimate the true intensity of predation. Phena N and S dominate, as they do at the other contact exposures.

Higher in the Midway, other phena appear, although N and S continue to be most numerous. Adult mortality due to predation declines somewhat (to 7 percent) but remains well above Cretaceous levels. Minor differences in predation intensity at different localities may result from poorly known environmental differences.

The species distribution of these phena shows, once again, that abundance, size, and smooth exterior control predation intensity, or at least the preservation of evidence for predation. The intensification of naticid predation is especially conspicuous in species of *Cytherella, Bairdoppilata,* and *Brachycythere,* which have the most pelecypod-like shape. Recorded mortality rates for adult individuals of *Brachycythere plena* range as high as 49 percent (transitional interval) and 26 percent (Paleocene). We know this species survived this intense predation in the earliest days of its existence and went on to become a common and characteristic member of Paleocene faunas throughout the Gulf and Atlantic Coastal Plains. It should be pointed out that, because of the time-averaged and condensed nature of the rock and fossil record, predation can be recorded only for those species that successfully tolerate it and continue to reproduce themseves abundantly, generation after generation. A species that succumbs to increased predation would probably do so too rapidly to leave a decipherable record of its last days. It may be, for example, that this increased naticid predation caused the extinction of *Brachycythere ovata* and *Brachycythere rhomboidalis,* but there is no direct evidence for this, beyond the fact that both are very rare in the lower part of the transitional interval and absent higher. The origin of *Brachycythere plena* is also unknown. It does not occur in the Cretaceous, except where burrowed contacts make sampling likely to yield mixed faunas, and its first appearance marks the base of the Paleocene in this region. In size, smooth exterior, and weakly alate venter, *B. plena* is intermediate between *B. ovata* and *B. rhomboidalis.* Its amazing tolerance of predation may have been due to some characteristic not recorded on the skeleton, such as great fecundity.

Claiborne Group (Lutetian)

These Middle Eocene assemblages (Table 8) have high species diversity and 10 phena of predation scars. The 33 prey species account for 95 percent of the total fauna and include virtually all species that are either large or abundant. Naticid drillholes predominate, but other gastropod drillholes are also common, especially in the younger assemblages. Adult mortality due to predation reached as high as 16 percent and averaged 12 percent, slightly higher than in the Midway and much higher than at any time in the Cretaceous.

At the Stone City outcrop, molluscan fossils are almost unbelievably abundant. Here Nelson (1975, Table 4) reported that 11 percent of gastropod, 11 percent of pelecypod, and 10 percent of scaphopod shells bear naticid drillholes. According to Stanton and Nelson (1980, p. 125), three naticid species account for 16 percent of the total macrofossil assemblage (120 species). They also reported predatory muricids, cymatiids, octopus, fish, and arthropods in their trophic analysis of this community. The correspondance of adult mortality (11 percent) by gastropod predation for both ostracods and molluscs at Stone City is unexpected and perhaps not a coincidence. While it is not possible to compare the abundance data directly, it appears that juvenile gastropods preyed on adult ostracods to roughly the same degree (or with the same effect) as adult gastropods preyed on adult molluscs. It seems that ostracods provided a significant part of the diet of juvenile naticids at Stone City. The role of ostracods as alternate prey in this predator-prey system may be more important than commonly supposed.

Holocene, Gulf of Mexico

These 10 samples (Table 9) constitute a transect across the continental shelf south of Galveston. The individual assemblages have more species, better representation of very fragile or very small species, more numerous juveniles, and fewer fragments than would be expected in comparable fossil assemblages. Naticid drillholes are still the most abundant single phenon but do not dominate these assemblages as they do older ones, accounting for only 2 percent of adult mortality. Average mortality due to predation is about 7 percent, distinctly lower than in Early Cenozoic assemblages but higher than in the Cretaceous. Both overall mortality and mortality due to naticids decline into deeper water.

The lower incidence of naticid predation, by comparison with earlier assemblages, may result from the fact that thick-shelled species (on which such drillholes can be well preserved) are relatively less abundant. It is also likely that ongoing sedimentary transport, bioturbation, compaction, lithification, and diagenesis will modify these Holocene assemblages by selectively removing most specimens of the smaller and more fragile species. In this manner, naticid drillholes may become more abundant, relative both to other phena and to the total assemblage. Of course, it may also be that modern naticids more strongly prefer pelecypods over ostracods than did their ancestors. Kitchell *et al.* (1981) demonstrated that living *Polinices* selects its molluscan prey species in such a way as to maximize the cost-benefit function (searching and drilling energy expended to food-energy gained), and that Neogene evolutionary trends in molluscan prey species reflect directional selection to withstand this predation. We should ask whether the miniaturization of many lineages of Cytheracea and the relative decline of *Cytherella* (infaunal in habit) represent strategies by which late Cenozoic ostracods have adjusted to this predation.

Holocene, Coastal Lagoons

Assemblages from estuarine and lagoonal environments of Sabine Pass, Galveston Bay, West Bay, the San Bernard River, Tres Palacios Bay, and eastern Matagorda Bay were examined (Table 10). Solution features (H) predominate in upper and midbay biofacies. Naticid drillholes occur only in very robust species of the inlet and lower bay biofacies. The somewhat nondescript phenon E is also characteristic of the lower bay biofacies. Estimated adult mortality averages at least 8 percent. The preceding remarks about taphonomic processes also apply here. Solution features were also conspicous in the fossil assemblages from nearshore settings (Glen Rose Formation, the Cretaceous part of the Littig Quarry exposure). These solution features may prove to be useful indicators of coastal environments, and their origin deserves further investigation.

CONCLUSIONS

Twenty ichnophena of gastropod drillholes and other predation scars were recognized in Albian to Holocene assemblages of Texas. Younger assemblages have greater diversity of ichnophena. The oldest gastropod drillholes were found in the Albian, but the oldest definitely naticid holes were in the Cenomanian. Naticid drillholes increased in abundance and morphological quality during the Campanian. Abrupt increases in naticid predation on ostracods occurred near the end of the Campanian and at the Cretaceous-Tertiary boundary. High levels of naticid and other predation continued to characterize Paleocene and Middle Eocene assemblages. The somewhat lower levels for naticid predation in Holocene assemblages may be explained by environmental, taphonomic, and evolutionary factors. These recorded fluctuations in predation intensity have obvious paleoecological and biostratigraphical applications, limited at present by the absence of corresponding data for molluscs. Although in theory these trends might explain the evolution or extinction of certain ostracod taxa, in practice, evidence of predation can be recorded only in those populations that successfully survive it. It follows that extinction resulting from predation is not likely to leave a decipherable record. Nevertheless, predation should be considered as a potential cause for some Cenozoic evolutionary trends in ostracods.

Abundance, size, and smoothness of carapace control vulnerability of ostracod species to gastropod predation, or control preservation of the evidence for this predation. The accepted criteria for distinguishing muricid from naticid drillholes in mollusc shells cannot be applied consistently to ostracods. Although modern naticids seek infaunal prey, fossil naticid holes occur on some taxa not likely to have been infaunal (Bairdiidae, Cytherideidae). In the Middle Eocene Stone City Formation, naticid predation was equally intense on Mollusca and Ostracoda. It appears that ostracods provided a significant food resource for juvenile naticids.

Three phena are attributed to digestive solution. They are most abundant in coastal settings and never occur on infaunal taxa (*Cytherella*).

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DISCUSSION

De Deckker: Isn't the change in the percentage of predators across the Cretaceous-Tertiary boundary simply the result of a change in environment?

Maddocks: No, not in the sections studied. Thor Hansen, who has studied molluscan diversity at these same Cretaceous-Tertiary sections, reports that many taxa on which molluscs prey disappear at or near the boundary, while naticid gastropods continue to be abundant. Perhaps the intensification of predation on ostracods reflects the decreased abundance of the preferred molluscan prey.

De Deckker: Are you aware of any papers discussing predation by ostracods on those gastropods, because if ostracods did eat the gastropods, your percentages of gastropods drilling on ostracods would simply be a result of size of the gastropod population (that is less predators, their numbers having been reduced by ostracod predation on juvenile gastropods) being able to predate on ostracods?

Maddocks: Sohn and Kornicker reported that some freshwater ostracods prey on snails, and

I have also seen this, but this predation leaves no marks on the shell. I do not see how this could be recognized in fossils. Stanton and Nelson (1975) did not include ostracods in their elaborate trophic analysis of the Stone City fauna. Larval gastropod shells are very common in the microscopic residues of this formation, so clearly juvenile naticid mortality was very high, but the cause is not obvious. Stanton and Nelson reported that one very abundant and two rare species of Naticidae comprise the single most abundant family at this locality.

Hartmann: Were you able to distinguish naticids and other gastropods, and between other drillers and predators such as Polychaeta?

Maddocks: Good naticid drill holes are easy to recognize in robust shells, but other kinds are not so easy to distinguish. There is a large literature on boring organisms, but I did not know that polychaetes drilled ostracods. I would like to learn how to recognize holes made by these other predators.

Oertli: You are talking in your very interesting paper about mortality rate. Are we sure that living ostracods were attacked (like a jaguar jumping on his prey) and not specimens just dead, *i.e.* still "eatable"?

Maddocks: The bevelled hole always has the larger (outer) perimeter on the exterior of the shell. As Reyment reported earlier, the holes tend to be located over the "meatier" regions of the animal. There is a large body of literature on the drilling behaviour of modern naticids. It has been reported somewhere that metabolites in the water guide them to their prey, and that in very crowded aquaria where the concentrations of these metabolites are very high, they have some trouble distinguishing live prey from empty shells. I do not know whether naticids would scavenge recently dead ostracods; someone should test this.

Reyment: Naticids operate below the sediment surface, muricids on the surface. Since the majority of gastropod holes, by far, found in ostracods are naticid (countersunk) holes, those ostracods must perforce be interstitial forms. That the mobile ostracods can be successfully attacked by drills, (for which several minutes elapse before sufficiently high grip can be achieved) is an outcome of the survival strategy of ostracods, whereby the animal tightly shuts its shell and remains still for a period of time until the danger has presumably passed. Drills seek prey a few minutes after hatching. They have an image-conditioned attack mechanism which can lead them to select unsuitable organisms (such as foraminifers) until the learning process has been completed. The choice of ostracods by juveniles is doubtless due to two causes (a) mistaken selection of prey by juveniles or (b) alternative selection of food in the absence of favourite nourishment (see Moore (1958) *Marine Ecology* for references concerning the switch to cirripedes in the absence of bivalves due to excessively heavy predation leading to temporary extinction of an accustomed food-source). Recently, we (Eva Reyment and I) were surprised to find naticid drill holes in ostracods from DSDP material from the W. Walvis Ridge, from a depth said to be about 3-4000 m in the Maastrichtian (Piveteau, 1960) Traité de Zoologie, Vol, Crustacées) reports naticids from 6000 m). Referring to your observations on the improvement of drilling technique over time, my own experience for Maastrichtian to Recent in the South Atlantic does not point to any difference in skill in this respect.

Maddocks: Very few (none?) of the species that are small enough to be interstitial (in the strict sense) or that show the morphologic adaptations associated with interstitial life (as described by Hartmann) ever bear naticid drillholes (in the collections I have examined). Except for *Cytherella*, the commonly attacked taxa do not seem likely (by analogy with living relatives) to be infaunal in habit. Perhaps naticids attack surface-dwelling prey from below, like submarines attacking a ship.

APPENDIX

TABLE 1—PREDATION IN GLEN ROSE (LOWER ALBIAN) ASSEMBLAGES.

	Ichnophenon (Specimens)				
Species	A	B	L	M	Total
16	3	1	22	—	26
40	—	—	6	1	7
48	—	—	1	—	1
66	—	—	5	—	5
67	—	—	1	—	1
Total	3	1	35	1	40
Mortality(%)	<1	<1	1	<1	1

TABLE 2—PREDATION IN WALNUT (MIDDLE ALBIAN) ASSEMBLAGES.

Species	Total Specimens	Percent of Fauna	Ichnophenon (Specimens)			Total
			I	M	Q	
13	8	<1	3	—	—	3
15	1,628	24	24	—	—	24
17	144	2	1	—	—	1
44	603	9	15	1	—	16
46	87	1	—	—	1	1
47	592	9	15	—	—	15
65	114	2	19	—	—	19
66	1,062	16	9	—	—	9
68	168	2	6	—	—	6
96	197	3	1	—	—	1
128	32	<1	1	—	—	1
138	118	2	—	2	—	2
Total	4,753	69	94	3	1	98
Mortality(%)	6,842		3	<1	<1	3

TABLE 3—PREDATION IN DEL RIO (CENOMANIAN) ASSEMBLAGES.

	Ichnophenon (Specimens)					
Species	I	M	N	R	T	Total
43	1	—	—	1	—	2
45	—	1	1	—	—	2
48	3	—	—	2	—	5
51	—	—	—	—	1	1
100	1	—	—	—	—	1
Total	5	1	1	3	1	11
Mortality(%)	<1	<1	<1	<1	<1	1

TABLE 4—PREDATION IN AUSTIN AND LOWER TAYLOR (LOWER AND MIDDLE CAMPANIAN) ASSEMBLAGES.

Species	Total Specimens	Percent of Fauna	Ichnophenon (Specimens)									Total
			A	B	I	L	M	N	Q	R	U	
7	364	2	—	—	2	—	1	—	—	—	—	3
8	158	1	—	—	—	—	1	—	—	—	—	1
9	19	<1	1	—	—	—	—	—	—	—	—	1
11	107	1	—	—	—	—	—	—	—	2	—	2
22	600	3	—	—	1	—	—	1	—	—	2	4
23	6,789	38	2	2	17	—	3	44	1	13	11	93
24	369	2	—	—	3	—	—	—	—	—	2	5
28	219	1	1	1	—	—	—	—	—	1	—	2
41	1,008	6	—	—	—	1	—	—	—	3	—	4
42	937	5	—	—	—	—	—	—	—	2	—	2
74	150	1	—	—	2	—	—	3	—	2	—	7
77	2,581	14	2	1	9	—	—	2	—	1	—	15
115	2,079	12	—	—	—	—	—	—	—	7	—	7
127	271	2	—	—	3	—	—	—	—	1	—	4
140	381	2	1	—	—	—	—	—	—	6	—	7
142	561	3	—	—	2	—	—	1	—	2	—	5
Total	16,593	93										
Sprinkle Formation		33	5	1	12	1	3	31	—	18	—	71
Burditt Formation		40	2	2	19	—	2	12	1	16	5	59
Dessau Formation		26	—	—	8	—	—	8	—	6	10	32
Total	18,099		7	3	39	1	5	51	1	40	15	162
Mortality(%)			<1	<1	<1	<1	<1	1	<1	<1	<1	2

TABLE 5—PREDATION IN MIDDLE AND UPPER TAYLOR (UPPER CAMPANIAN) ASSEMBLAGES.

Species	Specimens	Percent of Fauna	Ichnophenon (Specimens)							Total
			A	B	I	M	N	R	S	
25	6	<1	—	—	—	—	1	—	—	1
48	1,673	dominant	1	1	—	—	22	3	—	27
49	150	2	1	—	—	—	—	—	—	1
50	245	3	—	—	—	—	—	1	—	1
54	74	1	—	—	—	—	—	—	1	1
55	116	1	—	—	—	—	—	1	—	1
70	556	7	—	—	—	—	1	—	—	1
71	1,053	14	—	—	—	—	16	—	2	18
73	281	4	—	—	—	—	10	—	8	18
86	1,025	<1	—	—	1	—	—	1	—	2
95	27	<1	1	—	—	—	—	—	—	1
112	13	<1	—	—	—	—	—	1	—	1
143	461	6	—	—	—	1	—	—	1	2
145	315	4	—	—	—	—	—	1	—	1
Total	5,995	53 (exclusive of *Cytherella*)								
Bergstrom Formation Localities:										
Cottonwood Creek		17	2	—	1	—	39	—	12	54
Gilleland Creek		12	1	1	—	—	3	3	—	8
Rice's Crossing		28	—	—	—	—	6	1	—	7
Moore & Berry's Crossing		16	—	—	—	1	—	1	—	2
Pecan Gap Formation Localities:										
Sons of Hermann Hall		13	—	—	—	—	1	3	—	4

(*Continued*)

TABLE 5—*Continued*

Species	Specimens	Percent of Fauna	Ichnophenon (Specimens) A	B	I	M	N	R	S	Total
Old Manor Road		13	—	—	—	—	1	—	—	1
Total	9,953		3	1	1	1	50	8	12	76
Mortality(%)			<1	<1	<1	<1	1	<1	<1	2

TABLE 6—PREDATION IN NAVARRO (MAASTRICHTIAN) ASSEMBLAGES.

Species	Individuals	Percent of Fauna	Ichnophenon (Individuals) A	B	I	M	N	O	R	S	Total
10	10	<1	—	—	—	—	—	—	1	—	1
12	184	5	3	—	1	—	—	—	—	12	16
14	229	6	—	—	—	2	—	—	1	—	3
18	47	1	—	—	—	—	4	—	—	—	4
25	74	2	—	—	—	—	2	—	—	3	5
26	218	6	—	—	1	—	22	—	—	13	36
29	220	6	—	1	—	—	6	—	1	7	15
48	1,053	27	1	9	2	—	84	—	4	—	100
49	41	1	—	—	—	2	1	—	4	—	7
56	17	<1	—	—	2	—	—	1	—	8	11
69	157	4	—	—	—	—	1	—	—	—	1
70	106	3	—	—	—	—	2	—	2	—	4
72	78	2	—	—	—	—	8	—	—	10	18
73	698	18	—	—	4	—	39	—	—	11	54
79	65	2	—	—	1	—	4	—	—	—	5
80	101	3	—	—	—	—	—	—	—	3	3
118	14	<1	—	—	—	—	1	—	—	—	1
139	7	<1	—	—	—	1	1	—	—	—	2
141	15	<1	—	—	—	1	—	—	—	—	1
Total	3,334	84									
Brazos River		22	3	1	4	2	2	1	1	25	39
Littig Quarry		6	—	—	—	—	20	—	—	19	39
Walkers Creek		20	—	4	2	2	14	—	6	13	41
Onion Creek		51	1	5	5	2	139	—	6	10	168
Total	3,962		4	10	11	6	175	1	13	67	287
Mortality(%)			<1	<1	<1	<1	4	<1	<1	2	7

TABLE 7—PREDATION IN MIDWAY (DANIAN) ASSEMBLAGES.

Species	Individuals	Percent of Fauna	Ichnophenon (Individuals) A	B	C	I	L	M	N	O	P	R	S	Total
2	290	6	—	—	—	—	—	1	3	—	—	2	—	6
20	354	7	1	—	—	2	—	—	25	—	—	—	—	28
27	901	17	—	—	2	1	—	—	220	—	—	—	36	259
34	4	<1	—	—	—	—	—	—	1	—	—	—	—	1
48	1,659	32	1	4	—	5	—	1	136	1	—	1	—	149
77	76	1	1	—	—	—	—	—	2	—	—	—	1	4
80	20	<1	—	—	—	—	—	—	—	—	—	—	4	4
81	388	8	—	—	—	1	—	—	3	—	1	—	1	6
85	82	2	1	—	—	—	—	—	2	—	—	—	9	12
91	13	<1	—	—	—	—	—	—	—	—	—	—	2	2
107	99	2	—	—	2	—	—	—	2	—	—	—	1	5
108	7	<1	—	—	1	—	—	—	—	—	—	—	—	1

(*Continued*)

TABLE 7—*Continued*

Species	Indi-viduals	Percent of Fauna	A	B	C	I	L	M	N	O	P	R	S	Total
			Ichnophenon (Individuals)											
110	312	6	2	—	—	1	2	—	26	—	—	2	1	34
119	26	1	1	—	—	1	—	—	1	—	—	—	—	3
144	57	1	—	—	—	—	—	—	8	—	—	—	—	8
Total	4,288	83												
Wills Point Formation Localities:														
Caldwell & Limest. Co.		14	3	—	4	1	—	—	20	—	1	3	22	54
Kincaid Formation Localities:														
Ravine, Falls Co.		6	1	—	1	—	2	1	23	—	—	—	—	28
Littig Quarry		10	2	2	—	—	—	—	34	—	—	1	19	58
Walkers Creek		13	—	—	—	—	—	—	37	—	—	—	3	40
Brazos River		49	1	2	—	10	—	1	287	—	—	1	7	309
Transitional Interval		8	—	—	—	—	—	—	28	1	—	—	4	33
Total	5,149		7	4	5	11	2	2	429	1	1	5	55	522
Mortality(%)			<1	<1	<1	<1	<1	<1	8	<1	<1	<1	1	10

TABLE 8—PREDATION IN CLAIBORNE (LUTETIAN) ASSEMBLAGES.

Species	Indi-vinduals	Percent of Fauna	Ichnophenon (Individuals)										Total
			A	D	G	J	K	L	M	N	R	S	
1	7	<1	—	—	—	—	1	—	—	—	—	—	1
3	20	1	—	2	—	—	—	—	—	—	—	—	2
5	56	2	—	—	—	—	1	—	—	2	—	—	3
19	13	1	—	2	—	—	—	—	—	1	—	—	3
30	143	6	—	—	—	—	—	4	—	29	—	—	33
31	66	3	—	2	—	—	—	—	—	8	—	—	10
33	16	1	—	—	—	—	—	—	—	1	—	—	1
35	99	4	2	—	—	2	3	—	—	—	—	—	7
36	25	1	1	—	—	—	—	—	—	1	—	—	2
37	111	5	1	—	—	—	1	—	—	3	—	—	5
48	73	3	—	—	—	—	—	—	—	11	—	—	11
63	11	1	—	1	—	—	—	—	—	2	—	—	3
74	171	8	2	4	—	1	—	—	—	20	—	—	27
76	254	11	3	—	—	1	—	—	—	52	—	4	60
83	136	6	—	2	1	—	—	2	1	4	—	—	10
84	48	2	—	1	—	—	1	—	—	2	—	—	4
87	136	6	—	—	—	3	—	—	—	—	—	—	3
98	37	2	—	3	—	—	—	—	—	1	—	—	4
99	13	1	—	—	—	—	—	—	—	1	—	—	1
109	54	2	1	—	—	—	—	—	—	4	—	—	5
111	71	3	1	—	1	—	1	—	—	18	—	—	21
123	112	5	2	1	—	—	4	1	—	1	—	—	9
125	76	3	—	—	—	—	—	—	—	3	1	—	4
126	53	2	—	—	—	—	—	—	—	3	1	—	4
129	14	1	—	1	—	—	—	—	—	—	—	—	1
130	93	4	2	4	—	—	—	1	3	2	—	—	12
131	40	2	1	6	—	—	—	1	1	1	—	—	10
132	43	2	—	2	—	—	—	1	—	2	—	—	5
133	5	<1	—	—	—	—	—	1	—	—	—	—	1
134	19	1	—	—	—	—	—	—	—	1	—	—	1
135	46	2	1	4	—	—	—	—	—	—	—	—	5
136	33	1	—	3	—	—	—	—	—	—	—	—	3

(*Continued*)

Table 8—*Continued*

Species	Individuals	Percent of Fauna	Ichnophenon (Individuals)										Total
			A	D	G	J	K	L	M	N	R	S	
137	39	2	—	2	—	—	—	1	—	1	—	—	4
Total	2,133	95											
Cook Mtn., Pin Oak C		18	6	13	—	3	4	2	1	9	—	—	38
Cook Mtn., L Brazos		40	7	12	2	3	2	4	4	104	—	4	142
Stone City Fm.		19	1	15	—	1	—	6	—	36	—	—	59
Weches Fm.		23	3	—	—	—	6	—	—	25	2	—	36
Total	2,250		17	40	2	7	12	12	5	174	2	4	275
Mortality(%)			1	2	<1	<1	1	1	<1	8	<1	<1	12

Table 9—Predation in Holocene Gulf of Mexico Assemblages.

Species	Individuals	Percent of Fauna	Ichnophenon (Individuals)								Total
			A	D	E	H	J	L	N	P	
6	9	1	—	—	—	—	—	—	1	—	1
21	4	<1	—	—	1	—	—	—	—	—	1
32	6	<1	—	—	—	—	—	—	1	—	1
38	11	1	—	—	—	—	—	—	2	—	2
48	30	2	—	—	—	—	—	—	2	—	2
52	18	2	—	—	—	—	—	—	1	—	1
53	21	2	—	—	2	1	—	—	1	—	4
57	39	3	—	—	1	4	—	—	—	—	5
59	28	2	—	—	1	2	—	—	—	—	3
61	24	2	—	—	—	5	—	—	—	—	5
62	26	2	—	—	2	—	1	—	1	—	4
64	53	4	1	—	1	2	—	—	2	—	6
82	27	2	—	—	2	—	—	—	—	—	2
86	40	3	1	4	—	—	—	1	—	—	6
89	78	6	1	—	7	—	—	—	—	—	8
90	31	2	—	—	2	—	—	—	—	—	2
92	29	2	—	—	1	—	—	—	—	—	1
93	80	6	—	—	3	—	—	—	—	3	6
97	13	1	—	—	2	—	—	—	—	—	2
101	40	3	1	—	—	1	—	—	—	—	2
103	30	2	2	—	—	1	—	—	—	—	3
104	2	<1	—	—	—	—	—	—	1	—	1
113	79	6	—	—	1	1	—	—	—	1	3
114	51	4	—	—	1	2	—	—	3	—	6
117	3	<1	1	—	—	—	—	—	—	—	1
120	44	3	1	—	2	—	—	—	—	—	3
121	6	<1	1	—	—	—	—	—	—	—	1
122	86	6	—	—	—	—	—	—	9	—	9
146	23	2	1	—	—	—	—	—	—	—	1
Total	931	67									
Stat. Depth (m)											
4120 12	173	12	1	—	5	1	1	—	9	—	17
4121 15	111	8	—	—	—	—	—	—	5	—	5
4122 28	142	10	—	—	5	2	—	—	1	—	8
4123 40	196	14	—	—	3	5	—	—	1	—	9
4124 63	177	13	1	—	3	1	—	—	4	—	9
4125 91.5	255	18	3	4	2	—	—	—	1	3	13
4126 402	36	3	—	—	—	—	—	1	—	—	1

(*Continued*)

Table 9—*Continued*

Station Depth(m)	Individuals	Percent of Fauna	Ichnophenon (Individuals) A	D	E	H	J	L	N	P	Total
4133 24	23	2	—	—	1	1	—	—	—	1	3
4134 13	165	12	5	—	4	3	—	—	1	—	13
4135 13	114	8	—	—	6	6	—	—	2	—	14
Total	1,392		10	4	29	19	1	1	24	4	92
Mortality(%)			1	<1	2	1	<1	<1	2	<1	7

Table 10—Predation in Holocene Lagoonal Assemblages.

Species	Specimens	Percent of Fauna	Ichnophenon (Specimens) A	D	E	H	N	Total
4	339	5	1	1	2	1	—	5
39	969	15	—	1	7	1	1	10
53	74	1	—	—	1	—	—	1
58	47	1	—	—	2	4	—	6
60	109	2	—	—	2	6	—	8
61	253	4	—	1	—	25	—	26
88	137	2	—	—	—	8	—	8
89	812	13	—	—	4	20	—	24
94	139	2	—	—	4	—	—	4
101	133	2	—	—	—	4	—	4
102	3	1	—	—	1	—	—	1
103	11	<1	—	—	—	1	—	1
104	328	5	—	1	2	—	43	46
105	2,134	33	—	—	—	88	1	89
106	183	3	—	—	—	6	—	6
116	46	1	—	—	—	—	1	1
117	58	1	—	—	—	1	1	2
124	296	5	—	—	6	5	—	11
Total	6,071	94	1	4	31	170	47	253
Mortality(%)	6,453		<1	<1	1	5	1	8

Table 11—Stratigraphical Distribution of Predation.

	GLEN ROSE	WAL-NUT	DEL RIO	AUST-L.TAY	M-U TAYL	NAV-ARRO	MID-WAY	CLAI-BORNE	GULF MEXIC	LAG-OONS
Localities	11	5	2	9	6	4	8	4	10	6
Assemblages	21	86	6	56	40	46	97	14	10	25
Specimens	~6,300	6,842	1,708	18,099	9,953	9,673	12,868	3,832	3,637	6,453
Individuals	—	—	—	—	—	3,962	5,149	2,250	1,392	—
Species	~20	27	~20	36	54	50	49	61	117	39
MORTALITY(%):										
Naticid	—	—	<1	1	1	4	8	8	2	1
Gastropod	<1	<1	<1	<1	<1	1	<1	3	1	<1
Other	—	3	1	1	<1	1	<1	1	2	1
Solution	1	—	—	<1	<1	2	1	1	1	5
Total	1	3	1	2	2	7	10	12	7	8

TABLE 12—NAMES OF SPECIES LISTED IN TABLES 1–10.

1. *Acanthocythereis stenzeli* (Stephenson, 1946)
2. *Acanthocythereis washingtonensis* Hazel, 1968
3. *Actinocythereis davidwhitei* (Stadnichenko, 1927)
4. *Actinocythereis subquadrata* Puri, 1960
5. *Actinocythereis wechensis* (Sutton and Williams, 1940)
6. *Actinocythereis* sp.
7. *Alatacythere cheethami* Hazel and Paulson, 1964
8. *Alatacythere nadeauae* (Hill, 1954)
9. *Alatacythere ponderosana* (Israelsky, 1929)
10. *Alatacythere* aff. *A. serrata* (Bonnema, 1940)
11. *Amphicytherura dubia* (Israelsky, 1929)
12. *Antibythocypris macropora* (Alexander, 1929)
13. *Apatocythere* sp.
14. *Ascetoleberis hazardi* (Israelsky, 1929)
15. *Asciocythere goodlandensis* (Alexander, 1929)
16. *Asciocythere rotunda* (Vanderpool, 1928)
17. *Bairdia comanchensis* Alexander, 1929
18. *Bairdoppilata magna* (Alexander, 1934)
19. *Bairdoppilata platycoa* Howe, 1963
20. *Bairdoppilata suborbiculata* (Alexander, 1934)
21. *Bairdoppilata* sp.
22. *Brachycythere acuminata* Hazel and Paulson, 1964
23. *Brachycythere crenulata* Crane, 1965
24. *Brachycythere durhami* Hazel and Paulson, 1964
25. *Brachycythere ledaforma* (Israelsky, 1929)
26. *Brachycythere ovata* (Berry, 1925)
27. *Brachycythere plena* Alexander, 1934
28. *Brachycythere pyriforma* Hazel and Paulson, 1964
29. *Brachycythere rhomboidalis* (Berry, 1925)
30. *Buntonia alabamensis* (Howe and Pyeatt, 1934)
31. *Buntonia subtriangularis* (Sutton and Williams, 1939)
32. *Buntonia* sp.
33. *Clithrocytheridea oliveri* (Cushman, 1925)
34. *Clithrocytheridea ruida* (Alexander, 1934)
35. *Clithrocytheridea subpyriformis* (Sutton and Williams, 1939)
36. *Clithrocytheridea wechesensis* (Stadnichenko, 1927)
37. *Cocoaia smithvillensis* (Stephenson, 1942)
38. *Cushmanidea* cf. *C. seminuda* (Cushman, 1906)
39. *Cyprideis salebrosa* van den Bold, 1963
40. "*Cythere ornata*" of Vanderpool, 1928
41. "*Cythereis*" *bicornis* Israelsky, 1929
42. *Cythereis dallasensis* Alexander, 1929
43. *Cythereis dentonensis* Alexander, 1929
44. *Cythereis fredericksburgensis* Alexander, 1929
45. *Cythereis paupera* Jones and Hinde, 1889
46. *Cythereis* sp. C of Moysey and Maddocks, 1982
47. *Cytherella fredericksburgensis* Alexander, 1932
48. *Cytherella* spp.
49. *Cytherelloidea crafti* (Sexton, 1951)
50. *Cytherelloidea tollettensis* (Sexton, 1951)
51. *Cytherelloidea* sp.
52. *Cytheretta pumicosa* (Brady, 1867)
53. *Cytheromorpha paracastanea* (Swain, 1955)
54. *Cytheropteron castorensis* Butler and Jones, 1957
55. *Cytheropteron fossatum* Skinner, 1956

(*Continued*)

TABLE 12—*Continued*

56. *Cytheropteron navarroense* Alexander, 1929
57. *Cytheropteron* sp.
58. *Cytherura cybaea* Garbett and Maddocks, 1979
59. *Cytherura fiscina* Garbett and Maddocks, 1979
60. *Cytherura radialirata* Swain, 1955
61. *Cytherura sandbergi* Morales, 1966
62. *Cytherura valentini* Garbett and Maddocks, 1977
63. *Digmocythere russelli* (Howe and Lea, 1936)
64. *Echinocythereis margaretifera* (Brady, 1870)
65. *Eocytheropteron paenorbiculatum* (Alexander, 1933)
66. *Eocytheropteron trinitiensis* (Vanderpool, 1928)
67. *Eocytheropteron* sp.
68. *Eocytheropteron* sp. B of Moysey and Maddocks, 1982
69. *Escharacytheridea micropunctata* (Alexander, 1929)
70. *Haplocytheridea bruceclarki* (Israelsky, 1929)
71. *Haplocytheridea dilatipuncta* Crane, 1965
72. *Haplocytheridea* aff. *H. everetti* (Berry, 1925)
73. *Haplocytheridea globosa* (Alexander, 1929)
74. *Haplocytheridea habropapillosa* (Sutton and Williams, 1939)
75. *Haplocytheridea insolita* (Alexander and Alexander, 1933)
76. *Haplocytheridea montgomeryensis* (Howe and Chambers, 1935)
77. *Haplocytheridea multipunctata* (Alexander, 1934)
78. *Haplocytheridea nanifaba* Crane, 1965
79. *Haplocytheridea renfroensis* Crane, 1965
80. *Haplocytheridea* sp. 1 of Maddocks, 1985
81. *Hazelina* sp. A
82. *Henryhowella* ex. gr. *asperrima* (Reuss, 1850)
83. *Henryhowella orelliana* (Sutton and Williams, 1939)
84. *Henryhowella smithvillensis* (Sutton and Williams, 1939)
85. *Hermanites midwayensis* (Alexander, 1934)
86. *Krithe* sp.
87. *Loxoconcha claibornensis* Murray, 1938
88. *Loxoconcha matagordensis* Swain, 1955
89. *Loxoconcha moralesi* Kontrovitz, 1976
90. *Loxoconcha* aff. *L. moralesi* Kontrovitz, 1976
91. *Loxoconcha nuda* Alexander, 1934
92. *Loxoconcha* sp.
93. *Malzella* sp.
94. *Megacythere repexa* Garbett and Maddocks, 1979
95. "*Monoceratina*" spp.
96. "*Neocythere*" sp. of Moysey and Maddocks, 1982
97. *Neomonoceratina mediterranea* Ruggieri, 1953
98. *Opimocythere martini* (Murray and Hussey, 1942)
99. *Ouachitaia caldwellensis* (Howe and Chambers, 1935)
100. *Paracyprideis graysonensis* (Alexander, 1929)
101. *Paracytheroma stephensoni* (Puri, 1954)
102. *Paracytheroma texana* Garbett and Maddocks, 1979
103. *Pellucistoma magniventra* Edwards, 1944
104. *Peratocytheridea bradyi* (Stephenson, 1938)
105. *Perissocytheridea brachyforma* Swain, 1955
106. *Perissocytheridea rugata* Swain, 1955
107. *Phacorhabdotus formosus* (Alexander, 1934)
108. *Phacorhabdotus sculptilis* (Alexander, 1934)
109. *Phractocytheridea moodyi* (Howe and Garrett, 1934)
110. *Phractocytheridea ruginosa* (Alexander, 1934)

(*Continued*)

TABLE 12—*Continued*

111. *Phractocytheridea veatchi* (Howe and Garrett, 1934)
112. *Polylophus asper* Crane, 1965
113. *Pontocythere sandersi* (Puri, 1958)
114. *Pontocythere sulcata* (Puri, 1960)
115. *Praephacorhabdotus pokornyi* (Hazel and Paulson, 1964)
116. *Proteoconcha concinnoidea* (Swain, 1955)
117. *Proteoconcha edwardsi* Plusquellec and Sandberg, 1969
118. *Pterygocythere saratogana* (Israelsky, 1929)
119. *Pterygocythereis lemnicata* (Alexander, 1934)
120. *Pterygocythereis miocenica* van den Bold, 1967
121. *Pterygocythereis* sp. B
122. *Puriana krutaki* Kontrovitz, 1976
123. *Quadracythere bursilloides* (Stadnichenko, 1927)
124. *Radimella littorala* (Grossman, 1965)
125. *Ruggieria*? *evergreenica* (Stadnichenko, 1927)
126. *Ruggieria*? *suttoni* (Stephenson, 1946)
127. *Schuleridea travisensis* Hazel and Paulson, 1964
128. *Stillina* sp.
129. *Trachyleberis elmana* (Stadnichenko, 1927)
130. *Trachyleberis* aff. *T. montgomeryensis* (Howe and Chambers, 1935)
131. *Trachyleberis nitida* Howe, 1963
132. *Trachyleberis texana* (Stadnichenko, 1927)
133. *Trachyleberis* sp. 1
134. *Trachyleberis* sp. 2
135. *Trachyleberis* sp. 3
136. *Trachyleberis* sp. 4
137. *Trachyleberis* sp. 5
138. *Trachyleberis*? sp. of Moysey and Maddocks, 1982
139. *Veenia arachoides* (Berry, 1925)
140. *Veenia ozanana* (Israelsky, 1929)
141. *Veenia parallelopora* (Alexander, 1929)
142. *Veenia paratriplicata* (Swain, 1952)
143. *Veenia ponderosana* (Israelsky, 1929)
144. *Vetustocytheridea fornicata* (Alexander, 1934)
145. *Xestoleberis opina* Schmidt, 1948
146. *Xestoleberis* sp.

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Jurassic-Cretaceous Non-marine Ostracods from Israel and Palaeoenvironmental Implications

AMNON ROSENFELD, EPHRAIM GERRY AND AVRAHAM HONIGSTEIN
Geological Survey of Israel, Jerusalem,
Israel Institute of Petroleum and Energy, Ramat Aviv and Tel-Aviv University, Israel

ABSTRACT

In the Jurassic–Cretaceous strata of Israel non-marine ostracod assemblages occur in four major episodes. These ostracod species belong to the following genera: *Bisulcocypris* and *Darwinula* in the Early Jurassic; *Cypridea, Metacypris, Cypris, Clinocypris, Timiriasevia* and *Darwinula* in the Wealden facies of Berriasian-Barremian age; *Neocyprideis, Looneyella, Darwinula* and *Xestoleberis* in the Late Cenomanian-Early Turonian; *Neocyprideis, Candoniella* and *Xestoleberis* in the Late Turonian-Early Coniacian. *Bisulcocypris oertlii* is described as a new species. The non-marine ostracod assemblages are generally associated with shallow marine species. The mixed faunas indicate coastal marine environments with fresh–brackish water influence, up to hypersaline lagoonal conditions in Middle and Late Cretaceous.

INTRODUCTION

The Jurassic–Cretaceous sediments in Israel consist mainly of marine sequences of limestones, chalks, shales, marls and dolomites. Marine transgressions at that time were extensive and most of the sediments were deposited on flat shelf regions. Middle, and especially Late, Mesozoic rocks are widely distributed throughout the country both in surface and subsurface. The Jurassic ostracods from Israel have been studied by Maync (1966), whereas the Cretaceous ones were described by Sohn (1968), Gerry and Rosenfeld (1973), Rosenfeld and Raab (1974, 1984), Honigstein (1984) and Honigstein and Rosenfeld (1985). According to these studies, several ostracod assemblage zones could be distinguished within this succession. The ostracod biozonation in the Jurassic (Maync, 1966) is now under revision. Twenty ostracod zones have been established in the Cretaceous, of which seventeen contain exclusively marine species. Non-marine ostracods in Israel occur in a few localities in four major episodes within the Jurassic-Cretaceous strata (Text-fig. 1).

Mesozoic sediments in Israel, containing non-marine ostracods, are rather limited in their distribution and thickness. The observed non-marine species and the ratio between non-marine and marine specimens within the assemblages lead to significant conclusions on palaeosalinities (Text-fig. 1). The non-marine ostracods in the Cretaceous assemblage zones L-2*, UC-5 and UC-7 are associated with marine species and point to mixed environments, whereas in the Early Jurassic zone J-1* only non-marine ostracods occur. The distribution of the four non-marine biozones and

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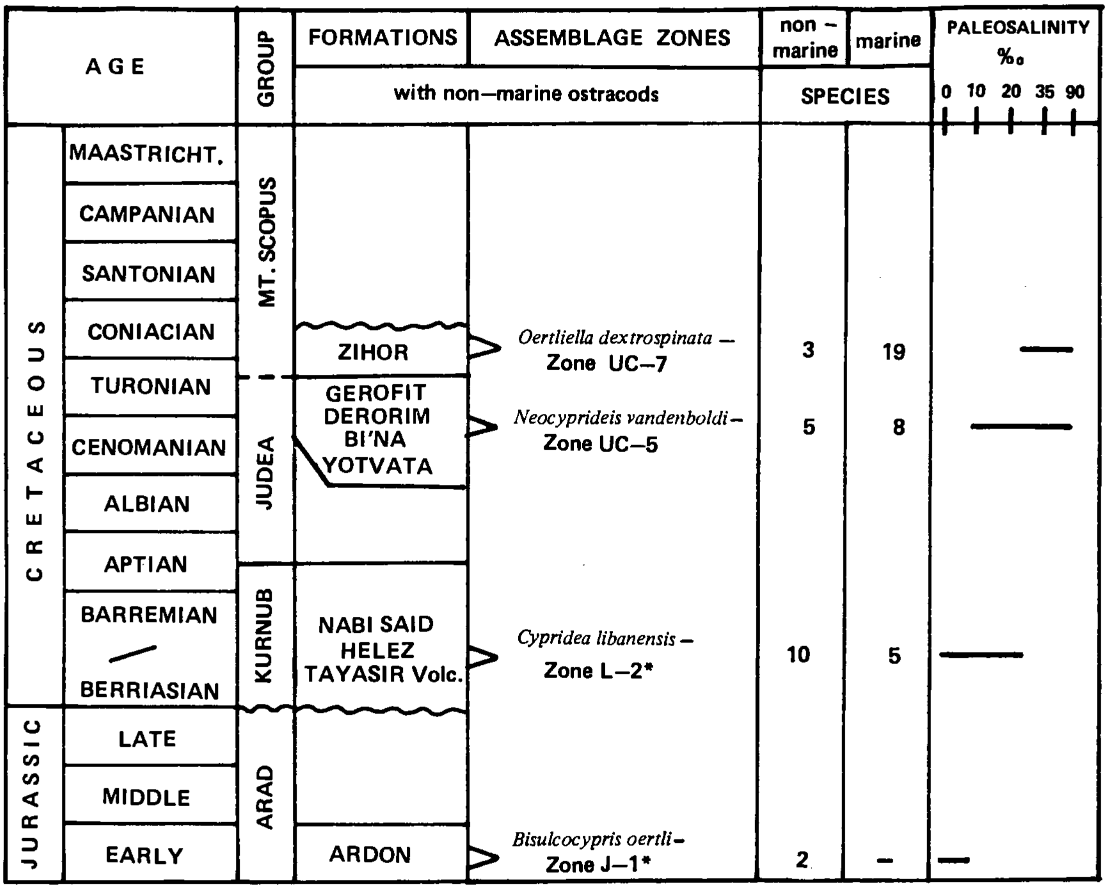
* L–2 and J–1 are zone symbols. Asterisks are used, if there are contemporaneous marine zones in other regions of local (see p. 662: L–2 *versus* L–2*).



TEXT-FIG. 1—Biozones with non-marine ostracods in the Jurassic–Cretaceous of Israel.

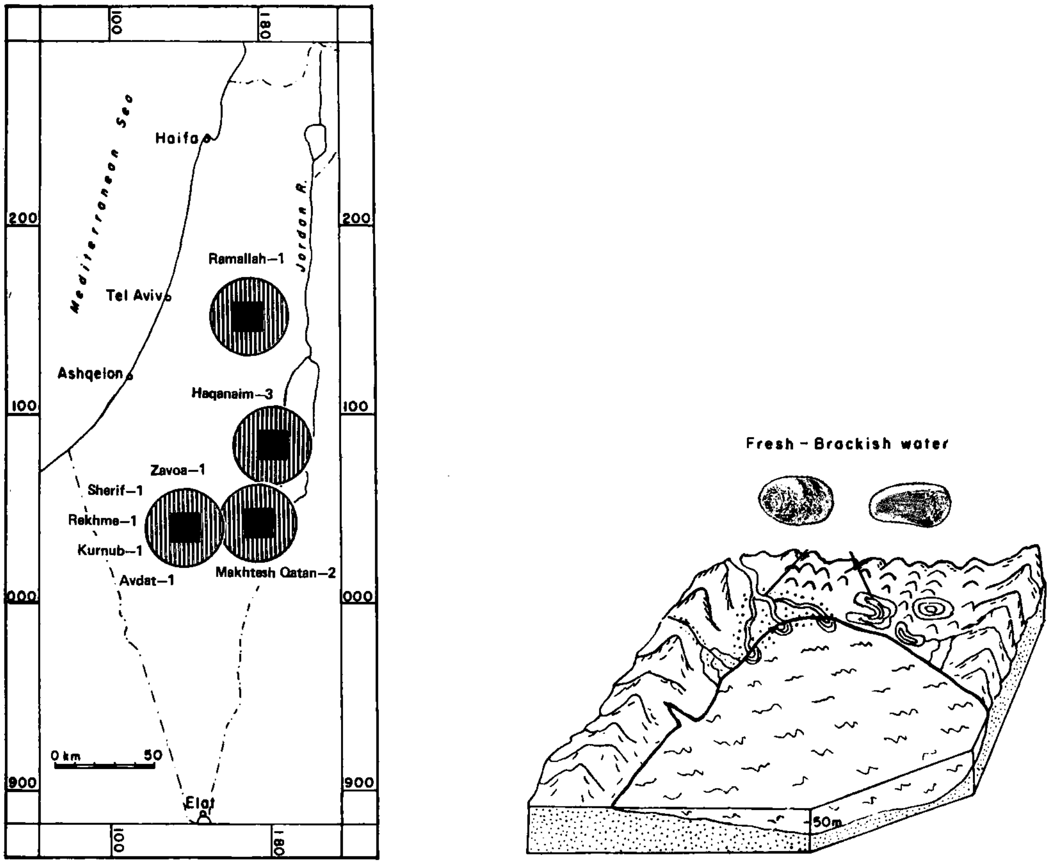
their percentage of species and specimens are illustrated in Text-figs. 2a–5a. All coordinates refer to the Israeli cartographic grid. The major ostracod components and their preferred biotopes are shown in Text-figs. 2b–5b. Characteristic species are illustrated in Pls. 1, 2.

ASSEMBLAGES OF NON-MARINE OSTRACODS

From the Early Jurassic–Late Cretacous the following four assemblage zones with non-marine ostracods have been recognized:

Bisulcocypris oertlii (J-1*) Assemblage Zone

This zone is newly established in the present paper and is characterized by the nearly monospecific occurrence of *Bisulcocypris oertlii* Gerry, n. sp. (Pl. 1, figs. 1–6). Only in very few cases this species is accompanied by *Darwinula* sp. (Pl. 1, fig. 7). Rare, indeterminable, doubtful, marine ostracod fragments were found in a few cuttings samples, but may have been caused by cavings. The ostracod density in the J-1* zone is low. This zone has a restricted occurrence of less than one meter thickness in different levels of eight boreholes (Text-fig. 2a) within the generally marine limestones of the Ardon Formation. The age determination of this zone (Early Jurassic) is based



TEXT-FIG. 2a (*left*)—Percentages of non-marine species (black squares) and specimens (striped circles) in samples of the *Bisulcocypris oertlii* (J-1*) Zone (Early Jurassic).

2b (*right*)—Ostracod biotope in the *Bisulcocypris oertlii* (J-1*) Zone. Fresh–brackish water. From left to right: *Bisulcocypris oertlii, Darwinula* sp.

on the appearance of the contemporaneous foraminifera *Orbitopsella primaeva* (Henson) in marine sediments (Derin and Gerry, 1975).

Bisulcocypris oertlii is described as a new species in the following taxonomic note:

Genus BISULCOCYPRIS Pinto and Sanguinetti, 1958
BISULCOCYPRIS OERTLII Gerry, n. sp.
(Pl. 1, figs. 1–6).

Derivation of name.—In honour of Dr. H. J. Oertli, SNEA(P)-Pau, France.

Holotype.—Female right valve (G.S.I. Type No. 440); Pl. 1, fig. 3.

Paratypes.—One female carapace (Pl. 1, figs. 1, 2) and one male carapace (Pl. 1, figs. 5, 6).

Type Locality.—Ramallah-1 well, 4,235 m; coord. 1667/1515.

Type Stratum.—Ardon Formation.

Diagnosis.—*Bisculcocypris* with smooth to fine reticulate surface. Dorsal and ventral margins straight to slighty convex. Pronounced sexual dimorphism.

Measurements (μm).—

l	h	w		
800	500	—	Holotype	F
760	440	510	Paratype	F
760	400	380	Paratype	M

Description.—Carapace ovate in females and ovate-elongate in males. Dorsal margin straight to slightly convex, ventral margin convex. Both ends well-rounded. Greatest height centrally. Two parallel sulci anterodorsally and middorsally. Sulci in juvenile forms less developed (Pl. 1, fig. 4). Posterior swollen, especially in females. Right valve slightly larger than the left. Surface smooth to finely reticulate. Internal features not observed. Pronounced sexual dimorphism; males lower and less tumid than females.

Remarks.—*Bisulcocypris oertlii* n. sp. is very similar to *B.*? *triassica* Gerry and Oertli, 1967 (p. 378, Pl. 1, figs. 1–6; Anisian of Israel). It differs from the latter in its larger size, the less oblique sulci and the straighter dorsal margin.

Material and distribution.—About twenty five carapaces and valves from Avdat-1, Haqanaim-3, Kurnub-1, Makhtesh Qatan-2, Ramallah-1, Rekhme-1, Sherif-1, Zavoa-1 (Gerry, 1975).

Stratigraphic range.—Early Jurassic.

Cypridea libanensis (L-2*) Assemblage Zone (Rosenfeld and Raab, 1984)

From the L-2* zone the following non-marine ostracod species are reported: *Cypridea libanensis* Bischoff, *C. heliopolisensis* Bischoff, *C. aaleyensis* Bischoff, *C.* cf. *C. ultima* Grekoff, *C. tayasirensis* Rosenfeld and Raab, *Darwinula* sp., *Cypris* sp., *Clinocypris* sp., *Metacypris polita* Grekoff and *Timiriasevia cardiformis* Rosenfeld and Raab. The major species are illustrated on Pl. 2. This assemblage is associated with marine forms, belonging to the genera *Antepaijenborchella, Metacytheropteron, Veeniacythereis, Fastigatocythere* and *Cytherura.* Ostracods are relatively frequent in the samples of the L-2* zone. Carapaces of *Darwinula* sp. are sometimes major components of the rock (Pl. 2, fig. 8). The L-2* zone is a few metres thick and was recognized in shales, marls and tuffs from four exposures and boreholes in northern and central Israel (Text-fig. 3a). This zone is related to the worldwide Wealden facies event and was found in short levels in different formations of the generally marine Kurnub Group (Text-fig. 1). A Berriasian–Barremian age is attributed to the L-2* zone according to the worldwide range of the Wealden ostracods, the contemporaneous marine *Schuleridea bullata* (L-2) Assemblage Zone (Rosenfeld and Raab, 1984), and the K-Ar absolute ages of the Tayasir Volcanics (Lang and Mimran, 1985).

Neocyprideis vandenboldi (UC-5) Assemblage Zone (Rosenfeld and Raab, 1974)

In the UC-5 zone the following non-marine species occur: *Neocyprideis vandenboldi* Gerry and Rosenfeld, *Looneyella sohni* Rosenfeld, *Xestoleberis*? *X. derorimensis* Rosenfeld, Cypridacea gen.? sp. (see Pl. 1, figs. 8–11) and *Darwinula* sp. This fauna is found together with marine types of the

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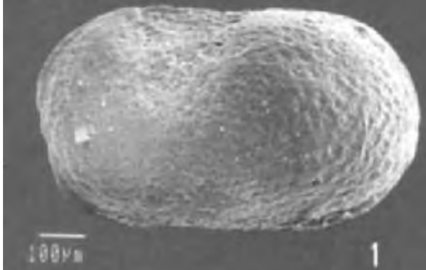
PLATE 1—Figs. 1–6. *Bisulcocypris oertlii* Gerry, n. sp., J-1* zone, Early Jurassic. 1. Paratype, female carapace, left side, Ramallah-1, 4,235 m. 2. Same carapace, dorsal view. 3. Holotype, female right valve, Ramallah-1, 4,235 m. 4. Juvenile carapace, left side, Rekhme-1, 1,819–1,125 m. 5. Paratype, male carapace, dorsal view, Kurnub-1, 1,175–1,185 m. 6. Same carapace, right side. Fig. 7. *Darwinula* sp., carapace, right side, Kurnub-1, 1,165–1,175 m, J-1* zone, Early Jurassic. Fig. 8. *Looneyella sohni* Rosenfeld, male carapace, left side, N. Yotvata, UC-5 zone, Late Cenomanian–Early Turonian. Fig. 9. *Neocyprideis vandenboldi* Gerry and Rosenfeld, female carapace, left side, N. Yotvata, UC-5 zone, Late Cenomanian–Early Turonian. Fig. 10. Cypridacea gen.? sp., carapace, left side, N. Yotvata, UC-5 zone, Late Cenomanian–Early Turonian. Fig. 11. *Xestoleberis*? *X. derorimensis* Rosenfeld, male carapace, dorsal view, Damun-7, 228–229 m, UC-5 zone, Late Cenomanian–Early Turonian. Fig. 12. *Neocyprideis flexeri* Honigstein and Rosenfeld, female carapace, left side, Biqat Qetura, UC-7 zone, Late Turonian–Early Coniacian. Fig. 13. *Candoniella*? *C. qeturaensis* Honigstein and Rosenfeld, carapace, right valve, Biqat Qetura, UC-7 zone, Late Turonian–Early Coniacian.



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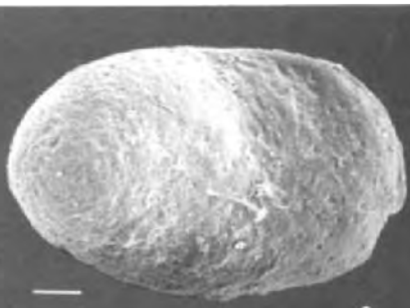

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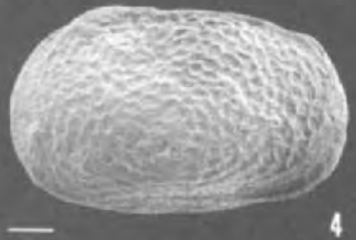

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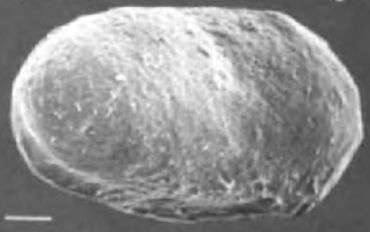

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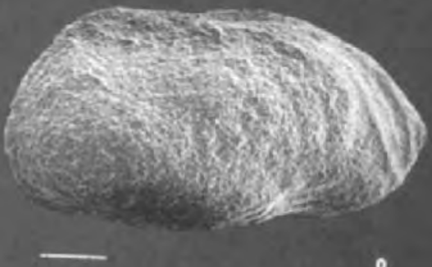

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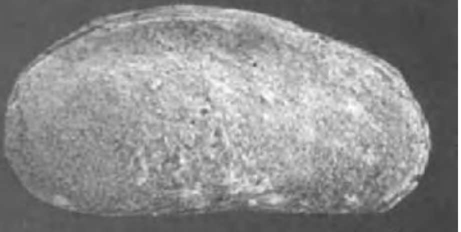

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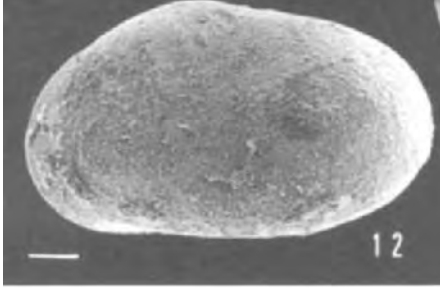

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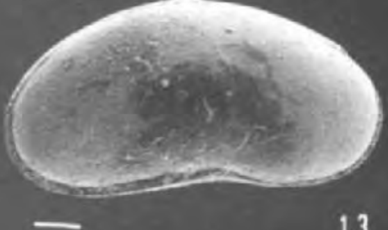

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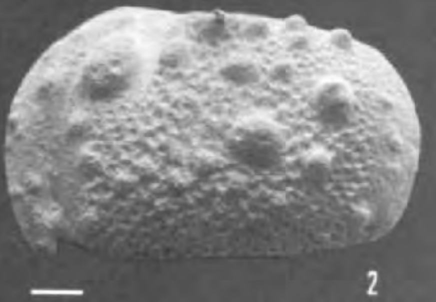
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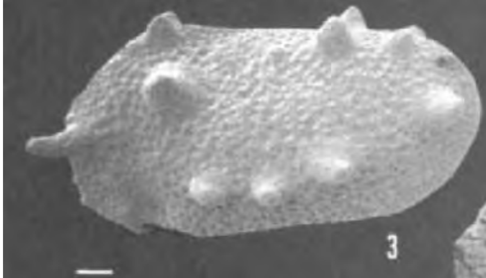
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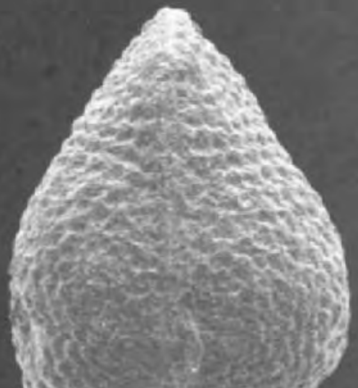
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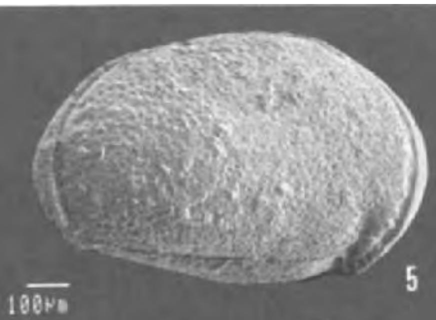

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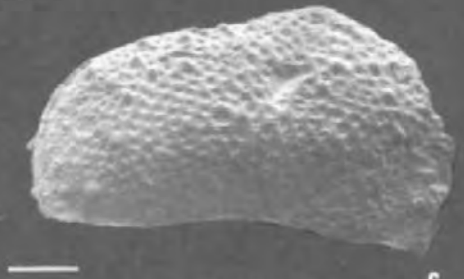
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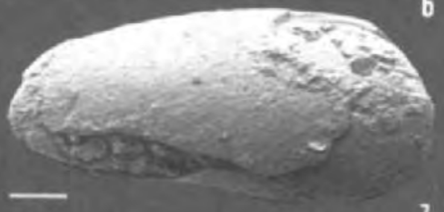
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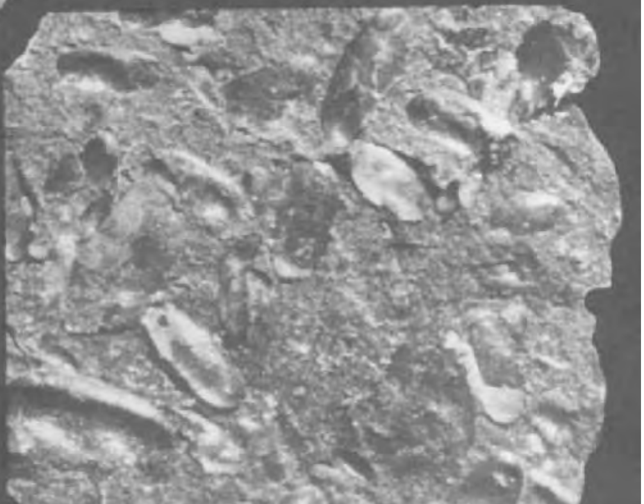
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genera *Bairdia, Paracypris, Metacytheropteron, Amphicytherura, Cythereis, Veeniacythereis, Limburgina* and *Planileberis*. Ostracods are abundant in samples of the UC-5 zone; *N. vandenboldi* is the dominant form in this zone and sometimes builds whole rocks in southern Israel (Gerry and Rosenfeld, 1973, Pl. 1, fig. 9). Species of *Xestoleberis* are reported from marine environments, but seem to tolerate lower salinities and thus may occur in brackish waters. *Limburgina*? *L. gerryi* Rosenfeld is the only marine type found together with abundant non-marine ostracods and is therefore considered as a transitional coastal marine species (Text-fig. 4b). The UC-5 zone is widespread in Israel and found in marls and limestones from eight exposures and boreholes (Text-fig. 4a). This zone can reach thicknesses of several tens of metres and was observed in different formations of the generally marine Judea Group (Text-fig. 1). The Late Cenomanian ammonite *Neolobites vibrayeanus* (d'Orbigny) is abundant in strata corresponding to this zone (Bartov *et al.*, 1972). A Late Cenomanian-Early Turonian age for the sediments of the UC-5 zone is suggested by its stragraphical setting below and above the Early Turonian marine *Cythereis rawashensis kenaanensis* (UC-6) Assemblage Zone (Rosenfeld and Raab, 1974).

Oertliella dextrcspinata (UC-7) Assemblage Zone (Honigstein and Rosenfeld, 1985)

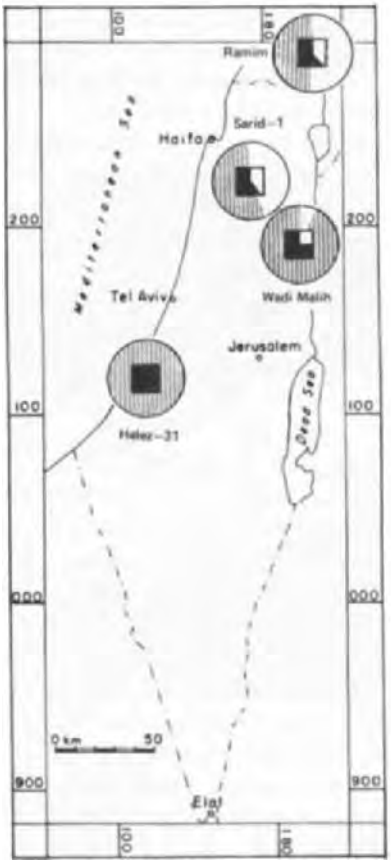
The following non-marine ostracod species occur in the UC-7 zone: *Neocyprideis flexeri* Honigstein and Rosenfeld, *Candoniella*? *C. qeturaensis* Honigstein and Rosenfeld (see Pl. 1, figs. 12, 13) and *Xestoleberis*? *X. derorimensis* Rosenfeld. These are associated with an abundant marine fauna of the genera *Cytherella, Cytherelloidea, Bairdia, Bairdoppilata, Paracypris, Ovocytheridea, Neocythere, Metacytheropteron, Cythereis, Spinoleberis, Cristaeleberis, Limburgina, Dumontina, Oertliella* and *Nucleolina*. Non-marine ostracods are frequent in some samples ofthe UC-7 zone, always accompanied by abundant marine species. *Limburgina galvensis* (Breman) in the UC-7 zone is also found only in samples containing *Xestoleberis* and *Neocyprideis* (see Text-fig. 5b). Non-marine ostracods occur in a few metres of thick marls and limestones from two exposures in the middle and upper parts of the Zihor Formation, which is restricted to southern Israel (Text-fig. 5a). The age of the UC-7 zone is Late Turonian–Early Coniacian, according to the ammonites *Coilopoceras zihoricum* Parnes and *Barroisiceras* sp. (Lewy, 1975).

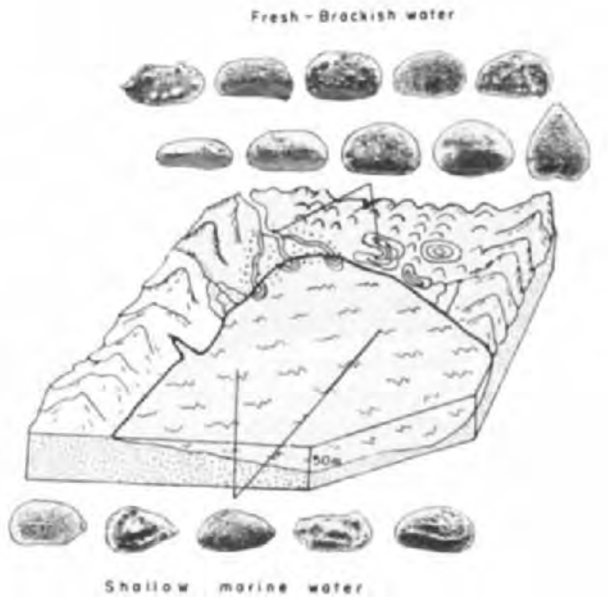
PALAEOENVIRONMENT AND CONCLUSIONS

During the Mesozoic, the sedimentation realm in Israel took place in mostly shallow marine regions. The sedimentary facies was determined by sea level fluctuations, as well as by tectonic activity. Facies changes were rapid and extreme. Sediments, deposited in fresh-brackish water or hypersaline conditions in the Jurassic-Cretaceous are limited both vertically and laterally. Non-marine ostracods occur in four major episodes (Late Jurassic, Berriasian-Barremian, Late Cenomanian–Early Turonian and Late Turonian–Early Coniacian). They are associated with marine fauna, which allow dating of the zones by ammonites, foraminifers and ostracods. The mixed ostracod assemblages indicate estuarine, lagoonal and coastal milieus. The non-marine zones are important for local stratigraphy, correlations and palaeoecology.

PLATE 2—Typical non-marine ostracod species from the L-2* zone (Berriasian-Barremian).

Fig. 1. *Cypridea tayasirensis* Rosenfeld and Raab, female carapace, left side, Wadi Malih. Fig. 2. *Cypridea libanensis* Bischoff, carapace, left side, Ramim. Fig. 3. *Cypridea heliopolisensis* Bischoff, carapace, left side, Ramim. Fig. 4. *Timiriasevia cardiformis* Rosenfeld and Raab, female carapace, dorsal view, Wadi Malih. Fig. 5. *Cypridea aaleyensis* Bischoff, carapace, right side, Ramim. Fig. 6. *Cypridea* cf. *C. ultima* Grekoff, carapace, right side, Helez-3, 1,508 m. Fig. 7. *Darwinula* sp., carapace, right side, Wadi Malih. Fig. 8. Rock sample with numerous specimens of *Darwinula* sp., Sarid-1, 1,613 m (photograph: courtesy of Dr. H. J. Oertli, Pau).





Text-fig. 3a (*left*)—Percentages of non-marine species (black squares) and specimens (striped circles) in samples of the *Cypridea libanensis* (L-2*) Zone (Berriasian-Barremian).

3b (*right*)—Various ostracod biotopes in the *Cypridea libanensis* (L-2*) Zone. Fresh–brackish water. From left to right:

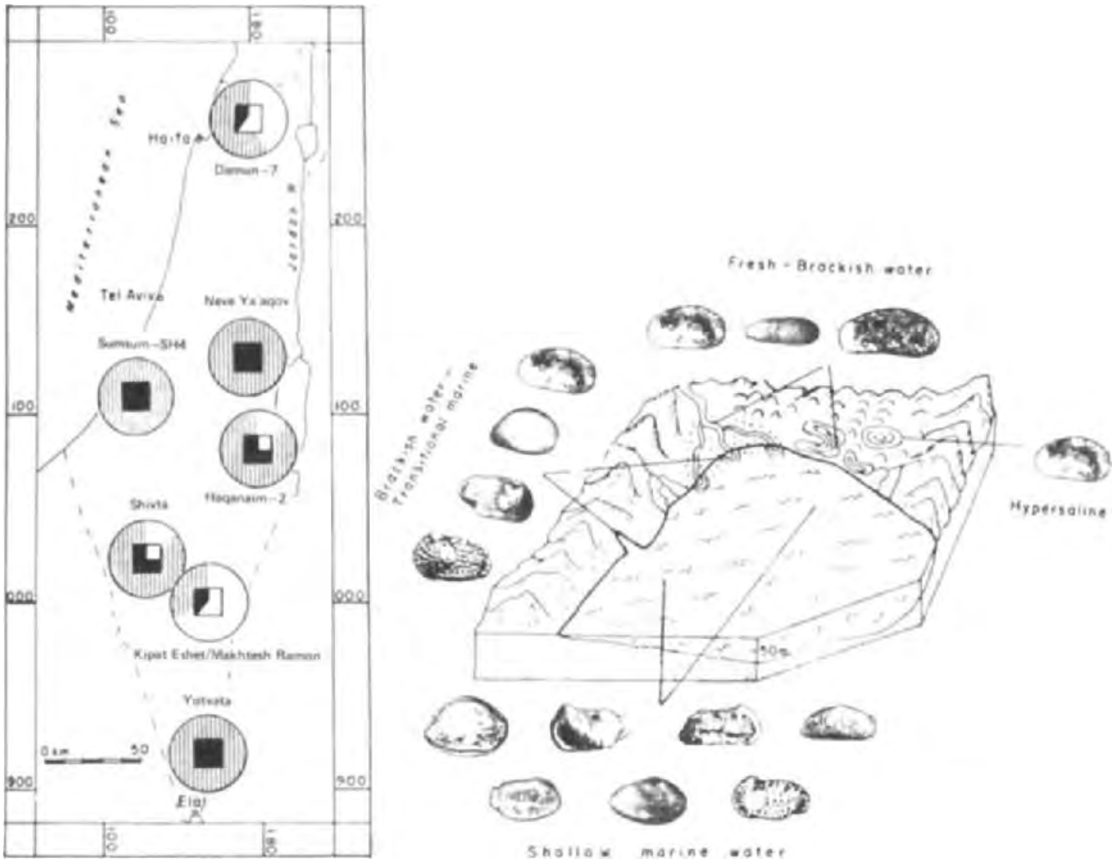
(Upper row) *Cypridea heliopolisensis, Cypridea* cf. *C. ultima, Cypridea libanensis, Cypridea aaleyensis, Cypridea tayasirensis.*

(Lower row) *Darwinula* sp., *Clinocypris* sp., *Cypris* sp., *Metacypris polita, Timiriasevia cardiformis.*

Shallow marine water. From left to right:

Cytherura qiriatshemonaensis, Antepaijenborchella menarica, Metacytheropteron parnesi, Veeniacythereis ghabounensis ghabounensis, Fastigatocythere naftaliensis.

A poor, but exclusively non-marine ostracod fauna is found in several stratigraphical levels in the Early Jurassic J-1* zone. These non-marine intercalations imply nearshore fresh-brackish water supply (Text-fig. 2b), probably due to local uplifts. The mixed marine and non-marine ostracod assemblages in the Early Cretaceous L-2* zone can be explained by the freshwater inland lakes, rivers and deltas, closely connected to the sea, affecting each other (Text-fig. 3b). The combination of fresh water and seawater in lagoonal and estuary milieus with a favourable high nutrient supply, would have encouraged the generation of a maximum number of forms. This non-marine episode may be related to sea level changes through regressions and volcanic activity, which is rather common in the Early Cretaceous of Israel. The combined occurrence of abundant non-marine and relatively rare marine ostracods in the Cenomanian-Turonian UC-5 zone point to coastal marine environ-



TEXT-FIG. 4a (*left*)—Percentages of non-marine species (black squares) and specimens (striped circles) in samples of the *Neocyprideis vandenboldi* (UC-5) Zone (Late Cenomanian-Early Turonian).

4b (*right*)—Various ostracod biotopes in the *Neocyprideis vandenboldi* (UC-5) Zone.

Fresh - brackish water. From left to right:

Neocyprideis vandenboldi, Darwinula sp., Cypridacea gen? sp.

Brackish water - transitional marine. From top to bottom:

Neocyprideis vandenboldi, Xestoleberis? *X. derorimensis, Looneyella sohni, Limburgina*? *L. gerryi.*

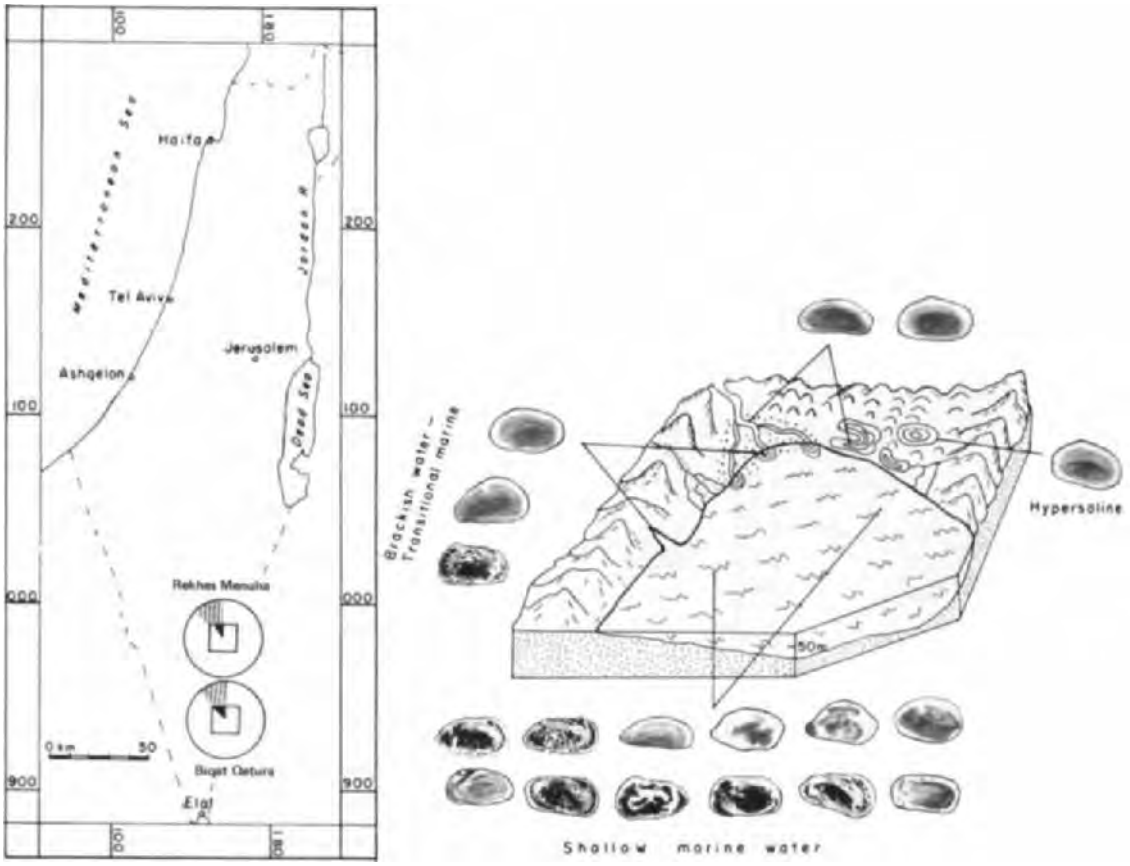
Hypersaline: *Neocyprideis vandenboldi.*

Shallow marine water. From left to right:

(Upper row) *Bairdia* sp., *Planileberis ziregensis, Cythereis namousensis, Paracypris mdaouerensis.*

(Lower row) *Amphicytherura sexta, Metacytheropteron berbericum, Veeniacythereis jezzineensis.*

ments with continental freshwater influence (Text-fig. 4b). This brackish water environment indicates development of lagoons and embayments, resulting from tectonic movements (Freund, 1962). Hypersaline conditions probably prevailed in this environment, as suggested by the presence of gypsum, alternating with marly beds, containing abundant *Neocyprideis vandenboldi.* In the Turonian–Coniacian UC-7 zone the marine palaeoenvironment is dominant. Brackish water ostracods are found only in parts of the section. Here, the biotopes are similar to that of the UC-5 zone, but with less continental water influence (Text-fig. 5b). *Neocyprideis* and nearby gypsum are also observed, pointing sometimes even to hypersaline conditions.



Text-fig. 5a—Percentages of non-marine species (black squares) and specimens (striped circles) in samples of the *Oertliella dextrospinata* (UC-7) Zone (Late Turonian-Early Coniacian).

5b—Various ostracod biotopes in the *Oertliella dextrospinata* (UC-7) Zone.

Fresh-brackish water. From left to right: *Candoniella*? *C. qeturaensis*, *Neocyprideis flexeri*.

Brackish water–transitional marine. From top to bottom:

Neocyprideis flexeri, *Xestoleberis*? *X. derorimensis*, *Limburgina galvensis*.

Hypersaline: *Neocyprideis flexeri*.

Shallow marine water. From left to right:

(Upper row) *Cythereis menuhaensis*, *Oertliella dextrospinata*, *Paracypris* sp., *Bairdia* cf. *B. cenomanica*, *Bairdoppilata cuvillieri omnipraesens*, *Cytherella* sp.

(Lower row) *Metacytheropteron* cf. *M. pagana*, *Cristaeleberis prisca*, *Spinoleberis yotvataensis macra*, *Nucleolina zihorica*, *Dumontina*? *D. almussatensis*, *Cytherelloidea glabra*.

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The authors express their thanks to Dr. Y. Mimran for critical reading of the manuscript, Mr. M. Dvorachek and Mr. Y. Levy, all from the Geological Survey of Israel, for the SEM photographs.

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DISCUSSION

Paik: What type of rocks did you examine in your study? How about population density?

Rosenfeld: Soft rocks, such as shales, tuffs, marls and marly limestones were examined. Population density in the Early Jurassic zone is very low, but in the Cretaceous zones non-marine ostracods are common to frequent. The population density is very high in sediments of hypersaline milieu where ostracods sometimes build whole rocks.

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Distribution and Diversity of Nearshore Ostracoda: Environmental Control in the Early Permian

ROGER L. KAESLER AND LARRY E. DENVER
University of Kansas, Lawrence, U.S.A.

ABSTRACT

Limestone and shale beds in the lower Americus Limestone (Permian, Wolfcampian) of the Midcontinent of North America were deposited in four contemporaneous environments: tidal flat, incipient lagoon, carbonate shoal, and open-marine shelf. Morphology of tabular cryptalgal limestones in the basal few centimeters of the Americus suggests that the four environments developed quite early in the depositional history of the Americus. An abundant but low-diversity, characteristically nearshore ostracode fauna of sixteen species was extracted from the cryptalgal limestones by crushing them and then following standard micropaleontological procedures. The dominant species in the ostracode assemblages are *Paraparchites humerosus, Sansabella bolliaformis,* and *Bairdia beedei.* All three are typical of rocks deposited in nearshore, Midcontinent environments of the Late Pennsylvanian and Early Permian. In terrigenous rocks, however, they are rarely dominant. On the other hand, such species as *Cavellina nebrascensis, Hollinella bassleri, Pseudobythocypris pediformis,* and *Healdia simplex,* the typically dominant species in nearshore terrigeous rocks, are comparatively rare in these cryptalgal limestones. *Paraparchites humerosus* was most abundant in the lagoon and adjacent parts of the carbonate shoal and tidal flat. *Sansabella bolliaformis* increased in abundance from the tidal flat across the lagoon and the carbonate shoal to the open-marine shelf. *Bairdia beedei* is less common than the other two dominant species. It was least abundant on the carbonate shoal and increased in abundance both landward onto the tidal flat and seaward toward the open-marine environment. The index of species diversity from information theory increases from the tidal flat to the open-marine environment.

INTRODUCTION

As a result of the development of carbonate petrology during the past three decades, environments of deposition of most limestones are readily discernible petrographically. On the other hand, study of such fine-grained terrigenous rocks as shale, mudstones, and claystones, many of which are source rocks for petroleum, has not kept pace with carbonate petrology. The environments of deposition of these rocks are still best determined by study of their enclosed microfossils, including the ostracodes. Thin-section petrology of shale is grim work indeed, and it is rarely productive.

No doubt the use of ostracodes to determine environments of deposition has stimulated our science; an appreciable proportion of the work reported at this symposium, for example, would not have been done were it not for the impetus of the petroleum industry. Nevertheless, the lack of a well-developed science of shale petrology analogous to carbonate petrology and the utilitarian aspect of the study of ostracodes have been a mixed blessing. On the one hand, they have provided a wealth of biostratigraphical and paleogeographical information. On the other, they have in large part thwarted the development of a comprehensive paleoecology of the Ostracoda. The rocks that are best understood paleoenvironmentally, the limestones, rarely yield identifiable ostracodes. Yet our understanding of the paleoenvironments of rocks that yield most ostracodes, the shales, is determined by studying the ostracodes themselves. Thus, a degree of freedom is lost, and the ostracode paleoecologist is typically at risk of what has euphemistically been called *reciprocal illumination,* termed *circular reasoning* in most circles.

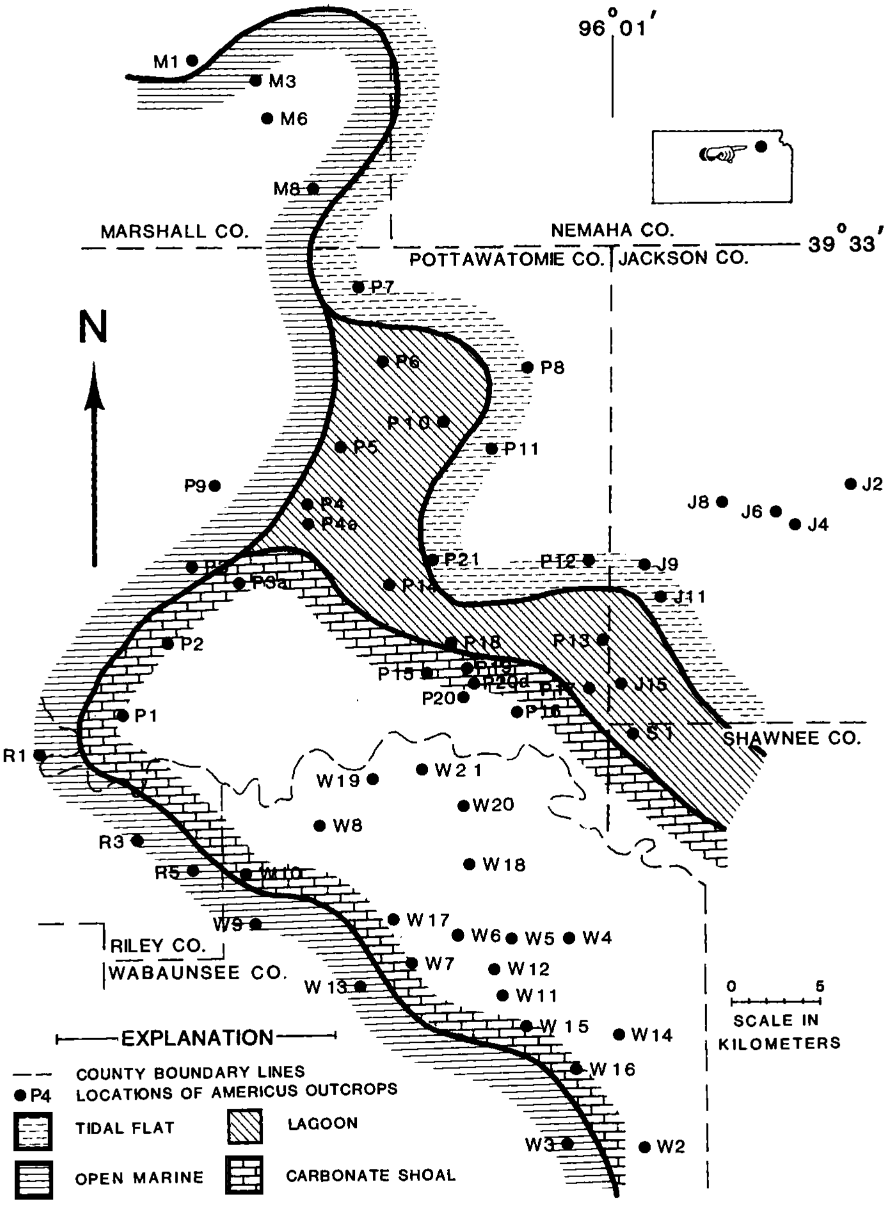
We contend that the paleoecology of ostracodes will be enhanced if more effort is directed to the study of ostracodes from limestones, especially limestones that have been analysed petrographically. Our purpose here is to report the results of such a study of nearshore, Early Permian, cryptalgal limestones from the North American Midcontinent (Text-fig. 1) from which an abundant, low-diversity ostracode fauna was extracted by crushing. We show that each of the three dominant species in the assemblage responded differently to subtle differences in environments of deposition, which ranged from a tidal flat to a shallow, open-marine environment and included a carbonate shoal and an incipient lagoon. The joint occurrences of these three species and other, rarer ones produced an assemblage with a species diversity that is predictable from independent knowledge of the environment of deposition as determined by carbonate petrology.

Until fairly recently, study of the thin, widespread, cyclothemic, late Paleozoic rocks of the Midcontinent of North America has typically stressed vertical change and lateral similarity of lithology and environments of deposition. This circumstance stems in part from the underlying philosophy of the founding fathers of Midcontinent geology (see, *e.g.*, Moore, 1964), which was itself colored by an outcrop pattern that closely parallels depositional strike. The Lower Permian Americus Limestone Member of the Foraker Limestone (Text-fig. 2), however, provides a splendid opportunity to depart from this pattern of study and to investigate environments of deposition in three dimensions. The outcrop pattern of the Americus Limestone in northeastern Kansas is controlled in part by the surface expression of the buried, late Paleozoic, Nemaha anticline (Kluth and Coney, 1981). As a result, it is well exposed in three dimensions over an area of nearly 2,000 square kilometres.

Fisher (1980) has done the most recent and comprehensive study of the carbonate petrology of the Americus Limestone. In rocks of the lower part of the Americus he found evidence of four environments of deposition (Text-fig. 1): tidal flat, lagoon, carbonate shoal, and open-marine shelf. More recently, Peterson and Kaesler (1980) studied assemblages of ostracodes in shales from the localities sampled by Fisher.

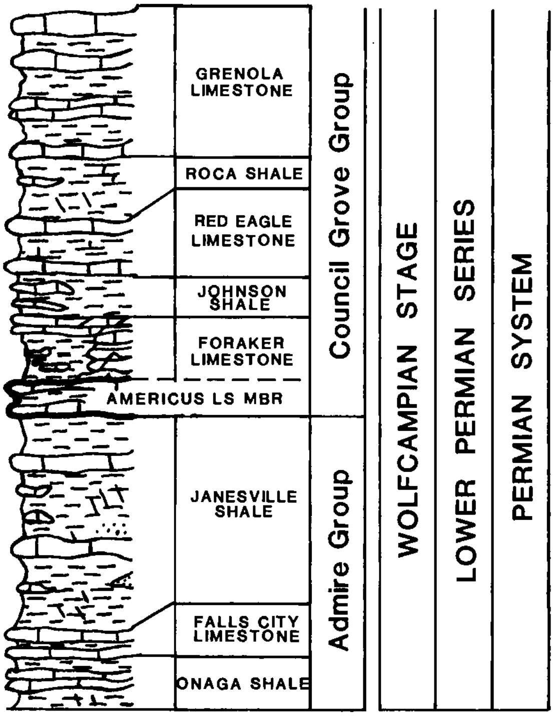
Throughout north-central Kansas the lowermost bed of the Americus is a cryptalgal limestone that ranges in thickness from 2 to about 15 cm. Denver (1985) studied microfacies of the cryptalgal limestones. Associated with the cyanobacteria that formed the cryptalgal structures he found numerous ostracodes, tiny gastropods, encrusting foraminifers, and *Spirorbis* worm tubes. The ostracodes are the subject of this investigation.

Fisher (1980) based his paleoenvironmental interpretations on study of the entire lower portion of the Americus, not on the cryptalgal limestones alone. He attributed the environmental differentiation that took place during deposition of the lower Americus to minor tectonic activity along the Nemaha anticline, perhaps accentuated by differential compaction of underlying shale beds. His interpretation is supported by Denver's (1985) findings. The four environments of deposition that Fisher recognized occur in the basal cryptalgal limestone bed as well as higher in the section, although neither the carbonate shoal nor the lagoon were as well differentiated at the beginning of Americus deposition as later.

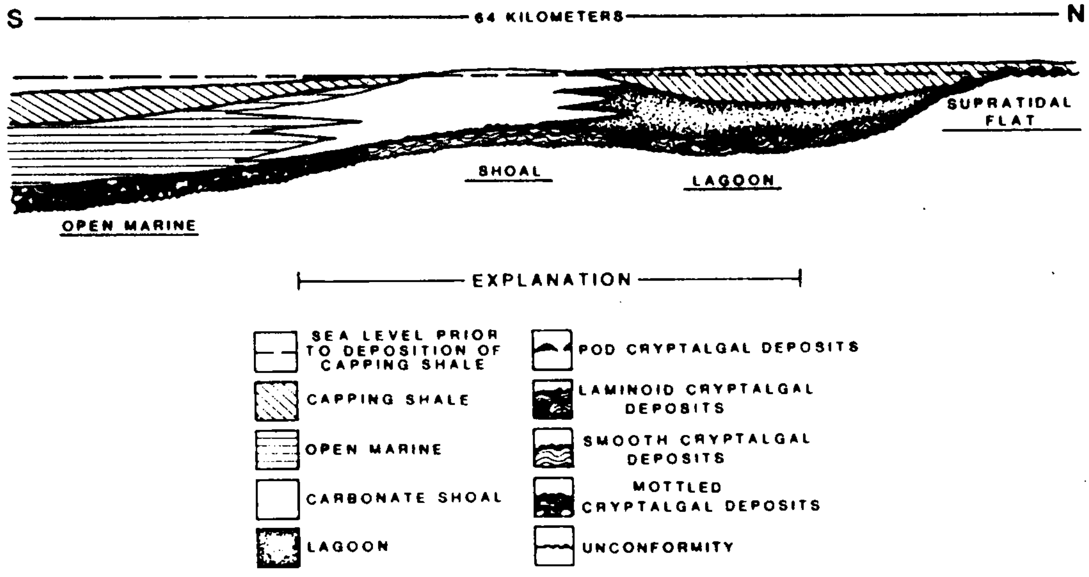


TEXT-FIG. 1—Location map of study area in northeastern Kansas showing numbers of outcrops studied, not all of which were sampled, and geographical extent of the tidal flat, lagoon, carbonate shoal, and open-marine shelf (after Fisher, 1982).

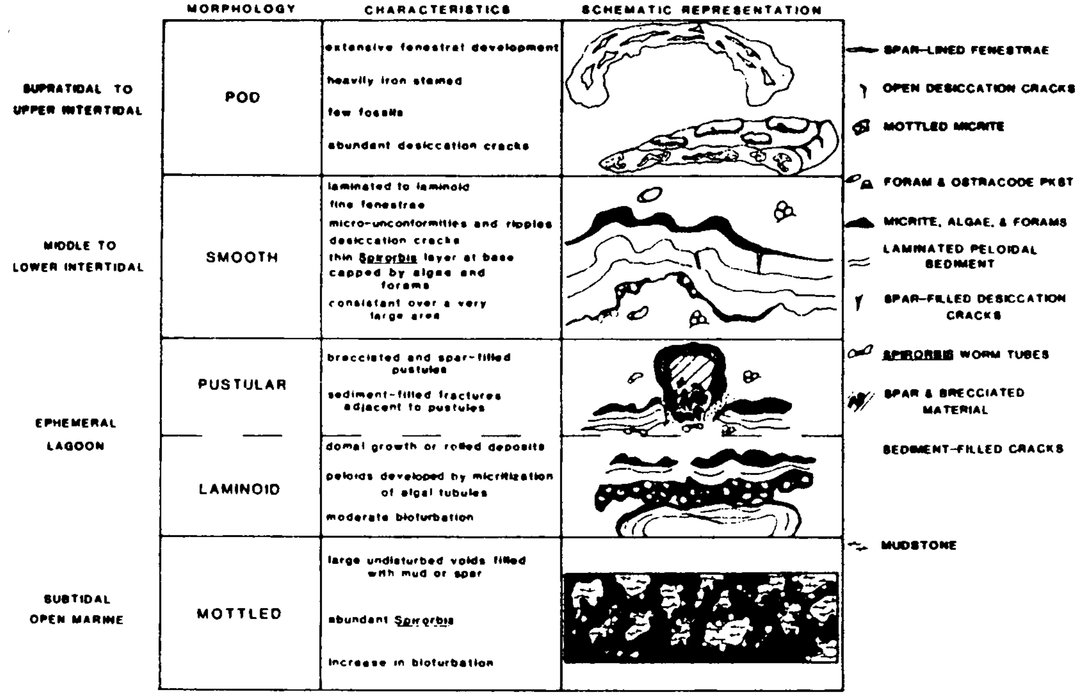
The four environments of deposition are shown in Text-fig. 3, a diagrammatic cross section from north to south across the study area. These environments are marked by distinctly different morphologies of the cryptalgal deposits, shown schematically in Text-fig. 4. The supratidal to



TEXT-FIG. 2—The Americus Limestone Member and related stratigraphical units (after Zeller, 1964).



TEXT-FIG. 3—Schematic cross section through the study area showing configuration of depositional environments, locations of types of cryptalgal morphologies, and position of sea level prior to deposition of the shale that caps the lower Americus Limestone beds. Evidence of the four depositional environments in the basal cryptalgal limestone bed demonstrates that the environments were differentiated quite early in Americus deposition (after Fisher, 1980).



TEXT-FIG. 4—Morphologies and characteristics of cryptalgal deposits from four nearshore environments.

upperintertidal part of the tidal flat is characterized by cryptalgal structures with pod morphology. This morphology is marked by the occurrence of spar-lined fenestrae, open desiccation cracks, and mottled micrite. Cryptalgal structures with smooth morphology occur in the middle to lower intertidal environments of the carbonate shoal. Such structures are characterized by laminated peloidal sediment, spar-filled desiccation cracks, *Spirorbis* worm tubes, micrite with associated algae and foraminifers, and an overlying foraminifer-ostracode packstone. The lagoonal environment, which was probably quite ephemeral early in its depositional history, was the site of deposition of both pustular and laminoid cryptalgal structures with *Spirorbis,* domal and rolled cryptalgal structures, spar and brecciated material, and sediment-filled cracks. Rocks of the open-marine environment are characterized by mottled cryptalgal deposits that have large, undisturbed voids now filled with mud or spar, abundant *Spirorbis,* and evidence of more bioturbation than occurred in the other environments.

MATERIALS AND METHODS

Ostracode-bearing samples of cryptalgal limestone about 10 cm square were collected at twenty-five of the localities studied by Fisher (1980) and subsequent authors. Following microstratigraphical and petrological study (Denver, 1985), a portion of each limestone sample was crushed to a maximum size of about 4 mm using a small crusher with ceramic jaws and cheeks. The crushed

TABLE 1—RESULTS OF CRUSHING AND FURTHER PROCESSING TWO SAMPLES OF CRYPTALGAL LIMESTONES FROM LOCALITIES P14 AND W18. SIEVE MESH SIZES ARE U.S. STANDARD SERIES SIZES.

Status	Mass of Samples	
	P14	W18
before crushing	329 g	815 g
after initial washing in water		
20< size	267 g	671 g
40< size <20	20 g	39 g
60< size <40	11 g	21 g
80< size <60	5 g	11 g
100< size <80	2 g	3 g
sum	305 g	745 g
100< size (washed away)	24 g	70 g
processed with Amosol		
20< size	252 g	670 g
40< size <20	23 g	35 g
60< size <40	13 g	21 g
80< size <60	7 g	11 g
100< size <80	3 g	3 g
sum	298 g	740 g
100< size (washed away)	7 g	5 g
processed with Quaternary-O		
20< size	241 g	634 g
40< size <20	19 g	34 g
60< size <40	11 g	20 g
80< size <60	5 g	10 g
100< size <80	1 g	2 g
sum	277 g	700 g
100< size (washed away)	21 g	40 g
	ostracods per gram	
original, unprocessed	8.2/g	3.6/g
fully processed, total	9.7/g	4.2/g
fully processed, size <20	74.7/g	44.3/g

material was washed through sieves and processed with both Amosol (Stoddard's solvent) and Quaternary-O using standard micropaleontological procedures. Table 1 gives results of analyses of two of the samples, P14 and W18, to show how the effectiveness of various procedures of processing limestones. The number of identifiable ostracodes found in the samples varied from about 4 per gram to about 10 per gram. Processing the samples with Amosol and Quarternary-O reduced the mass of material to be picked by 5 or 10 percent over washing with water. It also provided cleaner, more easily identified ostracodes. From each of the twenty-five samples, 100 ostracodes were selected at random for study.

We have not assessed whether crushing limestones biases samples and produces a distorted view of the ostracode assemblage. We suspect intuitively that during crushing smooth ostracodes pop out of limestone more readily than ornamented ones. Most late Paleozoic ostracodes from nearshore environments of the Midcontinent, however, are smooth. Many of our samples included a few ornamented ostracodes belonging to such genera as *Hollinella, Kindlella,* and *Monoceratina,* but whether these were found in the same proportions in which they occur in the rock is not known.

Indices of species diversity (H) from information theory (Brillouin, 1961; Pielou, 1977; Kaesler and Mulvany, 1977) were used to help assess the structure of the ostracode portion of the community associated with the cryptalgal limestones.

RESULTS AND DISCUSSION

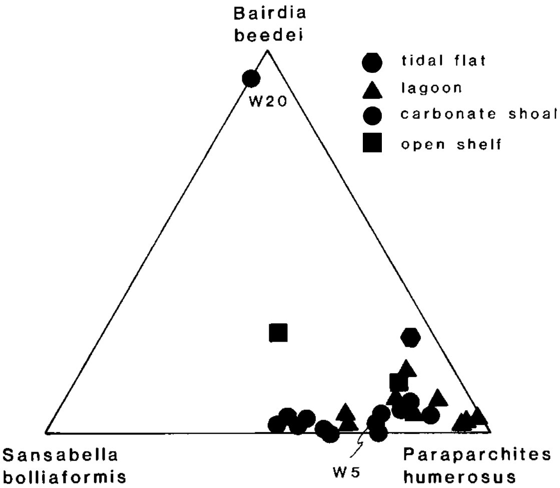
The 2,500 ostracodes selected for study comprise sixteen species (Table 2). Such low species richness is typical of nearshore, late Palaeozoic ostracode assemblages. The fauna includes many of the species found in previous studies of terrigenous depositional environments of the Midcontinent (Brondos and Kaesler, 1976; Haack and Kaesler, 1980; Peterson and Kaesler, 1980; Melchert, 1982). In general, however, the fauna is dominated by different species from those that are most abundant in terrigenous rocks. Faunas of nearshore terrigenous mudstones, for example, typically contain abundant *Cavellina nebrascensis, Hollinella bassleri, Pseudobythocypris pediformis,* and *Healdia simplex.* In our samples these species are comparatively rare, and none comprises more than 2.5 percent of the total fauna (Table 2).

TABLE 2—SPECIES FOUND, AUTHORS, TOTAL NUMBERS, AND MEAN PERCENTAGE OF FAUNA.

Species and Author	Number	Percentage (%)
Paraparchites humerosus Ulrich & Bassler	1,600	64.0
Sansabella bolliaformis (Ulrich & Bassler)	504	20.1
Bairdia beedei Ulrich & Bassler	236	9.3
Cavellina nebrascensis (Geinitz)	60	2.4
Pseudobythocypris pediformis (Knight)	25	1.0
Kindlella sp.	15	0.6
Bairdia acuminata Cooper	14	0.6
Fabalicypris acetalata (Coryell & Billings)	14	0.6
Hollinella bassleri (Knight)	12	0.5
Healdia simplex Roundy	5	0.2
Cryptobairdia folgeri (Kellett)	4	0.2
Carbonita sp. cf. *C. inflata* (Jones & Kirkby)	4	0.2
Monoceratina lewisi Harris & Lalicker	3	0.1
Acratia typica Delo	2	0.1
Bairdia sp.	1	0.1
Genus A species A	1	0.1
Total	2,500	100.0

The ostracode assemblages collected from cryptalgal deposits of the Americus Limestone are dominated by three species: *Paraparchites humerosus, Sansabella bolliaformis,* and *Bairdia beedei.* These species comprise, respectively, 64 percent, 20 percent, and 9 percent of the total fauna. A ternary diagram in which the sums of these species are adjusted to 100 percent shows subtle differences in their relative abundances (Text-fig. 5) that appear to be strongly correlated with depositional environment. The two samples from the open-marine shelf (shown by squares) are comparatively rich in *B. beedei.* The same is true of the single sample from the tidal-flat environment (hexagon), although this result is somewhat surprising given *Bairdia's* preference for environments with normal-marine salinity.

With one notable exception, samples from the carbonate shoal (circles) tend to have lower relative abundances of *Bairdia beedei* than samples from the lagoon (triangles). Analysis of microfacies of the cryptalgal structures of the carbonate shoal suggests that the shoal was frequently subaerially exposed (Denver, 1985). If so, it is not surprising that *B. beedei* was less well adapted to survive there than in the lagoon or open-marine environments. Note, however, that both lagoonal and carbonate shoal samples tend to contain proportionately more *B. beedei* as the relative abundance of *Paraparchites humerosus* increases (toward the *P. humerosus* corner of the ternary diagram).



TEXT-FIG. 5—Ternary diagram with percentages of the four dominant species adjusted to 100 percent.

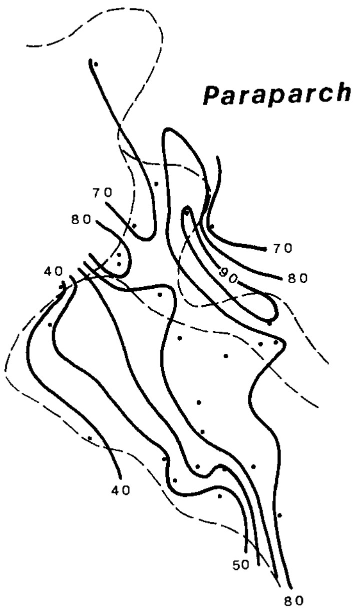
It is not clear if the two species interacted biologically or environmentally or if this apparent correlation is an artifact caused simply by lower relative abundances of *Sansabella bolliaformis.*

The notable exception mentioned above is sample W20. It is plotted near the *Bairdia beedei* apex of the ternary diagram (Text-fig. 5), which species comprises about 90 of its ostracode assemblage. Sample W20 is from the heart of the carbonate shoal where *B. beedei* is expected to be rare. The sample's apparently aberrant faunal assemblage defies explanation at this time.

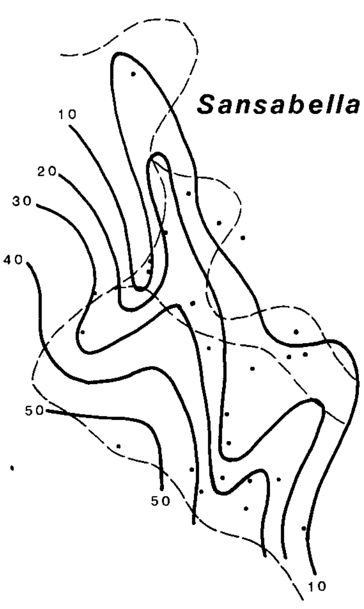
Except for sample W5 (see Text-fig. 1 for location), the group of six carbonate shoal samples that lie along the middle of the base of the ternary diagram (circles) are from the seaward margin of the carbonate shoal. This is a region in which *Paraparchites humerosus* and *Sansabella bolliaformis* are nearly equally dominant but in which *Bairdia beedei* is quite rare or altogether absent.

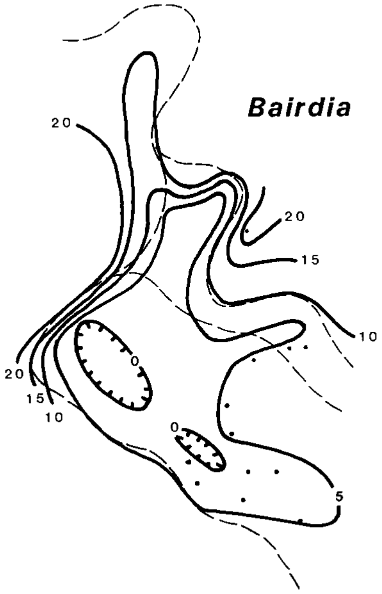
Paraparchites humerosus is the most abundant species in our samples. It comprises 64 percent of the total ostracode fauna and as much as 92 percent of the ostracodes from some samples. Text-fig. 6 shows its distribution by percentage contoured with an interval of 10 percent. *P. humerosus* was most abundant in the lagoon and adjacent parts of the tidal flat and carbonate shoal. Its abundance diminished across the carbonate shoal toward the open-marine environment. It also appears to have been quite abundant at the mouth of the lagoon where lagoonal waters are in contact with open-marine waters, although sampling density in that area is not sufficient to confirm this observation. Its abundance on the carbonate shoal and distal portions of the tidal flat suggests that *P. humerosus* could withstand at least brief intervals of subaerial exposure. The abundance of *P. humerosus* throughout the study area, moreover, suggests that it may have fed on the cyanobacteria that formed the cryptalgal structures. Some early Palaeozoic leperditacean ostracodes, with which *P. humerosus* is morphologically convergent, were confined to nearshore environments and may have had a similar mode of life. The sample from locality W20, which has a fauna rich in *Bairdia beedei,* contained no *P. humerosus* and was ignored when Text-figs. 6 to 8 were contoured.

Sansabella bolliaformis is the second most abundant species in our samples. It comprises 20 percent of the total ostracode fauna and ranges from 3 to 57 percent of the assemblages from individual samples. Text-fig. 7 shows its distribution across the study area contoured with an interval of 10 percent. It was least abundant on the tidal flat, where it comprised less than 10 percent of the ostracode fauna. It was also relatively rare near the mouth of the lagoon, although whether this condition prevailed into the open-marine environment near the mouth of the lagoon could



TEXT-FIG. 6—Percentage *Paraparchites humerosus* comprises of samples, contoured with an interval of 10 percent. Dashed lines mark boundaries of environments of deposition.





TEXT-FIG. 7 (*left*)—Percentage *Sansabella bolliaformis* comprises of samples, contoured with an interval of 10 percent. Dashed lines mark boundaries of environments of deposition.

TEXT-FIG. 8 (*right*)—Percentage *Bairdia beedei* comprises of samples, contoured with an interval of 5 percent. Dashed lines mark boundaries of environments of deposition.

TABLE 3—SAMPLE NUMBERS, ENVIRONMENT OF DEPOSITION, SPECIES RICHNESS (S), AND BRILLOUIN'S (1962) INDEX OF SPECIES DIVERSITY (H).

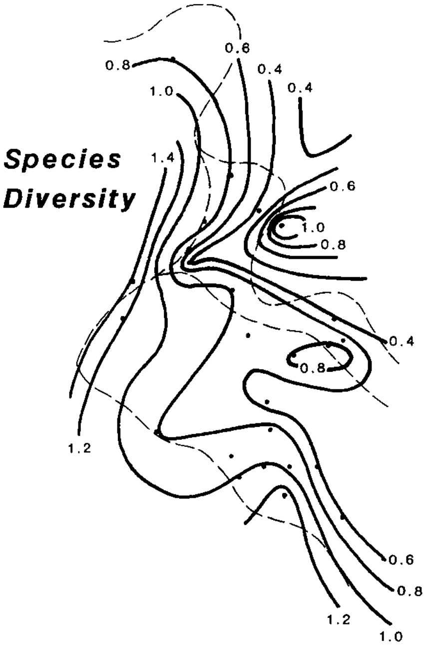
Sample Number	Environment of Deposition	Species Richness (S)	Species Diversity (H)
P11	tidal flat	9	1.13
P4	lagoon	5	0.64
P4A	lagoon	5	0.40
P5	lagoon	5	0.86
P6	lagoon	6	0.84
P10	lagoon	5	0.33
P13	lagoon	5	0.36
P14	lagoon	5	0.83
P17	lagoon	5	0.75
J15	lagoon	5	0.67
mean	lagoon	5.1	0.63
P2	carbonate shoal	5	1.19
P15	carbonate shoal	3	0.67
P16	carbonate shoal	5	0.77
W4	carbonate shoal	3	0.61
W5	carbonate shoal	6	0.90
W6	carbonate shoal	6	1.01
W7	carbonate shoal	8	1.01
W10	carbonate shoal	5	0.83
W11	carbonate shoal	7	1.33
W14	carbonate shoal	4	0.58
W17	carbonate shoal	6	0.94
W18	carbonate shoal	6	0.89
W20	carbonate shoal	4	0.53
mean	carbonate shoal	5.2	0.87
P3	open-marine shelf	10	1.39
M6	open-marine shelf	6	0.84
mean	open-marine shelf	8	1.12

not be determined. In general, *S. bolliaformis* increased in relative abundance seaward across the carbonate shoal.

The distribution and relative abundance of *Bairdia beedei* are shown in Text-fig. 8, which is contoured with an interval of 5 percent. *B. beedei* was absent from some areas of the carbonate shoal and had quite a low relative abundance in others, suggesting its typically bairdiacean preference for normal-marine conditions and its inability to withstand subaerial exposure. Its abundance increased seaward toward the open-marine environment. It was also somewhat more abundant higher in the lagoon. The fairly high relative abundances in some parts of the tidal flat are difficult to explain but suggest strong influence of marine waters in that region.

Thirteen other species were found, many of which are characteristic of late Paleozoic, nearshore environments (Table 2). One must exercise caution in interpreting their distributions, however. These species range in abundance from 2.4 percent to as low as 0.04 percent of the total fauna. Whereas the presence of such rare species might indicate specific environmental conditions, their absence does not necessarily convey any information at all. Instead, a rare species might be absent from a picked sample *by chance alone*. Dennison and Hay (1967) have computed the probability of failing to collect rare species due to sampling error. With a sample size of 100, the probability of failing *by chance alone* to find species that comprise 1 percent or less of the fauna is 0.366, quite a high probability of failure indeed. The *chance* of failing to find species that comprise 2.5 percent or less of the fauna is 0.08. One begins to gain confidence in the sampling only of more abundant species. For example, the probability of missing *by chance alone* species that comprise 5 percent of the fauna is quite low: 0.006. The implications of this for such studies as ours are clear. Species that make up less than 2.5 percent of the fauna—that is, all species except the three dominant ones—are quite likely to be absent from individual samples by chance rather than as a result of their ecology. Tripling the sample size to 300 would have improved the meaning of presence and absence of the rare species, but such action was precluded by the paucity of ostracodes in the samples.

An index of species diversity is a statistic that includes *or confounds* information on both the number of species (species richness) and the evenness with which they are distributed *in a sample* (Pielou, 1977, p. 292). Both species richness and species diversity of late Paleozoic marine ostracodes tend to be low in nearshore environments. In our samples, species diversity (Brillouin, 1962) ranges from 0.33 at locality P10 near the mouth of the lagoon to 1.39 at P3 in the open-marine environment (Table 3). In general samples from the carbonate shoal, with a mean diversity of 0.87, have higher species diversity than samples from the lagoon (mean = 0.63). Few samples were collected from either the open-marine environment or the tidal flat. The open-marine samples, nevertheless, have high species diversity as was expected (mean = 1.12). The only sample from the tidal flat (P11) has a surprisingly high species diversity of 1.13. Sample P11 also has a high species richness of 9 and one of the highest relative abundances of *Bairdia beedei*. Text-figure 9 summarizes species diversities,which are contoured with an interval of 0.2. Species diversity was generally quite low in the main body of the lagoon and increased both toward the mouth of the lagoon and across the carbonate shoal toward the open-marine environment. More work is needed on the tidal flat and the open-marine setting to determine the distribution of speciese diversities.



Text-fig. 9—Species diversity (Brillouin, 1962) contoured with an interval of 0.2. Dashed lines mark boundaries of environments of deposition.

CONCLUSIONS

1. Low values of both species richness and species diversity of ostracodes from cryptalgal limestones deposited in a nearshore setting are consistent with what is known of ostracode faunas from nearshore terrigenous environments.

2. The fauna is dominated by *Paraparchites humerosus, Sansabella bolliaformis,* and *Bairdia beedei* instead of the species that are typically dominant in nearshore terrigenous rocks. These three species are present but rarely dominant in nearshore terrigenous rocks.

3. *Paraparchites humerosus,* the most common species, has its greatest abundance in the lagoon and adjacent parts of the tidal flat and carbonate shoal. It seems likely that it could withstand periods of subaerial exposure and that it may have fed on cyanobacteria that formed the cryptalgal deposits.

4. *Sansabella bolliaformis* was least abundant on the tidal flat and increased in abundance across the lagoon and carbonate shoal toward the open-marine shelf. It was apparently not abundant, however, at the mouth of the lagoon where lagoonal waters met open-marine waters. *S. bolliaformis* may also have been able to withstand subaerial exposure.

5. *Bairdia beedei* was rare or absent on the carbonate shoal and more abundant both on the tidal flat and toward the open-marine shelf. Its rarity on the carbonate shelf suggests that it was unable to withstand subaerial exposure.

6. Species diversity was lowest in the lagoon and increased across the carbonate shoal and toward the mouth of the lagoon. Diversity was also high in the only sample from tidal-flat rocks.

7. Development of paleoecology of ostracodes from carbonate environments is enhanced by use of carbonate petrology and careful microfacies analysis.

ACKNOWLEDGMENTS

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Field work and subsequent laboratory research were supported by the Wallace E. Pratt fund from the Exxon Foundation, administered by the Department of Geology of The University of Kansas. All ostracode specimens have been deposited with the Museum of Invertebrate Paleontology of The University of Kansas as numbers 1,104,380 to 1,106,879. Slabs and thin sections of the cryptalgal limestones are also in the Museum with numbers 214,782 to 214,969.

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DISCUSSION

Adamczak: What kind of sedimentary structure did you observe in the rocks examined? Since the environment is of near shore character, you should have a lot of tempestites and such sediments indicate that the fauna is mixed.

Kaesler: First let me reiterate that these ostracodes occur in cryptalgal laminites, that is, low-relief, tabular stromatolites. The algal mat from which the cryptalgal structures were formed, was in places ripped up or rolled, probably as a result of storms. Nevertheless, the relief of the ancient seafloor on which the algal mat formed was so low that the storm waves were damped for the most part. By all means there is some mixing of these faunas, but once the ostracodes are stuck down by the cyanobacterial filaments, they are essentially immobile.

Schweitzer: Does the species diversity index include the rare species?

Kaesler: The index of species diversity we used is that of Brillouin which comes from information theory. It gives the diversity per species of a fully censused sample. The key words here are *fully censused and sample.* Yes, rare species are included because the sample must be fully censused, that is, all species must be distinguished and all individuals assigned to a taxon.

Schweitzer: Conclusions about lateral changes in abundance must be tempered with caveats when abundance is normalized to percentages.

Kaesler: Percentages are ratios. You are correct that they must be used with caution and can lead to spurious correlations. I think we have used the term *relative abundance,* which sufficiently tempers our conclusions with caveats.

Lower Carboniferous Ostracode Assemblages from Nova Scotia

CHRIS P. DEWEY
Mississippi State University, Mississippi State, U.S.A.

ABSTRACT

During the Lower Carboniferous, the Maritime Basin of eastern Canada was a tectonically active fluvial basin that was subjected to intermittent transgressive events. The duration and extent of the transgressive pulses was a function of both intrabasinal tectonics and eustatic sea level changes.

Windsor Group sediments from three carbonate marine environments in the Minas and Antigonish sub-basins of Nova Scotia were studied for their ostracode content.

The most diverse fauna was derived from an offshore, near normal salinity, bioclastic limestone. *Bairdia* spp., *Bairidacypris quartziana* and *Kirkbya* n. sp. A are the main ostracodes present, but other indicators include *Beyrichiopsis cornuta, "Gortanella"* sp. and *Monoceratina youngiana.* It is significant that paraparchitaceans are not very abundant in this assemblage.

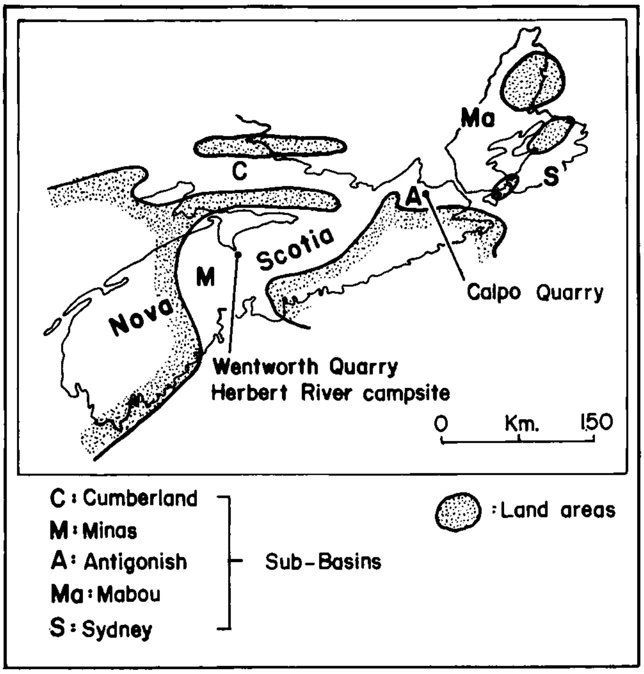
A less diverse fauna occurs in a bioclastic limestone that developed on a drowned topographic high. The fauna is dominated by paraparchitaceans such as *Chamishaella suborbiculata* and *Shishaella moreyi. Bairdia* sp. L. and *Amphissites* sp. aff. *A. centronotus* are also present but not common. This association suggests a more stressed environment.

The most restricted fauna was collected from the carbonate member of a carbonate-siltstone-gypsum triplet. Only five species are present, with *Beyrichiopsis lophota* and *Paraparchites* sp. aff. *P. kellettae* forming more than 90% of the preserved fauna. This assemblage represents the most saline and most restricted environment studied.

In the Maritime Basin the combined effects of a semi-arid climate, eustacy and tectonism resulted in low temporal and spatial stability. The transgressive pulses that affected the area were mostly short-lived, of limited geographical extent and often associated with hypersalinity. High grade faunal communities would therefore not be expected to develop under these conditions.

INTRODUCTION

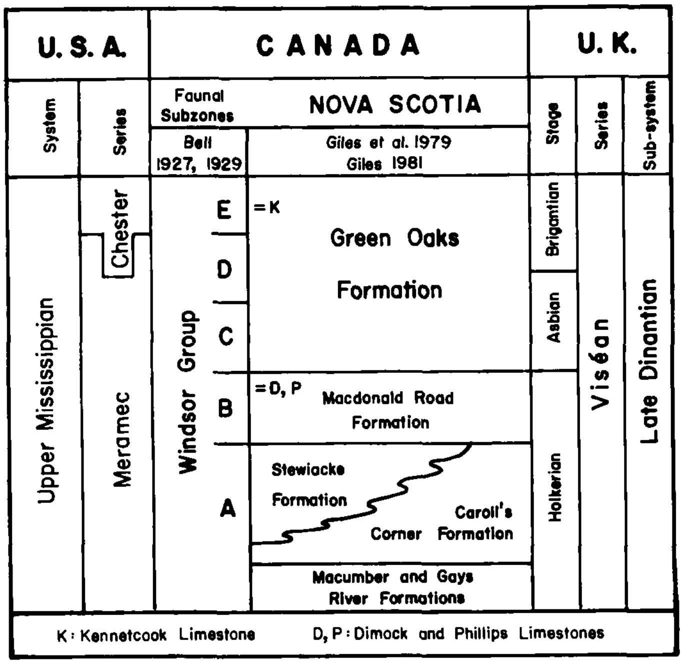
Marine sediments of the Lower Carboniferous Windsor Group in Maritime Canada were deposited within a series of interconnected, tectonically active sub-basins. Together the sub-basins formed a larger Late Palaeozoic structure known as the Maritime Basin, which included parts of New Brunswick, Nova Scotia, Newfoundland and Prince Edward Island. In this paper, only ostracodes from the Minas and Antigonish Sub-Basins of Nova Scotia will be discussed (Text-fig. 1). The Windsor Group sediments of Nova Scotia consist of thick fluvial sequences intercalated with marine deposits which are often associated with evaporites. Due to tectonic instability, sedimenta-



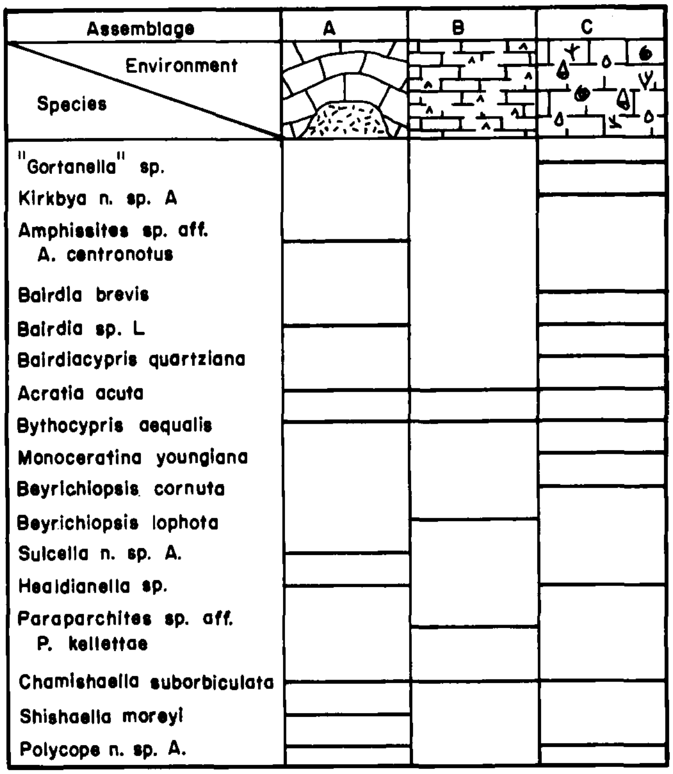
TEXT-FIG. 1—Location map of study area showing depositional sub-basins of Nova Scotia and sampling localities.

tion was neither continuous within, nor sychronous among the various sub-basins (Giles, 1981). Inter-sub-basinal correlation has therefore been a matter of much debate; however, a mega-faunal zonation (Bell, 1927, 1929) and formal lithostratigraphic subidivisions (Giles, *et al.*, 1979; Giles, 1981) have been developed for the Windsor Group (Text-fig. 2). The stratigraphic relationships of the Windsor Group with the upper Mississippian of the mid-continental U.S.A. and the Visean of Europe (Text-fig. 2) are based mostly on foraminifera and palynomorphs, (Mamet, 1979; Utting, 1980; Giles, 1981).

Ostracodes from three transgressive marine units of the Windsor Group form the basis of this study. The oldest ostracodes were collected from a biostromal limestone that occurs within the Gays River Formation in the Antigonish Sub-Basin. Ostracodes from the Phillips and Dimock Limestones were collected from the basal member of carbonate-siltstone-evaporite triplets that occur in the MacDonald Road Formation of the Minas Sub-Basin. The youngest ostracodes studied were collected from the Kennetcook Limestone in the Green Oaks Formation of the Minas Sub-Basin (Text-fig. 2).



TEXT-FIG. 2—Stratigraphical correlation chart for the Windsor Group.



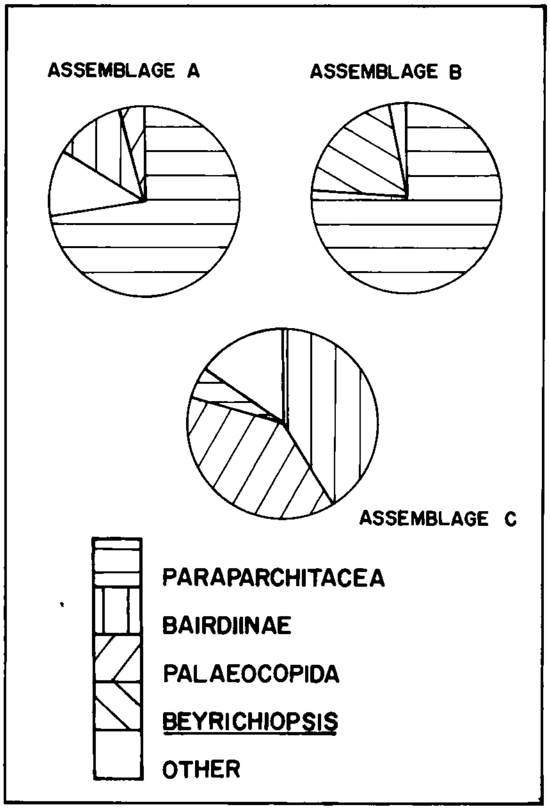
TEXT-FIG. 3—Chart showing assemblage distribution of ostracodes from the Windsor Group.

Ostracode Assemblages

The ostracode assemblages described herein form part of the first ecological study of Mississippian ostracodes from the Maritime Basin of Canada. The Nova Scotia assemblages can be related to similar assemblages described form Newfoundland (Dewey, 1983).

The three Nova Scotia assemblages all represent various types of marine conditions and show the effects that environmental stress can exert upon the ostracode fauna.

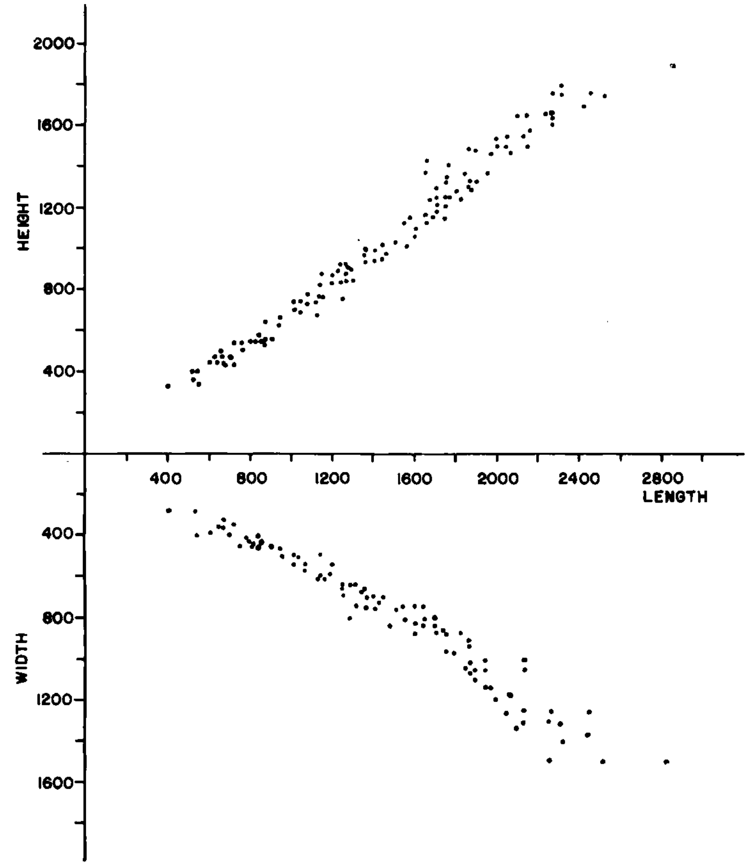
Ostracode assemblage A is based upon material collected from a massive buff-coloured, micritic limestone in Calpo Quarry, Antigonish. The limestone developed as a bioclastic association over a granodioritic pluton, blocks of which may be isolated, or form conglomeratic units within the limestone. A varied mega-fauna of brachiopods, bryozoans, conularids, bivalves and gastropods is found in the limestone, but corals and crinoids are notably absent. The environment of deposition is interpreted as a subtidal, drowned topographic high that occurred during the first marine transgression of Windsor times (Geldsetzer, *et al.*, 1980). Nine species of ostracodes were isolated from the limestone, (Text-fig. 3) and their relative proportions (Text-fig. 4) indicates a paraparchitacean dominated fauna. Almost 75% of the fauna is composed of the paraparchitaceans *Chamishaella suborbiculata* (Munster) and *Shishaella moreyi* Sohn. *Bairdia* sp. L. Sohn forms only about 10%



Text-fig. 4—Relative percentage diagrams for Nova Scotia ostracode assemblages.

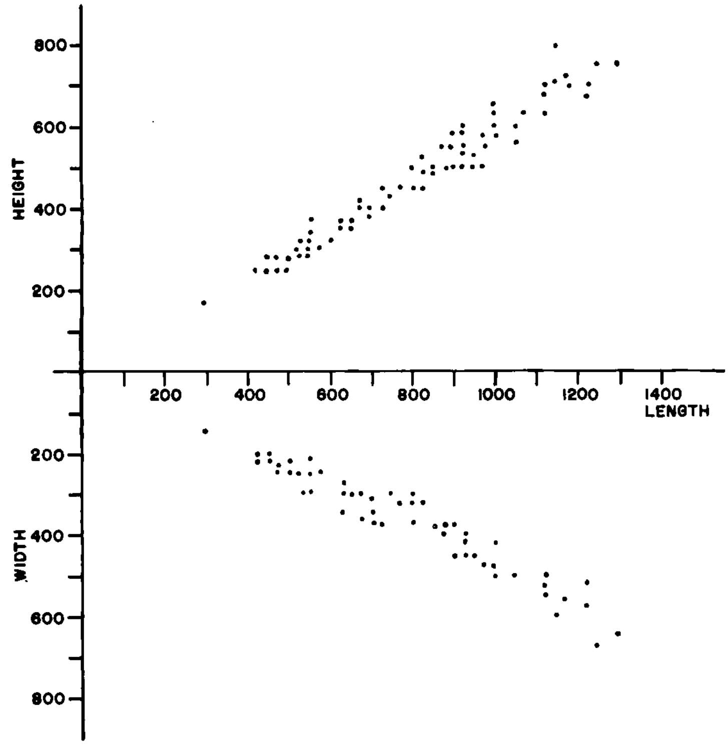
of the fauna and the only palaeocope present is *Amphissites* sp. aff. *A. centronotus* (Ulrich and Bassler), individuals of which represent 3 % of the fauna. None of the other components are significant ecological markers in this assemblage. Ostracode assemblage A is contemporaneous with Newfoundland Assemblage I (Dewey, 1983) and represents a similar, though less diverse fauna. The ostracode association may suggest a nearshore environment; however, the lack of forams, and corals or crinoids in the mega-fauna, together with the overlying evaporites that occur througout the area, also militate in favour of an abnormally saline environment.

Ostracode assemblage B is described from the Dimock and Phillips Limestone units in Wentworth Quarry. The limestones are dark brown/grey micrites that contain ostracodes, rare brachiopods and the ?bryozoan *Palaeocrisidia*. Both the Dimock and Phillips Limestones are overlain by siltstone and thick gypsum/anhydrite units. The repetitive nature of the carbonate-siltstone-evaporite triplets implies a series of transgressive-regressive cycles. The evaporites are considered to be of supratidal sabkha origin and the limestones are thought to represent a marginal marine environment (Geldsetzer, *et al.*, 1980). The limestones yield an ostracode fauna of only five species (Text-fig. 3). More than 75 % of the fauna is composed of *Paraparchites* sp. aff. *P. kellettae* Sohn and *Chamishaella suborbiculata* (Text-fig. 4); however, there are no spinose paraparchitaceans present. The sedimentological evidence associated with this occurrence supports the idea that high abundances of paraparchitaceans in a fauna may be related to a salinity-stressed environment



TEXT-FIG. 5—Growth chart for *Paraparchites* sp. aff. *P. kellettae* from Assemblage B, Nova Scotia. (Measurements are in microns).

(Sohn, 1971; Robinson, 1978; Dewey, 1983). An additional 20% of the fauna is composed of *Beyrichiposis lophota* Copeland, which is closely allied to the European species *B. plicata* Jones and Kirkby. *Beyrichiopsis* is thought to be an indicator of marginal environments (Becker, *et al.*, 1974). Growth curves of *Paraparchites* sp. aff. *P. kellettae* and *Beyrichiopsis lophota* (Text-figs. 5 and 6) indicate that the assemblage is an *in-situ* multigeneration fauna. *Acratia acuta* (Jones and Kirkby), a normally wide ranging species is only present as a few individuals, which may suggest that it is near the end of its ecological tolerance in this environment.



TEXT-FIG. 6—Growth chart for *Beyrichiopsis lophota* from Assemblage B, Nova Scotia (Measurements are in microns).

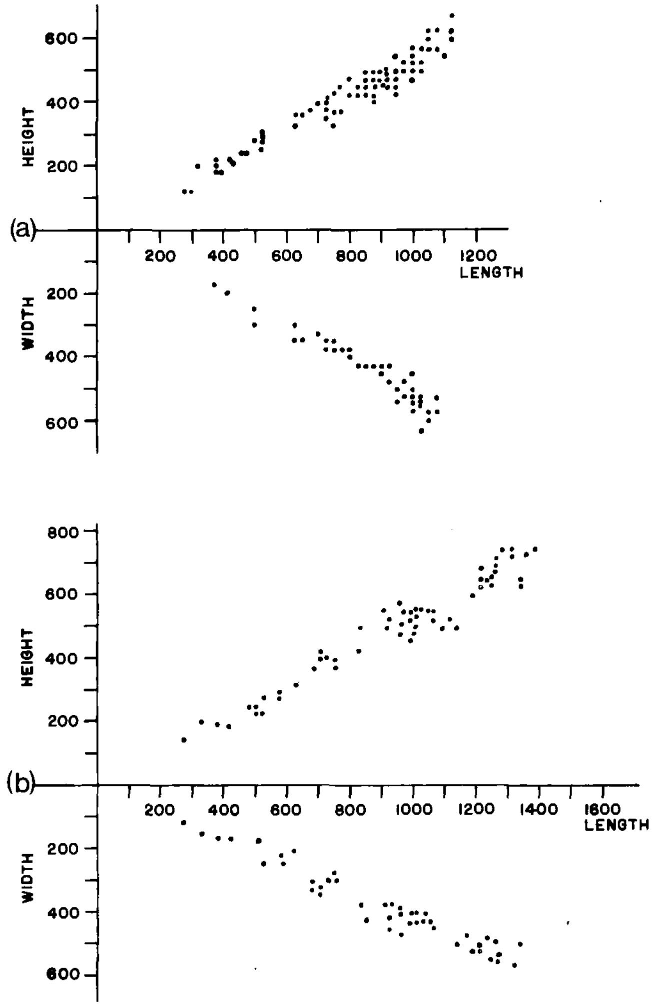
The low diversity and high abundance ostracode fauna is typical of a low level community and the very large numbers of individuals may reflect a lack of inter-specific competition, rather than a rich nutrient supply (Levinton, 1970). The assemblage is therefore interpreted as occurring in a nearshore hypersaline carbonate environment where less tolerant species were unable to survive, whereas the opportunistic eurytopic species would be abe to thrive in abundance.

Ostracode Assemblage C was derived from the Kennetcook Limestone at the Herbert River campsite. The massively bedded buff-coloured bioclastic limestone contains a rich fauna of brachiopods, gastropods, bivalves, bryozoans, corals, tentaculitids and crinoid ossicles as well as forams and twelve species of ostracodes (Text-fig. 3). The environment of deposition is considered to be a low energy, shallow subtidal environment of near normal marine salinity (Moore, 1967). The ostracodes present in the Kennetcook Limestone constitute the most diverse fauna of the present study, although the diversity is not as great as that of Newfoundland Assemblage I (Dewey, 1983).

The most important components of this assemblage are members of the Subfamily Bairdiinae, which, represented by ***Bairdia brevis*** Jones and Kirkby, ***Bairdia*** sp. L. and ***Bairdiacypris quartziana*** Egorov, constitute 42% of the fauna, (Text-fig. 4). Studies of both Recent and Carboniferous species of *Bairdia* (Kornicker, 1961; Kaesler, 1982) indicate that greatest abundances of the genus occur in stable shallow subtidal offshore environments of normal marine salinity.

The second most important group in Assemblage C is the Palaeocopida which accounts for 37% of the fauna. The most common plalaeocope is *Kirkbya* n. sp. A, although rare individuals of "*Gortanella*" sp. and *Beyrichiopsis cornuta* Jones and Kirkby are also present. Carboniferous palaeocopes are thought to be more abundant in nearshore environments, being commonly replaced in the offshore by podocopids, although kirkbyacean palaeocopes may also become important (van Ameron, *et al.*, 1970; Becker, *et al.*, 1974; Kaesler, *et al.*, 1977; Kaesler, 1982). This would account for the rarity of non-kirkbyacean palaeocopes in Assemblage C.

It is significant that the single paraparchitacean species present in Assemblage C, *Chamishaella*



TEXT-FIG. 7—Growth charts for a) *Kirkbya* n. sp. and b) *Bairdia* sp. L. from Assemblage C, Nova Scotia (Measurements are in microns).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suborbiculata accounts for only 5% of the total preserved population. It is probable that paraparchitaceans, which were more adaptable to unstable nearshore conditions, were replaced by bairdiaceans (which are less tolerant of environmental stress) in the more stable environments further from shore (Ferguson, 1962, 1974).

Other minor elements of the fauna include a few individuals of *Monoceratina youngiana* (Jones and Kirbky). The genus *Monoceratina* is often a rare component of ostracode faunas (Roth, 1928; Sohn, 1977) and is frequently associated with fine sediments in shallow marine environments (Donze, 1971; Swain and Kraft, 1975; Sokac, 1977). Also present are several specimens of *Polycope* n. sp. A which by analogy to modern species (Sars, 1928; Elofson, 1941; Joy, 1974) are interpreted as swimming or burrowing benthic ostracodes. A less significant member of the assemblage is bairdiocypridid gen. et sp. indet. which supports the idea that bairdiocypridids often co-occur with *Bairdia* (Becker, *et al.*, 1974). *Acratia acuta* is also present, but is a wide ranging species of little ecological significance.

When examined as a whole, the ostracode associations of this assemblage indicate that the environment of deposition may have been in a shallow subtidal offshore area. The assemblage shows a high carapace to valve ratio, which, combined with the instar series in *Bairdia* sp. L and *kirkbya* n. sp. A (Text-fig. 7) suggests a lack of *post-mortem* transport. The assemblage does not show a very high species diversity; however, the presence of corals, crinoids and foraminifers would suggest that salinity was not a controlling factor. It is more likely that there were fewer niches available for colonisation in this assemblage than in the biohermal Assemblage I from Newfoundalnd (Dewey, 1983).

CONCLUSIONS

Ostracode assemblages described from the three marine transgressive environments in Nova Scotia (Plates 1 and 2) show many faunal characteristics that are similar to those described from Newfoundland (Dewey, 1983). Most ostracode assemblages from both Newfoundland and Nova Scotia are indicative of fairly unstable, nearshore marine conditions. Sedimentological and faunal evidence also supports the notion that the transgressive cycles that produced these conditions were often associated with hypersalinity. The sum of these ecological controls led to the development of predominantly paraparchitacean dominated ostracode faunas in a variety of different nearshore environments (viz: Assemblages I to V in Newfoundland (Dewey, 1983) and Assemblages A and B in Nova Scotia). The only exception to this is Assemblage C in Nova Scotia. In Assemblage C the mega-faunal evidence indicates that salinity was not a major control in the environment, and the ostracode fauna suggests that the environment was sufficiently stable and far enough from shore to allow the devleopment of a *Bairdia* rich fauna.

ACKNOWLEDGEMENTS

I would like to express my gratitude to my Ph. D. supervisor, Lars Fahraeus, for guiding me

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PLATE 1—Fig. 1. "*Gortanella*" sp., right aspect, ×62. Fig. 2. "*Gortanella*" sp., left aspect, ×75. Fig. 3. *Kirkbya* n. sp. A, left aspect, ×60. Fig. 4. *Amphissites* sp. aff. *A. centronotus*, right aspect, ×82. Fig. 5. *Bairdia brevis*, right aspect, ×68. Fig. 6. *Bairdia* sp. L, right aspect, ×44. Fig. 7. *Bairdiacypris quartziana*, right aspect, ×45. Fig. 8. *Acratia acuta*, left aspect, ×62. Fig. 9. *Sulcella* n. sp. A, left aspect, ×60. Fig. 10. *Sulcella* n. sp. A, dorsal aspect, ×60.


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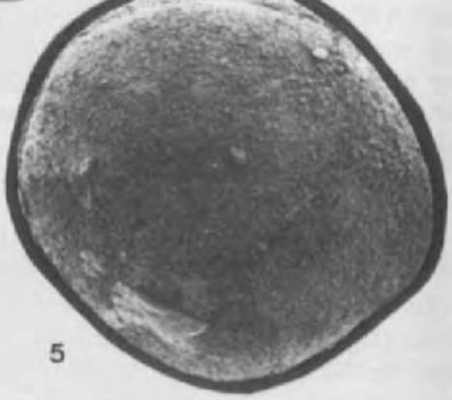
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through the doctoral program. I would also like to thank Ernie Russell for reviewing earlier versions of the manuscript; and Elisabeth Dewey for her drafting abilities.

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PLATE 2—Fig. 1. *Paraparchites* sp. aff. *P. kellettae,* right aspect, ×25. Fig. 2. *Chamishaella suborbiculata,* right aspect, ×40. Fig. 3. *Shishaella moreyi,* right aspect, ×80. Fig. 4. *Healdianella* sp., right aspect, ×70. Fig. 5. *Polycope* n. sp. A, right aspect, ×300. Fig. 6. *Beyrichiopsis cornuta,* left, aspect, ×70. Fig. 7. *Beyrichiopsis lophota,* left aspect, ×60. Fig. 8. *Monoceratina youngiana,* right aspect, ×115. Fig. 9. *Bythocypris aequalis,* right aspect, ×55.

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VII

Deep Sea Ostracoda

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Deep-Sea Ostracoda,
Taxonomy, Distribution and Morphology

GERD HARTMANN AND GESA HARTMANN-SCHRÖDER
Zoologisches Institut und Zoologisches Museum, Hamburg, F. R. Germany

ABSTRACT

The study of the deep-sea ostracoda has made much progress during the last few years. In particular, the paleontological investigations of the sea-floors of the oceans have contributed to this progress. Several statements have been made about the distribution, biology, morphology and ecology of deep-sea ostracods.

Based on a checklist of all living deep-sea ostracods known to date (Hartmann, 1985), the present paper discusses the following questions.

1. Do well-defined taxonomic groups of deep-sea ostracods exist?
2. Do morphological characters typical only of deep-sea ostracods and useable as deep sea indicators exist?
3. What do we know about the distribution of deep-sea ostracods?
4. What do we know about the ecology and biology of deep-sea species?

A critical evaluation of the existing data is given.

In a paper on deep-sea ostracods found at depths of between 1,630 and 5,330 meters and collected by the German Research Vessel *Meteor* in the Indian and Atlantic Oceans, the author (Hartmann, 1985) published a checklist of all Recent deep-sea ostracod species known to date. The present paper is an attempt to analyze this checklist with respect to taxonomy (taxonomic diversity), distribution, and morphology of these ostracods, as this has not been done in the above-mentioned paper. The author included all ostracod species (516 species and 4 subspecies) found regularly in depths of more than 1,000 meters in the checklist, even if they also live in shallow water or make vertical migrations.

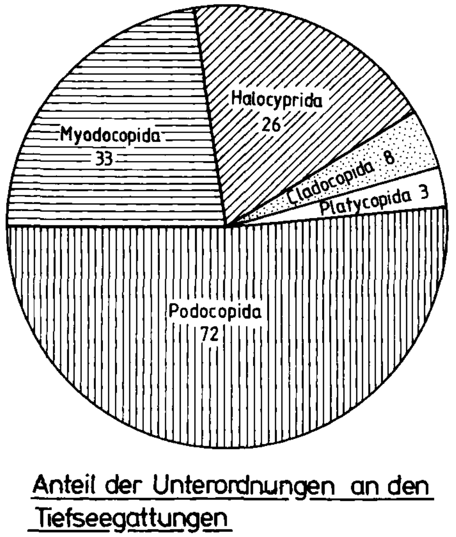
TAXONOMY

Text-figures 1 and 2 contain all genera and species of ostracod suborders found in the deep sea. It is clear at a glance that all suborders include deep-sea species and that none of the suborders or other higher systematic categories may be regarded as real deep-sea taxa. Let us look at the different suborders.

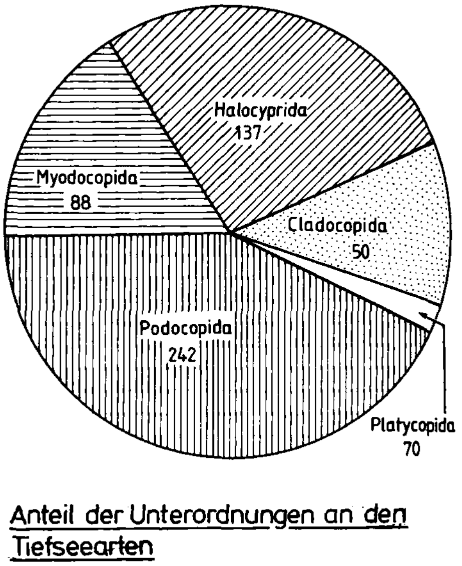
Table 1 and Text-figure 3 show representative deep sea Myodocopina. Checking the list, it is obvious that most genera are also represented in shallow water. Exclusively deep-water species are found only in:

Hadacypridina (monotypic), Azygozypridini with *Azygozypridina* (8) and *Isocypridina* (monotypic), and Gigantocypridini with *Gigantocypris* (7).

The Cylindroleberididae and Philomedidae, rich in species in littoral waters, are less important in the deep-sea. The Rutidermatidae are represented only by a single species. Among the Philomedidae *Igene* is a true deep-sea genus.



TEXT-FIG. 1—Diagram of the suborders of the deep-sea genera



TEXT-FIG. 2—Diagram of the suborders of the deep-sea species.

The *Halocypridina* are more difficult to judge since their species are nearly completely pelagic and many undertake vertical migrations thus occurring in water bodies of different depths. There are no deep-sea taxa of genera or higher taxonomic level.

Among the Archiconchoeciinae *Archiconchoecia* contains 14 deep-sea species, and among the Halocypridinae, *Bathyconchoecia*, with 10 deep-sea species, has the majority of its species in this environment. The entire family Thaumatocyprididae exists, though not exclusively, but with the majority of its species in deeper waters. *Danielopolina* also occurs in marine caves.

The same is nearly true for the Cladocopina. The family Polycopidae, rich in species, populates with many of its species the deep-sea bottom. In littoral biotopes this family lives in interstitial systems, both in the sublittoral and eulittoral regions. It is not possible to determine if this family invaded the interstitial systems of the littoral zone from the deep sea or vice versa.

Species of Platycopa are also found in the deep sea, but the number of species here remains small.

The Podocopa present a confusing picture in that most families of this subclass have representatives in the deep sea. Sometimes it is difficult to decide if their occurrence is autochthonous or if their shells have been transported to this biotope passively. In the tables, these species have been marked "questionable". Although this subclass is the richest in species, the number of exclusively deep-sea taxa is also small.

TABLE 1—DEEP-SEA GENERA AND NUMBER OF THE SPECIES OF MYODOCOPA–MYODOCOPIDA–MYODOCOPINA.

(Taxa with exclusively deep-sea distribution are *italicized*)

Family Cypridinidae:

Tribes Cypridini:
- Bathyvargula 2
- Cypridina 2
- Doloria 1
- *Hadacypridina 1 (only in deep-sea)*
- Macrocypridina 2
- Metavargula 3
- Paradoloria 2
- Vargula 4

Tribes Azygozypridini (only in deep-sea):
- *Azygocypridina 8*
- *Isocypridina 1*

Tribes Gigantocypridini (only in deep-sea):
- *Gigantocypris 7*

Family Cylindroleberididae (prevailing in littoral regions):

Subfamily Cylindroleberidinae:
- Archasterope 1
- Bathyleberis 2
- Diasterope 1
- Empoulsenia 2
- Parasterope 3
- Skogsbergiella 3
- Synasterope 6

Subfamily Cyclasteropinae:
- Cycloleberis 1
- Asteropterygion 1

Family Philomedidae (prevailing in littoral regions):

Subfamily Pseudophilomedinae:
- Angulorostrum 2
- Harbansus 1
- Paramekodon 2

Subfamily Philomedinae:
- Anarthron 1
- *Igene 2 (only in deep-sea)*
- Philomedes 11
- Scleroconcha 3
- Tetragonodon 2

Family Sarsiellidae:
- Parasarsiella 1
- Sarsiella 1
- Spinacopia 7
- Streptoleberis 1

Family Rutidermatidae (nearly exclusive to littoral regions):
- Alternochelata 1

TABLE 2—DEEP-SEA GENERA AND NUMBER OF SPECIES OF MYODOCOPA–HALOCYPRIDIDA–HALOCYPRIDINA AND CLADOCOPIDA–CLADOCOPINA.

Family Halocyprididae:

Subfamily Archiconchoeciinae:
- Archiconchoecia 14 (*many in deep sea*)

Subfamily Halocypridinae:
- Bathyconchoecia 10 (*many in deep sea*)
- Fellia 3
- Halocypris 2

Subfamily Conchoeciinae:
- Alacia 6
- Boroecia 3
- Conchoecetta 2
- Conchoecia 20
- Conchoecilla 3
- Conchoecissa 5
- Discoconchoecia 3
- Gaussica 2
- Loroecia 2
- Metaconchoecia 8
- Mikroconchoecia 4
- Mollicia 5
- Obtusoecia 1
- Orthoconchoecia 4
- Paraconchoecia 18
- Paramollicia 5
- Porroecia 1
- Pseudoconchoecia 1
- Spinoecia 2

Family Thaumatocyprididae (prevailing in deep sea):
- Danielopolina 1 (also found in caves!)
- Thaumatoconcha 11
- Thaumatocypris 1

Family Polycopidae:
- Archipolycope 9 (*many in deep sea*)
- Metapolycope 4
- Polycope 29
- Polycopsis 4
- Pontopolycope 2
- *Pseudopolycope 2 (all in deep sea)*

Among the Bairdioidea, only the family Bythocyprididae is frequent at depth. *Bythocypris* contains 15 species in this environment, this being a large part of its species spectrum. *Zabythocypris*, with 12 species known to date, exclusively inhabits the deep sea.

Very important for deep-sea ostracods is the genus *Argilloecia* of the Cypridoidea. The number of its deep-sea species is constantly rising with the progress of deep-sea research. Seventeen species have been found in the deep, and among ostracods sampled by the research vessels *Polarstern* and *Walther Herwig* in Antartica, more have been found by the authors.

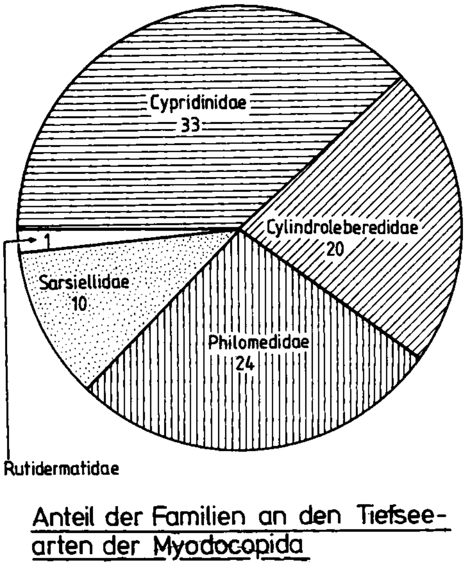
Among the Cytheroidea, generally rich in species, only occasionally have species been reported from deeper waters. This is, for example, true for the families Leptocytheridae and Cytherideidae which are very rich in littoral species. The Paradoxostomatidae, as forms which live mainly on algae and suck their sap, are not inhabitants of lightless depths. There are some exceptions among semi- and full-parasitic species. The Krithidae have, with the genus *Krithe*, a unit which includes 11, the Cytheruridae with *Cytheropteron* a unit with 16 deep-sea species. Most of the exclusivly deep-sea inhabiting genera contain however, only a few species or are monotypic:

> *Abyssocythere*—5 species, *Poseidonamicus*—4 species, *Abyssocythereis*—monotypic, *Pelecocythere*—monotypic, and *Vitjasiella*—monotypic.

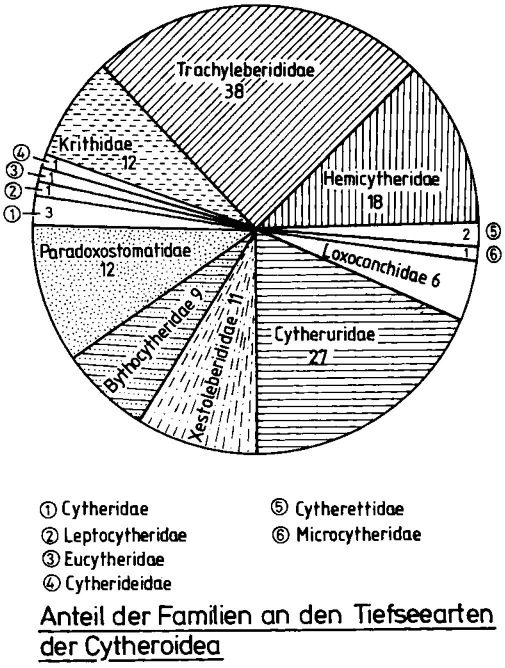
as well as the new genus *Profundocythere* with 3 species recently noted by the present author (1985).

Moreover, Table 3 shows that most of the remaining genera have at most 8, usually 1–5, deep-sea representatives.

Summing up, there is no doubt that many ostracod taxa inhabit the deep sea environment, but it must also be pointed out that the number of exclusively deep-sea living taxa is astonishingly small.



TEXT-FIG. 3—Diagram of the families of the deep-sea species of Myodocopida.



TEXT-FIG. 4. Diagram of the families of the deep-sea species of Cytheroidea.

TABLE 3a—DEEP-SEA GENERA AND NUMBER OF SPECIES OF PLATYCOPA AND PODOCOPA.

Family Cytherellidae:		
Cytherella	10	
? Cytherelloidea	1	*(uncertain)*
Family Sigilliidae:		
Saipanetta	1	
Superfamily Bairdioidea:		
Family Bairdiidae:		
Subfamily Bairdiinae *(prevailing in littoral regions):*		
Bairdia	10	
Bairdoppilata	4	
Neonesidea	1	
Paranesidea	3	
Pterobairdia		
Subfamily Pusselinae *(prevailling in littoral regions):*		
Anchistrocheles	2	
Family Bythocyprididae:		
Bythocypris	15	*(many in deep sea)*
Orlovibairdia	1	
Zabythocypris	*12*	*(all in deep sea)*
Superfamily Cypridoidea:		
Family Macrocyprididae:		
Macrocypris	8	
Family Pontocyprididae:		
Argilloecia	17	*(many in deep sea)*
Australoecia	3	
Pontocypria	1	
Pontocypris	6	
Propontocypris	1	
Family Candodidae (prevailing in littoral regions):		
? Aglaiocypris	1	*(uncertain)*
? Paracypris	2	*(uncertain)*

DISTRIBUTION OF DEEP-SEA OSTRACODA

Because of the great spatial, wide geographical, temporal and ecological continuity of the deep-sea environment, zoogeographers agree that many, if not most, deep-sea animal species have a wide distribution. Is this also true of deep-sea ostracods?

Analyzing the distribution of the 520 deep-sea species and subspecies it is not possible to confirm this general statement as applying to ostracods. On the contrary, most of the species appear to have only small vertical and horizontal ranges! This is possibly due to the lack of knowledge of deep-sea ostracods. However to postulate a wide distribution of deep-sea ostracods simply because this is true for other animal groups is not permissible.

Among the Myodocopina species of the checklist, only two species are found to be widely or circumtropically distributed. All others have a small range.

The pelagic Halocypridina naturally have a wider distribution. Twenty-three of the deep sea species have a circumtropical distribution, while 15 occur worldwide. However, the wide geographical distribution is mostly combined with a wide vertical distribution, that is, 18 of the 23 circumtropical species are also found in epipelagic communities, with the same being true for 12 of the 18 worldwide species.

Not a single species of the Cladocopina is recorded as having a wide distribution!

The Platycopa appear to be widely distributed with several species having been recorded from widely separate localities. It is however remarkable that only these three species appear to have a wide range, which clearly do not represent a single species. The Bairdioidea of the Podocopa show a similar picture. A wide distribution is also reported for species described by Brady (1880). The systematic status of these species, however, is not clear.

Among the Cytheroidea the following species are evidently widely distributed:

Krithe bartonensis, Krithe producta, Echinocythereis spp., and ***Bradleya dictyon.***

TABLE 3b—DEEP-SEA GENERA AND NUMBER OF SPECIES OF PODOCOPA (SUPERFAMILY CYTHEROIDEA).

Family Cytheridae:
? Cythere 2
Paijenborchella 1

Family Leptocytheridae:
Leptocythere 1

Family Eucytheridae:
Eucythere 1

Family Cytherideidae:
Cytheridea 1

Family Krithidae:
Krithe 11 *(many in deep sea)*
Parakrithella 1

Family. Trachyleberididae:
Bosquetina 2
Buntonia 1
Quasibuntonia 2
"Cythereis" 13
Abyssocythere 5 (all in deep sea)
Acanthocythereis 1
Henryhowella 1
Robertsonites 1
Trachyleberis 1
Ambocythere 2
Hiltermannicythere 1
Pterygocythereis 2
Bathycythere 1 *(deep sea of questionable)*
Echinocythereis 4
Basslerites 1

Family Hemicytheridae:
Agrenocythere 5
Cletocythereis 1
Tenedocythere 1
Thaerocythere 1
Bradleya 2
Poseidonamicus 4 (all in deep sea)
Caudites 1
? Orionina 1 *(questionable)*
? Aurila 1 (2) *(questionable)*
? Mutilus 1 *(questionable)*

Family Cytherettidae:
Abyssocythereis 1 (monotypic)
Pelecocythere 1 (monotypic)

Family Microcytheridae:
Microcythere 1

Family Loxoconchidae:
Loxoconcha 5 *(3 uncertain)*
? Phlyctocythere 1 *(questionable)*

Family Cytheruridae:
? Cytherura 3 *(questionable)*
? Hemicytherura 2 *(questionable)*
? Semicytherura 4 *(questionable)*
Cytheropteron 16 *(many in deep sea)*
Pedicythere 2

Family Xestoleberididae:
Microxestoleberis 2
? Ornatoleberis 1 *(questionable)*
Xestoleberis 8 *(some questionable)*

Family Bythocytheridae:
Bythocythere 2 *(1 questionable)*
Monoceratina 2
Vitjasiella 1 (monotypic)
Bythoceratina 2
Pseudocythere 2

Family Paradoxostomatidae:
Acetabulastoma 1
Cytherois 2
? Paracytherois 4 *(3 questionable)*
? Paradoxostoma 4 *(all questioable)*
? Sclerochilus 1 *(questioable)*

Incertae sedis:
? Saida 1 (677 m)

The majority of species of this group have, based on present knowledge, a small range. Examples of wide distribution are also found among the Cyprioidea with these species: *Macrocypris similis, Argilloecia pusilla,* and *Aglaiocypris meridionalis.*

Most species of this superfamily also have a small overall range.

Summing up the findings it must again be emphasized, that on the basis of present knowledge, only a few species show a wide distribution that has been proved. Among these, pelagic species with a broad vertical distribution predominate.

THE MORPHOLOGICAL CHARACTERS OF DEEP-SEA OSTRACODA

Morphological characters, influenced by the environment, are known from ostracod shells as well as from the soft parts. This has been studied especially in brackish water species, several characters of which respond to different environmental factors. It is to be expected that characters of deep-sea ostracods will show reactions to their deep-water environment.

A study of the literature on deep-sea ostracods and their morphological characters demonstrates, however, that general statements are as difficult to make as for taxonomy and distribution. Nevertheless, different authors (Benson, 1971, 1972; Poulsen, 1965) have drawn attention to characters obviously influenced by the deep-sea environment. It is difficult however, to generalize these findings.

A morphological change easy to correlate with depths is shown by the ostracod eye, by that of the nauplius as well as the lateral eyes.

For example, the lateral eyes of the Myodocopina reduce the number of ommatids with increasing depths (Poulsen, 1965 for the Cylindroleberididae). In deeper water the lateral eyes are often completely reduced. This is true for nearly all real deep-sea forms, such as *Hadacypridina,* the *Azygocypridini, Gigantocypridini, Igene, Bathyleberis,* and *Spinacopia.*

The nauplius or median eye is often also reduced in deep-sea ostracods. This trend is, however, not uniform. Well known, although not yet studied morphologically in detail, is the median eye of *Gigantocypris,* which is transformed into a paired large reflector eye, surely a specialisation for the deep sea. Kornicker (1969) also found a large median eye by reduced lateral eyes in *Spinacopia* (Sarsiellidae).

The Podocopa generally reduce the median eye when living in greater depths while lateral eyes have never been found in this group. Frequently, the valves form eye spots or transparent zones in their outer lamella above the median eyes. These spots disappear in the deep-sea environment (*Poseidonamicus,* Benson, 1972; *Xestoleberis,* Bonaduce and others).

In spite of this trend, a reduction of eyes cannot alone be regarded as a deep-sea character. Halocypridina, Cladocopida, Platycopida Darwinuloidea and Cytherettinae among the Cytheroidea do not possess lateral or median eyes. Other ostracods, such as cave-dwelling forms or species living in interstitial environmenta also reduce their eyes. Another character frequently observed in deep-sea animals is the prolongation of extremities, *i.e.* antennae, legs and their bristles. Indeed, many deep-sea ostracods possess long antennae and walking or swimming legs, and often, especially in Cytheroidea, terminal claws on the walking legs which are extremely long (*Zabythocypris, Pelecocythere, Vitjasiella* for example). Other real deep-sea species, however, do not show these adaptations. *Abyssocythereis* and *Poseidonamicus* can be named as examples. Moreover, it should not be forgotten that ostracods living in coral debris, on algae, or on soft substrates also show the same transformation of extremities.

The frontal organ of ostracods (better known as the organ of Bellonci) is reported to have a different form in deep-sea individuals of species with a wide vertical rang (*Igene,* Kornicker, 1975). It is, however, not clear, if this transformation is a deep-sea adaptation or not.

Morphological changes of the ostracod shell concern the thickness of their walls as well as their total length. Corresponding to the growing hydrostatic pressure and the inability of animals to build up strong calciferous skeletons in greater depths (4000 meter lysokline), deep-sea ostracods have thinner valves in deeper waters. This is true for both Myodocopa and Podocopa (*Hadacypridina, Bathyvargula,* several Podocopa). Benson (1972) mentioned the loss of marginal spines on the valves of deep-sea ostracods, regularly equipped with these features. A reduction in the number of marginal bristles is reported by Poulsen for *Hadacypridina.* Benson and Peypouquet (1983) believe that the variation of the marginal zone of *Krithe* is related to the changing hydrochemical and hydrophysical conditions in deeper waters.

Kornicker (1969) observed larger valves in deep-sea individuals of *Spinacopia* (Sarsiellidae). While Benson (1971) reported similar conditions for *Abyssocythere* and *Poseidonamicus*.

Finally, different authors believe that the ventral flattening of the ostracod shell and the development of wings, observed in several Cytheroidea (for example, Trachyleberididae, Cytheruridae, *Pelecocythere*) are a deep-sea character.

When the above-mentioned morphological characters, *i.e.* thickness of shell walls, size ventrally flattened shells, wings, etc., are analyzed, it is found that none of these characters may be called typical for the deep-sea environment. The calcification of ostracod shells depends on many factors. Weakly calcified shells are also frequent in brackish water and in species living on algae (such as *Xestoleberis* and *Paradoxostoma* species). The same is true for the ornamentation and size of the valves. Thus Kühl (1980) found in *Leptocythere* that different sizes and ornamentation could be correlated with the time of year. As flattened ventral surfaces and wings are frequently observed in ostracods living on soft substrates (Cytheruridae), the development of wings in deep sea ostracods may be related with soft substrates - also widespread in the deep.

Summing up, it must be stated that, similar to the statements given for taxonomy and distribution of deep-sea ostracods, there are no morphological characters exclusively present in deep-sea forms. Numerical methods (computer programs) should be applied to solve these problems.

SUMMARY

1. The deep-sea is populated by numerous taxa also present in littoral regions. Only a few taxa of higher systematic categories are exclusively deep-sea taxa.
2. The distribution of deep-sea ostracods is poorly known. A wide distribution is observed especially in pelagic species which also have a large vertical distribution.
3. There are no morphological characters which are exclusive to deep-sea Ostracoda.

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DISCUSSION

Adamczak: What about the carapace thickness in the deep-sea forms?

Hartmann: Generally it is accepted that deep-sea ostracods have thinner valves. However, as thin valves also occur in other biotopes such as the phytal and interstitial waters, it is not possible to generalize this statement. Intraspecific research has to be done on species which occur at different depths.

Maddocks: I believe you are aware of this already, but let me report for the record that nearly all subsequent reports of *Macrocypris similis* and other Challenger species are misidentifications, as are at least 50% of sightings of *Macrocypris minna.*

Hartmann: I am afraid that "accidents" like this one will happen often in the future. That is what makes work so difficult.

Sohn: Can you suggest to palaeonotologists criteria in Ostracoda for the recognition of deep-sea habitats? (I agree with your conclusions, but woud like to see your published statement for use by palaeontologists).

Hartmann: I am afraid that I cannot help you. Most of the characters which change with depth in Myodocopa are those of soft parts (the eye, etc.). Intraspecific work should be done to prove characters in fossil species paying attention at the same time to the entire fauna discovered in the sample in question.

The Anatomy of the Ostracod *Pelecocythere purii* sp. nov. and some Features connected with the Abyssal Mode of Life in this and some other Deep Water Forms

JOHN W. NEALE
University of Hull, England

ABSTRACT

The new species *Pelecocythere purii* is distinguished from *P. sylvesterbradleyi* and its anatomy compared with that of the shallow water type species of *Cytheropteron*. Some modifications, probably connected with its life in deep waters, are noted and attention is drawn to some features of other abyssal ostracods.

INTRODUCTION

In recent years, considerable ostracod faunas have been obtained from the abyssal regions of the North Atlantic. Many of the forms are new and show considerable modifications to their anatomy compared with the more commonly encountered shallow water species. Some of the smaller species belonging in genera such as *Rockallia*, "*Pedicythere*" and a new genus externally similar to *Cytherura* are only rarely encountered. Others are common and belong dominantly in the genera *Polycope, Cytherella, Bairdoppilata, Krithe, Bythocypris, Pelecocythere* and *Pseudocythere* amongst others. In dealing with the anatomy of a large new species of *Pelecocythere* it became apparent that there were considerable differences from the somewhat similar, but shallow water, type species of *Cytheropteron* which might be considered in connection with its habitat. The new species is described below and its anatomy discussed in relation to other forms.

TAXONOMY

Family CYTHERURIDAE G. W. Müller, 1894
Subfamily CYTHEROPTERINAE Hanai, 1957
Genus PELECOCYTHERE Athersuch, 1979
PELECOCYTHERE PURII sp. nov.
(Pl. 1, figs. 1–4, text-figs. 1–3)

Derivation of name.—In honour of Dr. Harbans Puri who was instrumental in organising the First International Ostracod Symposium at Naples in 1963.

Diagnosis.—A *Pelecocythere* species of elliptical shape in side view, with a short blunt caudal process in the right valve and ending in a short posteroventral point in the left. Surface finely pitted and showing incipient reticulation, but with a smooth alar rim and lateral surface just above the rim. *Pars incisiva* of mandible deep-bodied with relatively slender, toothed termination. Hemipenes with fairly blunt distal termination and oval in shape.

Holotype.—A male specimen OS 302a (left and right valves), 302b (dissection) deposited in the Museum National d'Histoire Naturelle, Paris.

Other Material.—This is a commonly encountered species between depths of 4,000 and 5,000 metres in the Eastern North Atlantic. Nine typical examples have been deposited in the MNHN, Paris, Nos. OS 303a, b - 311a, b.

Type Locality.—INCAL CP12: 46°00.5′N, 10°18. 3′W at a depth of 4,796 m.

Dimensions of figured specimens.—

		Length	Height
MNHN OS 302a Holotype	♂RV	1545 μm	840 μm
	♂LV	1580 μm	960 μm
MNHN OS 303a	♀RV	1555 μm	930 μm
	♀LV	1580 μm	1040 μm

Description.—Carapace large, alate, broadly elliptical in side view with the greatest height at about mid-length. Dorsal margin of left valve evenly rounded, dorsal margin in right valve straight. Surface appears smooth under ordinary optical examination; the SEM shows it to be finely pitted with incipient reticulation, but smooth where it approaches the alar rim. Alar rim smooth with four fine, anastomosing, longitudinal ribs on its ventral surface. Short blunt caudal process. A flange is present anteriorly, ventrally and posteriorly where it ends in a small posteroventral point (Pl. 1, fig. 4). The posterior part of this flange is apparent in lateral view (Pl. 1, figs. 1, 3) Hinge antimerodont in the right valve with five, well-developed teeth anteriorly and six or seven posteriorly, joined by a finely locellate groove of uniform width which may even become a little constricted at its extremities. Left valve complementary with straight accommodation groove to receive the dorsal margin of the right valve. Normal pore canals single, simple and sparse. Marginal pore canals straight and simple about five anteroventrally and three or four posteroventrally. Internally some ten or eleven orifices appear at the alar margin. These lead into the ala where they give rise to two pairs of porecanals, one pair opening on the dorsal surface of the ala, the other on the ventral surface. Just below the dorsal margin in the left valve the outer surface of the shell is perforated by six pores which end in pore conuli. The carapace shows clear dimorphism, the males being lower in proportion to their length than the females (Pl. 1, figs. 1, 3).

Appendages

Antennule robust, consisting of six segments. First two segments relatively long, protopodite with a fringe of strong bristles dorso-distally, second segment with pilose tufts proximo- and dorso-distally and ventrally together with an annulate ventro-distal seta. Third, fourth and fifth segments almost equidimensional. Third segment with one slightly curved, sword-like seta dorso-distally, fourth with two of different lengths and fifth with two in similar position. The fourth and fifth segments also have one rather finer seta latero-distally in the former and ventro-distally in the latter case. Both fourth and fifth segments are finely pilose dorsally. Distal segment more slender

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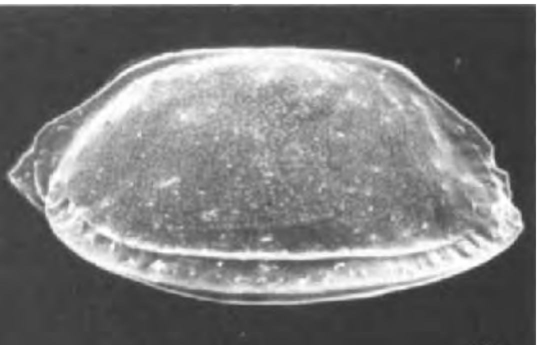
PLATE 1—*Pelecocythere purii* sp. nov. Stereographic paired photographs. All ×44. Figs. 1, 2, 4. Holotype, Male, MNHN 302a. INCAL CP12: 46°00.5′N, 10°18.3′W. Depth 4,796m. 1. Left valve in lateral view. 2. Right valve in lateral view. 4. Oblique ventral view of inside of right valve. Fig. 3. Female, left valve. MNHN OS 303a. INCAL CP13: 46°02. 1′N, 10°14.8′W. Depth 4,800m.


1a


2a


1b


2b


3a


4a


3b


4b

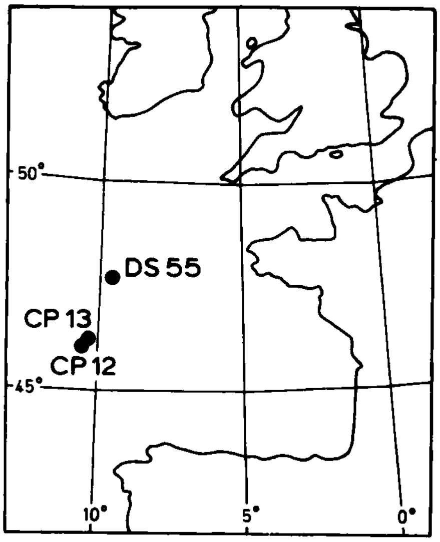
and armed with three long, smooth setae (two terminal, one set a little back from the others) and two smaller setae, one just over half the length of the others, one just over one-third the length.

Antenna of four segments, the long proximal and third segments almost the same length, the second and fourth segments short. Second segment with two-jointed exopodite proximo-distally which extends to just beyond the end of the distal segment; long flexible bristle ventro-distally which reaches well beyond the end of the distal segment to about half the length of the terminal seta. Long third segment with two fine, medium-length setae dorsally at just beyond half length and one long, strong, smooth seta with two finer, medium length setae immediately distal of it at about four-fifths length ventrally; there is one long, smooth seta and one rather finer, medium length seta postero-ventrally. Short fourth segment with one fairly long postero-ventral seta and one longer terminal seta.

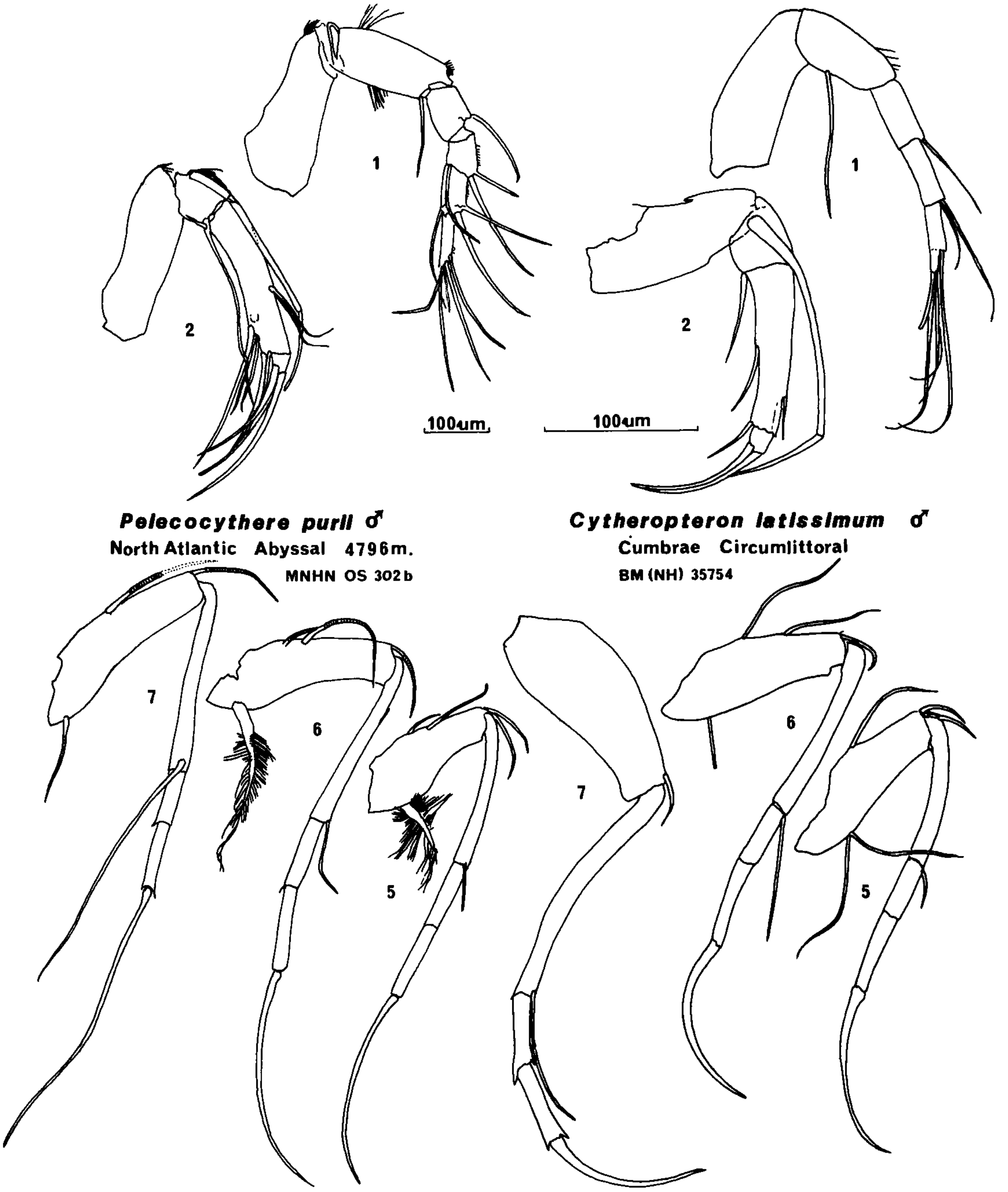
Mandible with deep-bodied *pars incisiva* with large dorsal tooth, four medium sized central teeth of which the most dorsal is the largest, three narrow ventral teeth and a ventral bristle. Palp large in relation to the *pars incisiva*. Palp originally of five segments of which segments two and three are indistinctly divided. Proximal segment short with five rayed epipodite and a thick-based ventro-distal seta with ventral bristles. Second segment long and consisting originally of two segments the division at two-thirds length being seen with varying clarity in various specimens. At this point there is a dorsal seta which is pilose and rather carrot-like, although in the figured specimen this is poorly represented. At this same point there are two lateral setae with ventral bristles the more dorsal of the two reaching level with the end of the terminal segment, the more ventral is just over half the length of the first; ventrally are two long smooth setae. Distally this segment carries seven smooth setae, two of short to medium length dorsally, and five long external lateral setae.

Maxilla with palp of four endites. Dorsal endite of two segments, proximal one with a dorsal annulate seta and two dorso-distal long, smooth setae; distal one with four setae. Other endites short in proportion to their depth, between one and a half and two times as long as deep, each armed with about eight setae. Vibratory plate with 16 strahlen.

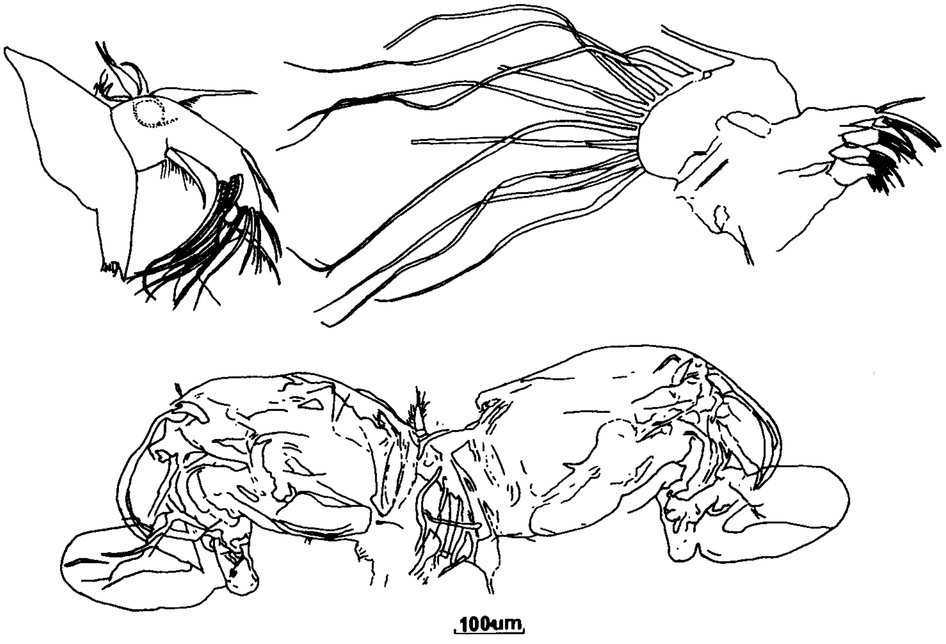
Fifth, Sixth and Seventh appendages are slender walking legs which are basically similar and consist of four segments with a long, narrow, terminal claw. There is a slight increase in length from the fifth to the seventh leg. In the fifth leg the protopodite has two median dorsal setae and two over-



TEXT-FIG. 1—Location of North Atlantic abyssal samples yielding specimens figured in this paper.

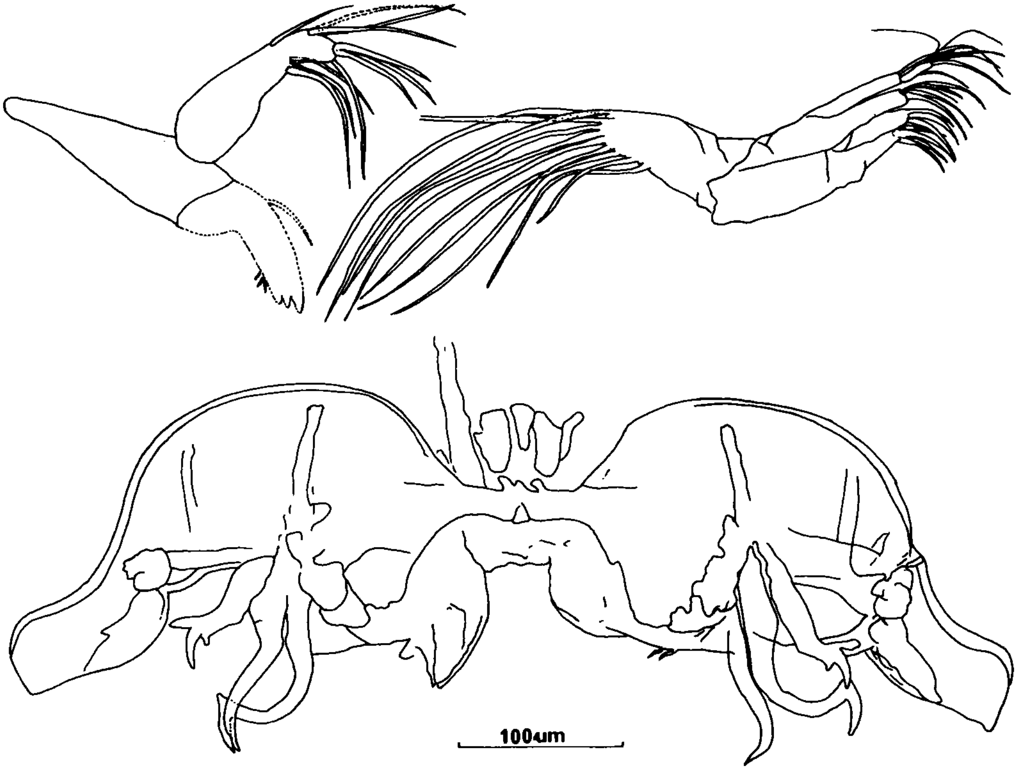


TEXT-FIG. 2—Antennules (1), Antennae (2) and Walking Legs (5, 6, 7) of *Pelecocythere purii*, Holotype MNHN OS 302b and *Cytheropteron latissimum* BMNH 35754. Scale has been adjusted so that they appear as though the carapaces were the same length and so the relative development of the appendages is directly comparable.



Pelecocythere purii **♂** **MNHN OS 302b**

Abyssal Depth 4796 m. Length 1545µm North Atlantic



Cytheropteron latissimum **♂** **BM (NH) 35754**

Circumlittoral Length 660µm Cumbrae

TEXT-FIG. 3—Mandibles, Maxillae and Copulatory Appendages in *Pelecocythere purii*, Holotype MNHN 302b and *Cytheropteron latissimum* BMNH 35754. Scale adjusted to give similar carapace lengths.

hanging the knee, the sixth limb is similar but with only one seta overhanging the knee, and the seventh is similar to the sixth but with only one median dorsal seta. All three walking legs have a ventral postero-proximal seta on the protopodite. In the fifth and sixth limbs this is a large, pilose carrot shaped seta, in the seventh it is annulate. These pilose setae occur in both sexes.

Male copulatory appendage rather elongate with oval hemipenes.

Affinities and Differences.—Pelecocythere purii is closely related to *P. sylvesterbradleyi* Athersuch but shows consistent differences and occupies a deeper niche (4,000–5,000 metres). In the shell of *P. purii* the right valve does not develop a posteroventral spine, but terminates in a blunt point posteriorly, whilst in contrast the left valve in both sexes develops a small, distinct posteroventral spine. Traces of subdivision have not been observed in the muscle scars of *P. purii.* It is difficult to compare the ornamentation between the two species, but to judge from Athersuch's enlarged figure of the posterior end on *P. sylvesterbradleyi* there is probably no significant difference. In the appendages and soft parts, *P. purii* differs in having a deeper bodied *pars incisiva* with more slender toothed portion and less elongate hemipenes with a blunter distal termination.

The alate shape and general form of the carapace suggests comparison with *Cytheropteron* and some material of the type species *Cytheropteron latissimum* Norman collected by Norman himself off Cumbrae is figured here for comparison (Pl. 2, fig. 4. Text-figs. 2, 3). *Pelecocythere purii* is more than twice the size of *Cytheropteron latissimum* and lacks the strong pitting/ornamentation of the latter, but these are only minor differences of no particular taxonomic importance above the species level. The principal difference lies in the even elliptical outline of *Pelecocythere,* particularly in its smoothly curved dorsal margin in the left valve, the evenly curved smooth rimmed ala, the blunt caudal process set low compared with the posteroventral upward swing of *C. latissimum* and the flange which is seen behind the caudal process in side view. In addition the alar rim is perforate with its quadruple canals from the orifices.

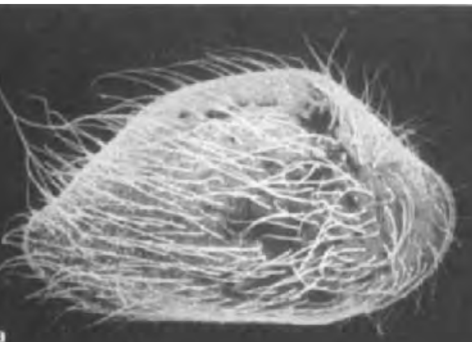
The hinge, while of the same general pattern, differs greatly in the even width of the median locellate groove in the right valve and in the greater number of teeth in the tooth plates. There are only three teeth at each end in *C. latissimum* and the locellate groove joining them is very narrow centrally and expands considerably at its extremities (Pl. 2, fig. 4).

The appendages also show striking differences. For comparative purposes, it has been assumed that the size of the appendages bears a linear relationship to the length of the carapace, and on this basis, the appendages of the two species have been figured as they would appear for the same size of adult shell. The antennules differ principally in the shorter, more equidimensional segments in the abyssal species and the strong more rigid setae. The antennae differ mainly in the lesser development of the exopodite in the abyssal form, coupled with the generally longer setae and in particular, the very long, flexible seta developed at the ventro-distal margin of the second segment which is over twice as long as the comparable seta in the type species of *Cytheropteron.* In *Pelecocythere* the mandibular palp is much larger in proportion to the *pars incisiva* and in the maxillary palp the endites are less elongate than in *C. latissimum.* Finally, the slender walking legs with their bushy proximal setae on five and six in *Pelecocythere* are in obvious contrast to *Cytheropteron.*

Features Connected with Abyssal Life

The above comparison raises the question of a connection between these features and the mode of life in deep waters, where the organisms live in complete darkness, in low energy environments on fine, soft substrates at considerable pressures. Abyssal ostracods develop a number of recurrent features as shown by the work of Benson (1972) who is one of the few workers to figure appendages of these deep water forms. A list would include:

1. Larger size
2. Loss of eyes and eye tubercles

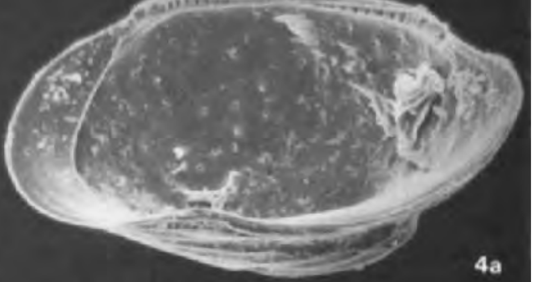

1a


2a


1b


2b


3a


4a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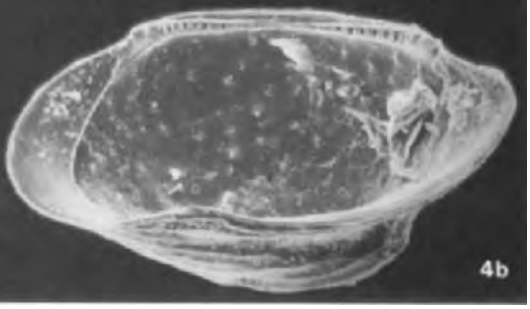
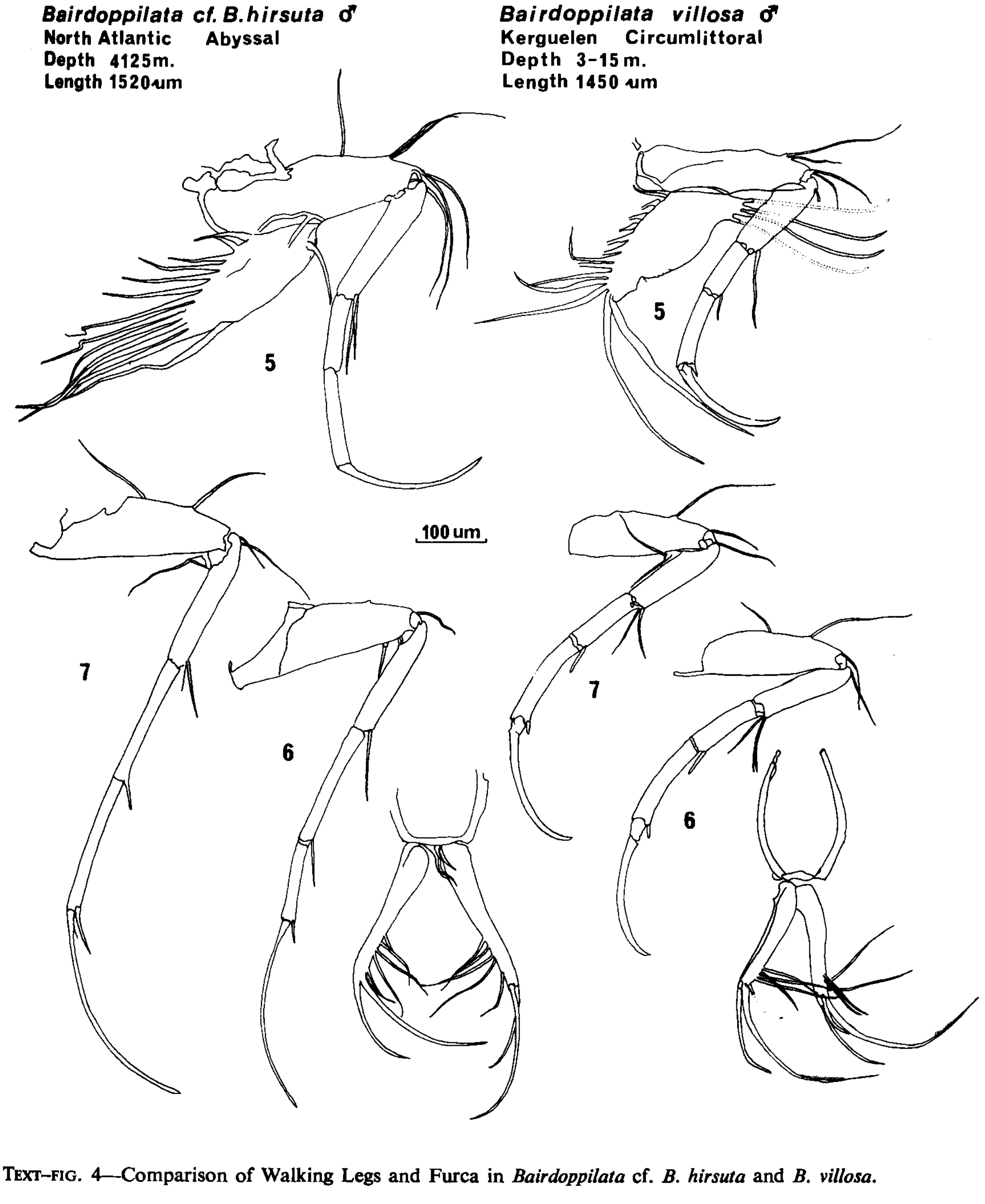

4b



TEXT-FIG. 4—Comparison of Walking Legs and Furca in *Bairdoppilata* cf. *B. hirsuta* and *B. villosa*.

PLATE 2—Stereographic paired photographs. Figs. 1,2. *Bairdoppilata* cf. *B. hirsuta* (Brady, 1880). MNHN 312a. BIOGAS IV, DS55: 47°34. 9′N, 9°40. 9′W. Depth 4,124m. ×38. 1. Right valve in lateral view. 2. Left valve in lateral view. Fig. 3. *Bairdoppilata villosa* (Brady, 1880). 3–15m, Kerguelen Island. Lateral view from right. ×41. Fig. 4. *Cytheropteron latissimum* Norman, 1865. BMNH 35754 Cumbrae. Circumlittoral. Oblique ventral view of inside of right valve. ×103.

3. Smooth shells or selective thickening along certain lines
4. The long and slender development of the last three pairs of appendages.

These features are all seen in *Pelecocythere*. Whilst caution is advisable in drawing generalisations, the last development of very slender walking legs is particularly widespread in a variety of families. Not only is it seen in the Trachyleberididae and Thaerocytheridae (Benson, 1972), but it is also seen in *Bairdoppilata* figured here where it is the most noticeable difference between the shallow and deep water hirsute forms. Maddocks (1969) in her work on the Bairdiacea shows this clearly in *B. villosa* from shallow water as compared with *B. hirsuta* from 1,000 m off Florida. The northeastern Atlantic has a considerable population of hirsute Bairdiacea in its deeper waters and whilst they appear to belong in a new species, this is a complex species group and needs thorough analysis before any attempt is made to delimit new taxa. One agrees with Maddocks that the group itself is probably worth separating as a new genus or subgenus, but fuller examination of a large number of species is advisable before taking this step. One of these northeastern Atlantic specimens from depths more than four times greater than those of Maddocks' material is figured here and shows a similar contrast with *B. villosa* (Text-fig. 4).

Rockallia and the new "*Cytherura*" show the same trend of slender, elongate walking legs and their detailed anatomy will be dealt with elsewhere. This trend is probably related to the low energy environment with a lack of bottom currents of any strength and the soft ooze of the sea floor at those depths. In *Pelecocythere* the first two pairs of walking legs develop large pilose carrot-like setae ventrally on the proximal segment and these occur in both sexes. Whilst by no means confined to abyssal ostracods, their enhanced development in the present form suggests a tactile/sensory function which may in some measure compensate for the loss of vision. A comparable development is seen in the thaerocytherid *Agrenocythere radula* as figured by Benson (1972), although this is not universal since the trachyleberid *Bradleya dictyon* apparently develops smooth setae in this position.

The mandibular palp in the Trachyleberididae and Thaerocytheridae develops a large plumose branch proximoventrally which is generally accepted as being associated with filter feeding and there is probably little difference between shallow and deep-water forms. However, in other genera such as *Rockallia* and the new "*Cytherura*", this development is carried to excess. Not only does the plumose branch become as large as the whole palp itself but, coupled with the fact that the latter become very thin and slender, it suggests an enhanced tactile/sensory function in addition to filter feeding. In *Pelecocythere* the type of response in this appendage differs. The palp is large and robust and a number of long, smooth setae are developed in the distal part of the palp forming a sort of fringe (Text-fig. 3). In addition a number of pilose, rather carrot-like setae are developed at various points on the appendage. It is difficult not to regard these as tactile/sensory developments which partially redress the lack of vision. In contrast to the development of slender walking legs, the reverse occurs in the anterior appendages in *Pelecocythere* (Text-fig. 2) where the antennule segments and maxillary endites are much more robust and equidimensional than in *Cytheropteron*. This same feature is seen in a number of other genera, but it is not a universal trend and it is not linked in any way to the abyssal mode of life. Finally, a specialised feature in *Pelecocythere* is seen in the development of quadruple pore canals and setae from the orifices in the alae which clearly gives the lateral extremities in this particular organism a highly tactile/sensory information gathering system.

The conclusions to be drawn are that there are two general trends in the appendage anatomy of abyssal ostracods. One is directed towards the development of slender walking legs and the other towards the provision of a wide range of tactile sensors to compensate for the lack of vision. Nevertheless, reference to the slender legs of the shallow water Paradoxostomatidae serves to emphasise that such trends are not absolute and that any evidence in this field must be treated with caution.

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DISCUSSION

Hartmann: I agree that we can note a tendency of prolongation of extremities in the deep sea. However, I do not think that the plumose (filter) bristles of the mandible are linked with depth.

McKenzie: I would endorse Prof. Neale's remarks on the precocious development of the plumose mandible bristle in Rockallidae and interpret this as having something to do with filter-feeding, analagous to the hypostomal fans illustrated by Schornikov for *Vitjasiella.*

Neale: I am in complete agreement with the first of the above comments and Dr. McKenzie's comment drawing attention ot *Vitjasiella* is most useful. In the full text I make the point that in some groups there is no significant difference in structure with depth, but that in representatives of two different families, the plumose bristle is developed to excess. This, coupled with the thin, attenuated flexible nature of the rest of the mandibular palp leads me to suggest that besides the filter feeding function, there may also be an enhanced secondary sensory function. The analogy with the hypostomal fans in *Vitjasiella* is worth pursuing further, although there are considerable differences as regards placement and orientation.

Maddocks: I have seen these trends also in deep-sea Bairdiidae, and I think that some of them may just be allometric functions of increased size. Somebody should investigate this. What do you think?

Neale: We have known for some time that these trends occur in different genera of very different size and so are clearly independant of absolute size. At the same time, in species of the same genus, size seems to be of little consequence. In the paper I figure the very differently proportioned walking legs of *B. villosa* and *B.* cf. *B. hirsuta* where the difference in carapace length is less than 5%.

Thus I assume that you are referring to size in the same taxon. This may be taken at two levels, either with regard to adults of different sizes or with regard to the growth of individuals. My own work on the North Atlantic faunas suggests that in adults of the same taxon at comparable depths the development is uniform and proportional to size. As regards the development and growth of the individual, I have not made a detailed analysis of growth patterns in the limbs of these taxa and this type of study is rare. The only really rigorous statistical study of which I am aware formed the basis of a Ph. D. Thesis at the University of Manchester (A. L. Gulshan, 1977, Development of the Appendages of *Heterocypris incongruens* (Ramdohr) (Crustacea, Ostracoda) 2 volumes), a work which deserves to be better known. It would be wrong to transfer the conclusions based on a study of a freshwater species to marine species such as *Bairdoppilata* and its allies, but a similar study on a marine species would certainly be of considerable interest in ascertaining the nature and comparability of growth patterns.

Whatley: I can confirm that the length of the thoracic limb is not necessarily related to size. Some very small deep sea cytherurids which we have dissected also have disproportionately long limbs. Your new cytherurid genus is rare in the North Atlantic, but very common in the deep sea of the Indo-Pacific back to the Eocene. The plumose structure also, within certain taxa, increases proportionately in size with depth.

Neale: I am interested to hear of the latter, which I suspected for some time, and look forward to publication of your detailed measurements and statistics.

Mediterranean Deep-sea Ostracods, the Species Poorness of the Eastern Basin as a Legacy of an Early Holocene Anoxic Event

DICK VAN HARTEN AND HENK J. DROSTE
University of Amsterdam, Netherlands

ABSTRACT

The benthonic ostracods of the Mediterranean show a major bathymetric divide which separates the faunas of shallower waters from those of the deep sea. This divide mostly lies at about 250–300 m and is marked by a faunal turnover and a decrease in diversity and density with greater depth. As opposed to the faunas above the divide, the deeper ostracod faunas of the western and eastern Mediterranean are strongly different: the eastern deep-sea faunas are much poorer in species than those of the west.

Bottom cores taken in the eastern Mediterranean show that normal deep-sea faunas, comparable with those still extant in the western basin, disappear abruptly at the base of the Early Holocene sapropel S-1 which was deposited between approximately 9,000 and 7,000 YBP. *Bathycythere vanstraateni, Cytherella* sp. Breman, *Krithe monosteracensis,* and *Macrocypris adriatica* do not return above the sapropel.

Our observations indicate that water anoxy associated with S-1 sapropel formation caused the extinction of many of the original eastern Mediterranean deep-sea ostracods. Recolonisation from the western basin has still failed to occur and is believed to be impeded by the relatively small depth of the sill of the Sicilian Ridge. There is no conclusive evidence that differential food conditions are playing a significant role in preventing recolonisation.

INTRODUCTION

Present-day knowledge of Mediterranean ostracods is biased in both a geographical and a bathymetric sense. Geographically, the emphasis has clearly been on the western rather than the eastern Mediterranean basin, the Adriatic Sea excepted. Bathymetrically, the bathyal and abyssal regions have received much less attention than the areas above the shelf edge.

Insufficient though available data are, there is no doubt that eastern Mediterranean deep-sea ostracod faunas are quite poor (Bonaduce *et al.*, 1983; Brambati *et al.*, 1983). Faunal diversities and densities tend to be distinctly lower than they are at corresponding depths in the western basin and this is remarkable as similar differences are much less in evidence in the shallow-water ostracods.

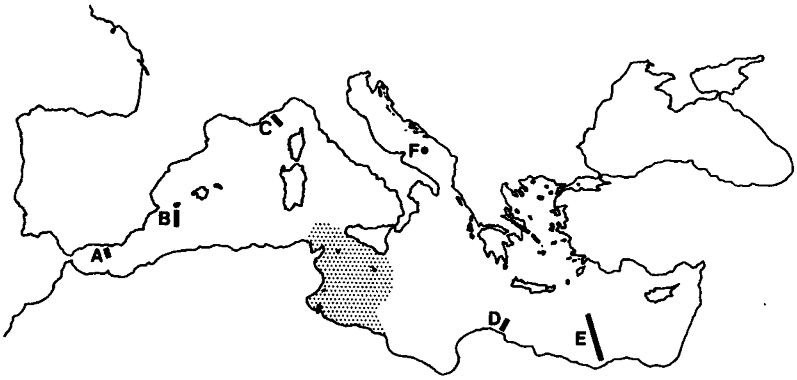
In this paper, we report the results of comparative investigations in the western and eastern Mediterranean with particular reference to the deep sea and offer an explanation for the differences observed.

MATERIALS AND METHODS

The materials for this study were collected during cruises of N/O Cathérine Laurence (Ligurian Sea; 1981), B/O Cornide de Saavedra (Alboran and Balearic Seas; 1982), and R/V Tyro (eastern Mediterranean; 1983) using grabs and boxcoring devices.

For analysis of fauna considered Recent, only the soft surface sediment (1–2 cm thick) was used. Minimum sample size was *ca.* 50 cc of raw sediment. Most samples were processed by simple washing, additional cleaning by boiling with soda being hardly ever necessary. The ostracods were picked from the fraction coarser than 150 μm.

In collecting, no attempt was made to discriminate between dead and living Recent fauna. Our data thus relate to taphocoenoses: communities of remains buried, or to be buried, together. Owing to *post-mortem* transport, much of which would be downslope, taphocoenotic depth ranges are expected to be broader than those of the corresponding biotopes.



TEXT-FIG. 1—Schematic map of the Mediterranean showing sampling sites. A: Alboran Sea transect (105–1,720 m). B: Balearic Sea transect (100–2,400 m). C: Ligurian Sea transect (130–2,575 m); two stations lying to the west of the main transect are not separately shown. D: Libyan Sea transect (165–2,291 m). E: transect off Alexandria (100–2,880 m). F: site of core 353 in the Adriatic Sea used by Van Straaten (1966), Breman (1975), and Van der Zwaan (1980). Shaded area southwest of Sicily: submerged part of Sicilian Ridge, connecting Europe with Africa and separating the western from the eastern Mediterranean basin.

RESULTS

Five bottom sampling transects in the Mediterranean are reported, each covering both shallow and deep waters. Three transects are located in the western basin, the other two lie in the eastern basin (Text-fig. 1). Identified ostracod taxa are listed in Tables 1–5; to reduce the noise of downslope contamination (the transportation of specimens to greater depth by currents and mass transporting agents), finds of juveniles have been left out.

All transects show contrasting "shallow" and "deep" assemblages, the transition mostly occurring at about 250–300 m depth. The Ligurian Sea seems an exception with the first deep-sea taxa appearing at more than 400 m. The transition is marked by a faunal turnover and a decrease in diversity and density with greater depth. The faunal divide may be masked by the effects of

TABLE 1—ALBORAN SEA. OSTRACOD DISTRIBUTION IN TRANSECT (SURFACE LAYER; ADULT SPECIMENS ONLY).

depth in m	100		500	1000		2000 3000
Aurila spp.	●					
"Bairdia" spp.	●					
Buntonia sublatissima	●					
Celtia quadridentata	●					
Costa edwardsi	●					
Cytherella spp.	●					
Eucythere sp.	●					
Paracytheridea sp.	●					
Pontocypris spp.	●					
Tetracytherura angulosa	●					
Urocythereis sp.	●					
Xestoleberis spp.	●					
Bythocythere sp.	●	●				
Carinocythereis antiquata	●	●				
Echinocythereis spp.	●	●				
Krithe aff. praetexta	●	●				
Loxoconcha spp.	●	●				
Monoceratina oblita	●	●				
Phlyctocythere pellucida	●	●				
Sagmatocythere spp.	●	●				
Bosquetina dentata	●	●	●			
Pseudocythere caudata	●		●			
Pterygocythereis spp.	●	●	●			
Henryhowella sarsi	●	●	●	●	●	
Cytheropteron spp.	●	●	●	●		●
Paracypris sp.		●	●			
Rectobuntonia inflata		●	●			
Macrocypris ligustica		●	●	●		
Argilloecia acuminata		●	●	●	●	●
spp.		●	●	●	●	●
Krithe monosteracensis			●			
Krithe sp.			●	●	●	
Cytherella sp. Breman			●		●	●
Macrocypris adriatica			●	●	●	●
Microxestoleberis profunda			●		●	●
Parakrithe dimorpha			●	●	●	●
Pseudocythere armata			●			●
Bythocypris tenera				●		
Bathycythere vanstraateni				●	●	●
Krithe keiji					●	●
Bythocypris obtusata						●
Polycope inflata				●		

downslope contamination (extremely heavy contamination can be seen in the Libyan Sea transect, Table 4). Unless their striking depth ranges are, in fact, due to this process, several *Polycope* species seem unaffected by the bathymetric divide. Within transects, an increase in shell size with increasing depth can be seen in *Argilloecia acuminata* (G. W. Müller) and *Bathycythere vanstraateni* Sissingh (Tables 6 and 7).

Between the western and eastern transects, there is reasonable similarity so far as the shallow-water ostracods are concerned. The deep-sea faunas are different, however, because several species that are quite common in the western basin are lacking entirely in the eastern transects (viz. *Bathy-*

TABLE 2—BALEARIC SEA. OSTRACOD DISTRIBUTION IN TRANSECT (SURFACE LAYER; ADULT SPECIMENS ONLY).

depth in m	100			500		1000		2000	3000
"Bairdia" spp.	●								
Occultocythereis dohrni	●								
Paracypris sp.	●								
Paracytheridea sp.	●								
Semicytherura spp.	●								
Aurila spp.	●	●							
Callistocythere spp.	●	●							
Celtia quadridentata	●	●							
Cytherella spp.	●	●							
Echinocythereis spp.	●	●							
Loxoconcha ex gr. rhomboidea	●	●							
Hiltermannicythere sp.	●	●							
Tetracytherura angulosa	●	●							
Urocythereis sp.	●	●							
Xestoleberis spp.	●	●							
Pontocypris spp.	●	●	●						
Microxestoleberis sp.	●	●	●	●					
Argilloecia spp.	●	●	●	●	●				
Pseudocythere caudata	●		●	●	●	●			
Bythocypris lucida		●							
Bosquetina dentata		●	●						
Parakrithe dimorpha		●	●						
Pterygocythereis jonesi		●	●						
Monoceratina mediterranea		●	●	●					
Macrocypris succinea			●						
Pseudocythere armata			●	●					
Cytheropteron spp.			●	●	●				
Bathycythere vanstraateni			●	●	●	●	●		
Rectobuntonia inflata			●				●		
Argilloecia acuminata			●	●	●	●	●	●	●
Henryhowella sarsi			●	●	●	●	●	●	●
Bythocypris tenera				●	●				
Krithe keiji				●	●	●			
Cytherella sp. Breman				●	●	●	●		
Macrocypris adriatica				●			●		●
Krithe monosteracensis							●		
Bythocypris obtusata								●	●
Pseudocythere hastata								●	●
Polycope tholiformis		●							
vasfiensis		●	●	●			●	●	
reticulata			●						
inflata			●	●	●	●	●	●	●
ovalis						●	●	●	
demulderi								●	
parareticulata								●	
quadridentata								●	

cythere vanstraateni, Cytherella sp. Breman, *Krithe keiji* Breman, *Krithe monosteracensis* (Seguenza), and *Macrocypris adriatica* Breman). The eastern deep-sea faunas are poor, by comparison, and hardly marked by distinctive genera. They are typically dominated by *Polycope* spp., not infrequently the only ostracods present, and may further contain *Argilloecia acuminata, Bairdia conformis* (Terquem), *Bythocypris obtusata* Sars, and *Pseudocythere* spp. *Pedicythere* spp., and *Tuberculocythere tetrapteron* (Bonaduce, Ciampo and Masoli) are sometimes found but tend to occur in only small numbers. *Bythocypris lucida* Seguenza inhabits shallow waters in the Balearic and Ligurian Seas whilst it apparently lives in the upper part of the deep zone in the Libyan Sea (*Bytho-*

TABLE 3—LIGURIAN SEA. OSTRACOD DISTRIBUTION IN TRANSECT (SURFACE LAYER; ADULT SPECIMENS ONLY).

depth in m	100			500		1000					2000		3000
"Bairdia" spp.	●												
Bythocypris lucida	●												
Carinocythereis bairdi	●												
Cytheridea neapolitana	●												
Echinocythereis sp.	●												
Parakrithe sp.	●												
Tetracytherura angulosa	●												
Urocythereis sp.	●												
Aurila spp.	●	●											
Bosquetina dentata	●	●											
Buntonia spp.	●	●											
Callistocythere spp.	●	●											
Cytherella spp.	●	●											
Krithe aff. praetexta	●	●											
Loxoconcha spp.	●	●											
Monoceratina oblita	●	●											
Occultocythereis dohrni	●	●											
Pterygocythereis jonesi	●	●											
Rectobuntonia miranda	●	●											
Sagmatocythere spp.	●	●											
Tenedocythere prava	●	●											
Phlyctocythere pellucida	●	●	●										
Pseudocythere caudata	●	●	●										
Semicytherura spp.	●	●	●										
Macrocypris ligustica	●	●	●	●									
Paradoxostominae	●	●	●	●									
Pontocypris spp.	●	●	●	●									
Xestoleberis spp.	●	●	●	●									
Henryhowella sarsi	●	●						●					
Argilloecia spp.	●	●	●			●	●	●	●	●	●		
Paracytheridea sp.		●											
Paracypris sp.		●	●										
Cytheropteron spp.		●	●	●							●	●	
Pseudocythere armata					●	●	●			●		●	
hastata					●							●	
Argilloecia acuminata					●	●	●	●	●	●	●	●	●
Krithe keiji					●	●	●	●	●	●	●	●	●
Bythocypris tenera						●							
Macrocypris adriatica						●	●		●	●	●	●	●
Bathycythere vanstraateni								●	●				
Cytherella sp. Breman								●	●	●			
Bythocypris obtusata											●	●	●
Polycope reticulata	●	●											
tholiformis	●		●	●									
inflata	●						●	●	●	●	●	●	●
vasfiensis	●	●		●	●	●				●	●	●	●
n. sp.		●											
ovalis				●				●	●	●	●	●	●
quadridentata					●	●	●	●	●	●	●	●	●

cypris nomenclature seems confused in the literature; see Plate 1 for usage of *B. lucida* and *B. obtusata* in this paper).

Several deep-sea cores in the Libyan Sea and off Alexandria penetrated the dark-coloured organic-rich layer (sapropel) generally referred to as S-1 (see Cita *et al.*, 1977) and reached pre-sapropel sediment underneath (Text-fig. 2). It has become customary to divide Mediterranean organic-rich layers into sapropels proper and mere sapropelic layers according to whether their organic carbon content is greater or smaller than 2% by weight (Kidd *et al.*, 1978). This distinction is not

TABLE 4—LIBYAN SEA. OSTRACOD DISTRIBUTION IN TRANSECT (SURFACE LAYER; ADULT SPECIMENS ONLY).

depth in m	100			500			1000			2000		3000
Macrocypris succinea	●											
"Bairdia" spp.	●	●										
Occultocythereis dohrni	●	●										
Cytherella vulgata	●	●	●									
Pontocypris spp.	●	●	●									
Argilloecia spp.	●	●	●	●								
Microxestoleberis sp.	●	●	●	●	●							
Paradoxostominae	●	●	●	●	●							
Semicytherura spp.	●	●	●		●							
Pseudocythere caudata	●	●	●	●	●		●					
Phlyctocythere pellucida		●										
Echinocythereis sp.		●	●									
Monoceratina oblita		●	●									
Bosquetina dentata		●	●	●	●							
Bairdia conformis		●	●	●	●	●	●	●				
Tetracytherura angulosa			●									
Bythocypris lucida				●	●	●	●	●				
Pseudocythere aff. caudata				●	●				●			
hastata				●	●	●	●		●	●	●	
Pedicythere spp.				●	●	●		●	●		●	
Pseudocythere armata					●	●		●				
Tuberculocythere tetrapteron					●			●	●			
Bythocypris obtusata									●	●		
Polycope reticulata	●	●	●	●	●							
rostrata	●	●	●	●				●				
n. spp.	●		●	●	●	●		●	●		●	
quadridentata	●	●		●		●			●		●	
inflata	●	●		●	●	●	●	●	●	●	●	●
vasfiensis	●	●	●	●	●	●	●	●	●	●	●	●
demulderi		●	●	●		●	●					
ovalis		●	●	●	●	●	●	●	●		●	●
orbulinaeformis			●	●	●	●		●	●	●		
parareticulata			●	●				●		●		
tholiformis				●								

made in the present paper. Here we are using the term sapropel in its original, loose sense to denote any markedly organic-rich interbed in an otherwise normal sediment sequence.

Sapropel S-1 is considered to be deposited in the Early Holocene, viz. between about 9,000 and 7,000 YBP (Ryan, 1972; Van Straaten, 1972; Stanley and Maldonado, 1977). Radio-carbon dating of our Libyan Sea sapropel gave 7,530±160 YBP, confirming its identity as S-1.

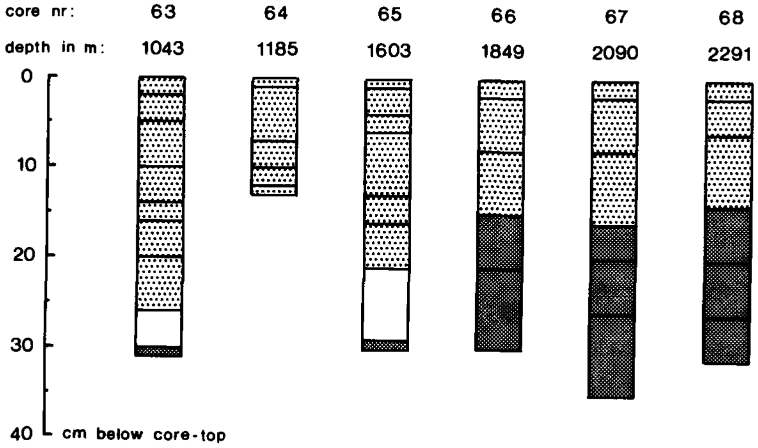
Barren of benthic fauna itself, S-1 marks a distinct faunal break in our cores: *Bathycythere vanstraateni, Cytherella* sp. Breman, *Krithe monosteracensis,* and *Macrocypris adriatica* are present below the sapropel but, apart from some rare cases of obvious reworking, absent above it. Some cores (*e.g.* core 63, Libyan Sea, Table 8) are suggestive of sustained upcore faunal impoverishment above the sapropel; this point needs future elucidation but should not detract from the significant turnover across S-1. In the pre-sapropel assemblage of cores 66, 67, and 68 (Libyan Sea), *Bythocypris reflexa* Breman is replaced upcore by *Bythocypris obtusata.*

Argilloecia acuminata and *Bathycythere vanstraateni* grew considerably larger in the pre-sapropel populations than they do nowadays at comparable, or even greater depths (Tables 6 and 7, Text-fig. 3). Maximum observed variation of mean shell length and height is on the order of 10% in these species. Assuming a similar figure for the variation in shell width, the difference in shell volume amounts to about 30%.

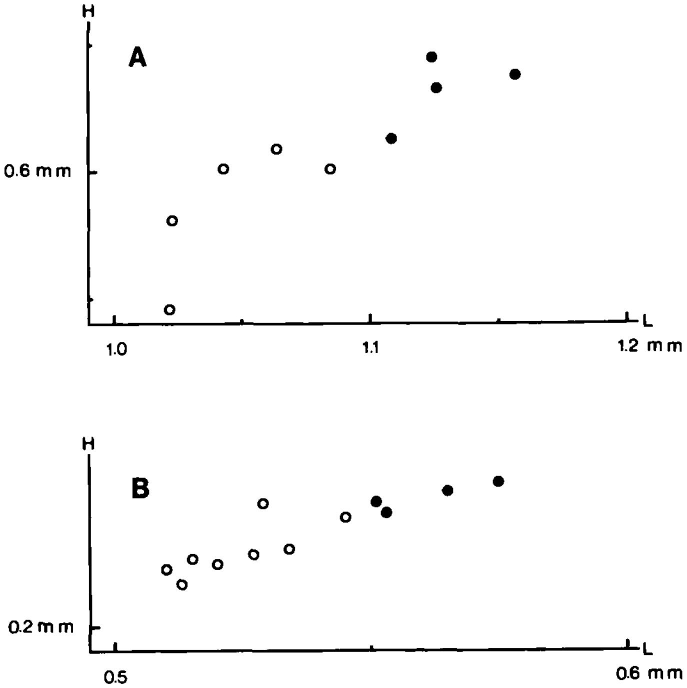
TABLE 5—OFF ALEXANDRIA. OSTRACOD DISTRIBUTION IN TRANSECT (SURFACE LAYER; ADULT SPECIMENS ONLY).

depth in m	100					500		1000				2000				3000
Carinocythereis antiquata	●															
Cytheridea neapolitana	●															
Hiltermannicythere sp.	●															
Krithe aff. praetexta	●															
Loxoconcha ex gr. rhomboidea	●															
Pseudopsammocythere similis	●															
Sagmatocythere sp.	●															
Aurila convexa	●	●														
Callistocythere adriatica	●	●														
Occultocythereis dohrni	●	●														
Xestoleberis communis	●	●														
Cytherella spp.	●	●	●													
Macrocypris succinea	●	●	●													
Semicytherura spp.	●	●	●													
Acanthocythereis hystrix	●	●	●	●												
Bosquetina dentata	●	●	●	●												
Buntonia spp.	●	●	●	●												
Phlyctocythere pellucida	●	●	●	●												
Pterygocythereis jonesi	●	●	●	●												
Argilloecia spp.	●	●	●	●	●											
Cytheropteron spp.	●	●	●	●	●											
Pontocypris spp.	●	●	●	●	●											
Henryhowella sarsi	●	●	●	●	●	●										
Monoceratina spp.		●	●	●												
Paracytheridea spp.		●	●	●												
Bairdia conformis		●	●	●			●		●							
Tetracytherura angulosa			●	●												
Parakrithe dimorpha				●	●											
Argilloecia acuminata				●	●	●	●	●	●	●	●	●	●			
Pedicythere phryne					●											
Pseudocythere hastata								●	●			●	●		●	●
Bythocypris obtusata								●	●	●	●					
Pseudocythere aff. caudata								●	●			●			●	●
? Microxestoleberis sp.									●							
Polycope reticulata	●	●	●	●	●	●	●	●								
inflata		●	●	●	●	●	●	●	●	●	●	●	●	●	●	
vasfiensis		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
demulderi			●	●	●	●										
ovalis			●	●	●	●	●	●	●	●	●	●	●	●	●	●
quadridentata			●		●		●	●	●		●		●		●	●
truncatula					●											
parareticulata					●	●				●		●	●	●	●	●

No organic-rich layer is found in cores 66, 67, and 68 (Libyan Sea). However, approximately 15 cm below the top of these cores, there is an abrupt faunal break which is equivalent to the turnover across S-1 in the other cores (Text-fig. 2, Tables 8 and 9). This suggests that a sapropel was present initially but has since been removed by some process of submarine erosion leaving a hiatus in the sedimentary record.



TEXT-FIG. 2—*Libyan Sea.* Boxcore profiles in sapropel area. Horizontal lines separate sampled intervals. Dark shading: samples yielding species of the group *Bathycythere vanstraateni* Sissingh–*Cytherella* sp. Breman–*Krithe monosteracensis* (Seguenza)–*Macrocypris adriatica* Breman; light shading: samples yielding assemblages with these marker species missing; white: barren (sapropel S-1).



TEXT-FIG. 3—Length-height plots of sample means listed in Tables 6 and 7. A: *Bathycythere vanstraateni* Sissingh; B: *Argilloecia acuminata* (G.W. Müller). Open circles: samples taken from surface layer; solid circles: samples taken from subsurface pre-sapropel levels.

Table 6—*Bathycythere vanstraateni* Sissingh. Size of adult left valves. Asterisks indicate samples taken from presapropel levels.

transect and depth in m		length in mm		height in mm		n
		mean	s	mean	s	
Alboran Sea	810	1.064	0.039	0.609	0.006	2
	1720	1.085		0.601		1
Balearic Sea	900	1.023	0.018	0.581	0.031	4
	1500	1.043	0.013	0.601	0.016	3
Ligurian Sea	1235	1.022		0.546		1
Libyan Sea	1849*	1.158	0.018	0.638	0.018	3
	1849*	1.125	0.011	0.645	0.018	2
	2090*	1.109	0.037	0.613	0.010	3
	2291*	1.127	0.018	0.633	0.027	3

Table 7—*Argilloecia acuminata* (G.W. Müller). Size of adult left valves. Asterisks indicate samples taken from presapropel levels.

transect and depth in m		length in mm		height in mm		n
		mean	s	mean	s	
Alboran Sea	810	0.510	0.010	0.211	0.005	7
	1720	0.529	0.020	0.224	0.008	4
Balearic Sea	900	0.513	0.007	0.208	0.002	3
	1500	0.545	0.007	0.221	0.002	3
Ligurian Sea	1235	0.515	0.006	0.213	0.006	9
	1580	0.527	0.009	0.214	0.007	8
off Alexandria	985	0.520	0.003	0.212	0.004	6
	2034	0.534	0.008	0.215	0.004	3
Libyan Sea	1043*	0.553	0.017	0.222	0.008	5
	1849*	0.565	0.010	0.226	0.007	7
	1849*	0.551	0.010	0.224	0.002	2
	2090*	0.575	0.019	0.228	0.008	5

Table 8—Libyan Sea. Ostracod distribution (adult specimens only) in core 63 (see Text-fig. 2 for core profile). Hatching indicates barren sapropel interval.

cm below core-top	0–2	2–5	5–10	10–14	14–16	16–20	20–26	26–30	30–31
Argilloecia acuminata					●		●	▨	●
Bairdia conformis	●	●	●	●	●	●	●	▨	
Bythocypris lucida	●	●	●	●	●	●		▨	●
obtusata					●	●	●	▨	●
Cytheropteron sp.						●	●	▨	
Paradoxostominae		●			●	●		▨	●
Pedicythere phryne					●		●	▨	
Polycope spp.	●	●	●	●	●	●	●	▨	●
Pseudocythere spp.	●	●	●		●	●		▨	●
Bathycythere vanstraateni								▨	●
Cytherella sp. Breman								▨	●
Henryhowella sarsi								▨	●
Krithe monosteracensis								▨	●
Macrocypris adriatica								▨	●
Xestoleberis sp.								▨	●

TABLE 9—LIBYAN SEA. OSTRACOD DISTRIBUTION (ADULT SPECIMENS ONLY) IN CORE 66 (SEE TEXT-FIG. 2 FOR CORE PROFILE).

cm below core-top	0	2	8	15	21	30
Argilloecia acuminata			●	●	●	
Bythocypris obtusata	●		●	●		
Paradoxostominae				●	●	
Polycope spp.	●	●	●	●	●	
Pseudocythere spp.	●			●	●	
Bathycythere vanstraateni				●	●	
Bythocypris reflexa					●	
Cytherella sp. Breman				●	●	
Krithe monosteracensis				●	●	
Macrocypris adriatica					●	
Xestoleberis sp.					●	

DISCUSSION

Depth-related Faunal Turnover

Benthonic ostracods, like other benthonic organisms, tend to be bathymetrically distributed in the sea. Actual depth, in terms of hydrostatic pressure, may play a role but it is abundantly clear from the pertinent literature that several other factors must be involved as well. It is beyond the scope of this paper to discuss this issue in any detail. We are only concerned with the existence of typically shallow and deep faunas which, in most of our transects, merge into one another at about 250–300 m depth. This major divide in the Mediterranean was recognized earlier by Ascoli (1964), Puri *et al.* (1969), and Breman (1976a), all of which authors placed it at approximately 250 m.

Division of marine ostracods into distinct shallow and deep assemblages seems world-wide (Peypouquet, 1980) but the boundary lies somewhat deeper in the Mediterranean than it does elsewhere (outside the Mediterranean it lies between 150 and 200 m; *e.g.* Van Morkhoven, 1972; Peypouquet, 1980). The world-wide occurrence of the divide taken together with the deeper position in the Mediterranean with its relatively clear waters supports the idea of a relationship with the photic zone, in accordance with a suggestion originally put forward by Pokorny (1971). This relationship may depend on food or oxygen requirements. We tentatively propose that ostracods restricted to the shallow zone need resources available only in the photic zone and immediately beneath it. Depth-indifferent forms and the true deep-sea taxa may be less exacting in their requirements.

Sapropel-related Faunal Turnover

Our results are much in line with those of Breman (1975) from core 353 (1,207 m depth) in the Adriatic Sea. There too, *Bathycythere vanstraateni, Cytherella* sp. Breman, *Krithe monosteracensis,* and *Macrocypris adriatica* disappear from the record at the base of S-1; at some depth below the sapropel, *Bythocypris reflexa* is replaced by *Bythocypris obtusata,* a replacement we also observed in some of our Libyan Sea cores. Above the sapropel, Breman too found poor faunas mainly composed of *Argilloecia acuminata, Bairdoppilata supradentata* (=*Bairdia conformis* of this paper; see

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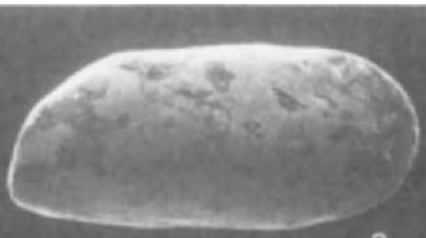
PLATE 1—Fig. 1. *Bathycythere vanstraateni* Sissingh. ×45. Balearic Sea, 1,720 m. Fig. 2. *Krithe monosteracensis* (Seguenza). ×75. Balearic Sea, 1,180 m. Figs. 3, 4. *Cytherella* sp. Breman. ×70. Ligurian Sea, 1,810 m. Figs. 5, 6. *Krithe keiji* Breman. ×95. Ligurian Sea, 1,580 m. Figs. 7, 8. *Bythocypris obtusata* Sars. ×45. Balearic Sea, 2,400 m. Figs. 9, 10. *Bythocypris lucida* Seguenza. ×45. Libyan Sea, 642 m. Fig. 11. *Macrocypris adriatica* Breman. ×30. Ligurian Sea, 2,100 m.


1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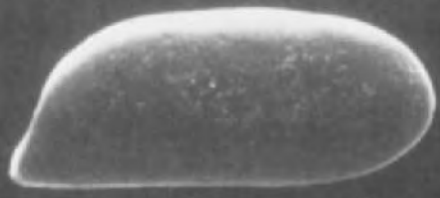
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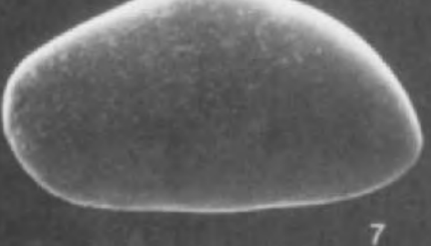
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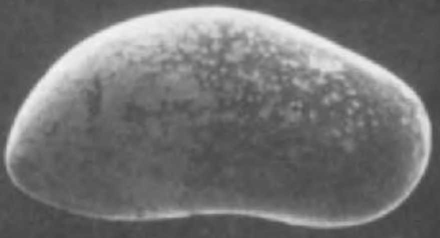
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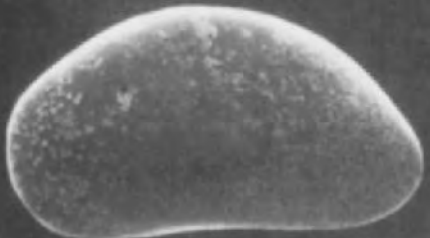
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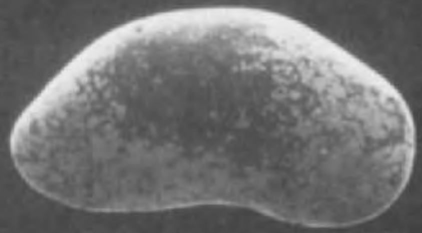
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11

Bonaduce *et al.*, 1975), *Bythocypris obtusata*, and *Polycope* spp. Poor Recent faunas of the same kind were reported by Brambati *et al.* (1983) from the deep Cretan Sea.

On account of these similarities, we propose that *Bathycythere vanstraateni*, *Cytherella* sp. Breman, *Krithe monosteracensis*, and *Macrocypris adriatica* disappeared from the entire eastern Mediterranean at the onset of sapropel deposition, about 9,000 years ago. This possibly also applies in the case of *Krithe keiji*, a species described by Breman (1976b) from the "Pleistocene (?)—Holocene" of the Adriatic Sea (Breman initially used the preoccupied name *K. caudata;* in Breman (1978), the specific epitheton was changed into *keyi* which was an unintentional misspelling for *keiji*). We found this form in all our western transects but it is apparently missing in the eastern ones, both above and below the sapropel.

Still extant in the western Mediterranean, these species became extinct in the eastern basin as a result of water anoxy associated with sapropel formation. The post-sapropel deep-sea ostracod faunas in the eastern Mediterranean are strongly different from those preceding this layer and much poorer. This can be considered a direct legacy of the S-1 anoxic event.

Some published reports may seem to rebut our claim. Ascoli (1964, Pl. 4 and 1966, Pl. 5) depicted *Krithe monosteracensis*, *Macrocypris* sp. 1 (=*M. adriatica*), and *Pterygocythereis*? sp. 1 (=*Bathycythere vanstraateni*) from a core taken at 1,192 m in the Adriatic Sea, believing them to represent Recent fauna. We subscribe to Breman's (1976a) suspicions, however, that Ascoli's pictures in reality refer to fossil specimens from the Pleistocene or Early Holocene which would crop out at the site of the core. Since Ascoli, as he mentioned in his 1964 paper, used unspecified samples from core-tops 30 or even 40 cm in length, there is the added possibility that his material did not come from the actual sediment surface.

The faunal poorness of the present-day deep eastern Mediterranean is very obvious indeed from the distribution chart in Bonaduce *et al.* (1983). Yielding a considerable number of *Bathycythere vanstraateni*, their station Ch 31 (Ionian Sea; 1,087 m) is notably out of tune, however. It is, in fact, the only eastern Mediterranean station in their chart to yield this species. The same sample is reported to contain *Cytherella bathyalis* (this is apparently a *nomen nudum;* the species is probably identical to *C.* sp. Breman of this paper) and suspiciously numerous *Bythocypris obtusata*. The deviant compositon of this sample and the isolated occurrence strongly suggest that fossil, pre-sapropel material rather than Recent fauna is involved. The composition does not point to reworking, in our opinion. But pre-sapropel sediment may have cropped out on the sea floor at the site of Ch 31 or be so shallowly buried that it entered the core-tops (of unspecified length) used by Bonaduce and his co-workers. Note, in this connection, that we found pre-sapropel sediment lying only 14 cm below the surface in core 68 in the Libyan Sea (Text-fig. 2). The single specimen of *Krithe monosteracensis* reported by Bonaduce *et al.* (1983) from their station Li 3 (Ionian Sea; 2,392 m), again a sole find in all of the eastern Mediterranean, seems inconclusive.

Sapropels are being generally associated with anoxic bottom-water conditions and the abrupt disappearance of benthonic ostracods at the base of S-1 is consistent with this. Animals do need free oxygen for respiration and will die of asphyxia in an anoxic environment. The fact that several preexisting species did not return after the anoxic event was over suggests that they had become effectively annihilated all over their regional biotope. As sapropel S-1 is geographically restricted to the eastern Mediterranean (Stanley *et al.*, 1975; Stanley, 1978; Cita and Grignani, 1982), anoxy-induced extinction would also have been limited to that region. After the annihilation in the east, recolonisation could only occur from the unaffected western basin, across the Sicilian Ridge. But the shallowness of this area (present-day sill depth approximately 400 m) and the concurrent elevated water temperatures to be expected would have tended to counteract re-invasion.

As opposed to the deep-sea fauna, the eastern Mediterranean shallow-water ostracods do not seem to have suffered much from the S-1 anoxic event. The similarity between our western and eastern transects in this depth range may either indicate that anoxy did not strongly affect the shallow waters or mean that locally annihilated shallow-water taxa did successfully re-capture their lost territories in the meantime. We favour the former alternative.

There are conflicting data on the minimum depth of occurrence of sapropel S-1. Van Straaten (1972) reported 699 m as the shallowest depth at which he had found this sapropel in the Adriatic Sea. Stanley (1978) mentioned 800–1,000 m as a minimum for the Ionian Sea. Perissoratis (1982), on the other hand, found S-1 in water as shallow as 280 m in the central northern Aegean Sea and Shaw and Evans (1984) gave 400 m for the Cilicia Basin (northeastern Mediterranean). The shallowest depth at which we found S-1 was 1,043 m (Libyan Sea, core 63) but higher upslope, core penetration may well have been too low for the sapropel to be reached. All quoted depths are uncorrected for Early Holocene global sea level which must have been some tens of metres lower than it is today.

However this may be, the deep-sea ostracod fauna was killed by anoxy, not sapropel deposition, and former anoxy need not necessarily be preserved in the form of sapropels. It can be argued (Van Harten, in press) that the anoxic ceiling (the minimum depth of full water anoxy) may have lain considerably higher in the watercolumn than the depth at which actual sapropels began to form. Allowing for some local variation, a depth of 200–300 m seems a reasonable estimate for the anoxic ceiling. This depth corresponds approximately with that of the main bathymetric faunal divide because both levels are apparently tied to the photic zone (Van Harten, in press).

The semi-coincidence of the two critical levels explains why S-1 anoxy selectively killed off deep-sea ostracod species, even those with a range reaching far above general sapropel depth whilst leaving the shallow-water fauna untouched. If our interpretation is correct, this phenomenon could be a general principle, to be expected with any major anoxic event in the eastern Mediterranean.

It should be borne in mind, however, that S-1 anoxy did not annihilate all the pre-existing deep-sea ostracods. *Argilloecia acuminata, Bythocypris lucida, Bythocypris obtusata, Henryhowella sarsi* (G.W. Müller), and some of the rarer species are found above as well as below the sapropel. *Argilloecia acuminata, Bythocypris lucida,* and *Henryhowella sarsi* may have survived by retreating upslope but this seems hardly likely in the case of *Bythocypris obtusata.* With an upper depth level of about 1,700 m in our western transects and about 1,000 m in those in the eastern basin (Tables 1–5), this is probably an obligatory deep-sea species in the Mediterranean, possibly even the deepest-dwelling ostracod to occur there, apart from some *Polycope* species (see also Bonaduce *et al.*, 1983). It is hard to accept that such a species could have escaped anoxy by retreating to depths of less than 200–300 m. An alternative explanation is admittedly speculative: perhaps full anoxy did not reach the bottom of all deep eastern Mediterranean sub-basins so that relict populations could survive. Several species of *Polycope* are also present on both sides of the sapropel; the depth ranges of these forms seem to be extremely broad, however, extending from the abyss to well above the critical depth inferred for the anoxic ceiling.

Significant faunal changes associated with eastern Mediterranean anoxic events were also described in the foraminifera (Cita and Podenzani, 1980; Van der Zwaan, 1980; Mullineaux and Lohmann, 1981; Parisi and Cita, 1982). The nature of the turnover across S-1 is very similar to that seen in the ostracods. To quote Cita and Podenzani (1980): "The benthic foraminiferal fauna above S-1 is completely different from that predating the Flandrian transgression" (*i.e. the pre-sapropel fauna;* note by present authors) "whereas it is similar to that presently living in the mesobathyal zone of the eastern Mediterranean basins" and "The colonizing population postdating the anoxic episode differs entirely from the Pre-sapropel community, both in terms of genera and species".

Van der Zwaan (1980) drew attention to a change in the foraminifera at about 95 cm (his sample 10) below the sapropel in core 353 of the Adriatic Sea. He ascribed this change, which is also reflected in the pelagic molluscs (Van Straaten, 1966) and the ostracods (*Bythocypris reflexa* is replaced upcore by *B. obtusata;* Breman, 1975), to a decreasing supply of nutrients and/or oxygen. We agree with this interpretation so far as oxygen is concerned. It seems reasonable to suppose that the onset of full anoxy was preceded by a gradual decline of oxygen in the water. The observed change in the fauna might reflect the passing of some critical threshold. In this connection, the *Bythocypris* replacement would support the view that *B. obtusata* is able to cope with relatively low oxygen levels, which is in keeping with our suggestion that this species possibly survived the S-1 event by retreating to deep refugia.

However, we disagree with Van der Zwaan's view about decreasing nutrient supply, *i.e.* nutrients in terms of food for the deep, benthonic communities. Firstly, on theoretical grounds, the oxygen decline heralding the onset of full anoxy should have been attended by increasing, not decreasing, amounts of organic matter reaching the bottom (Van Harten, in press). Parisi and Cita (1982) tentatively used this line of reasoning to explain peak abundances in benthonic foraminifera immediately preceding many older sapropels in the eastern Mediterranean. Secondly, ostracods below the sapropel in the Libyan Sea tend to be larger than their Recent congeners (Text-fig. 3). If ostracod size correlates positively with food availability (*e.g.* Peypouquet, 1977), the condition observed would suggest high rather than low food levels just before full anoxy killed all benthonic life. Unfortunately, our Libyan Sea cores are too short to allow a study of size variation approaching the sapropel from downcore.

The clear, blue Mediterranean is nutrient-poor and of notoriously low photosynthetic activity. Also, the concentration of nutrients in the eastern basin is only about half that of the western basin (McGill, 1961, 1965). This of course raises the question as to what extent the current nutrient distribution might be held responsible for the contrast between the deep-sea ostracods of the two parts of the Mediterranean. Might it be food shortage rather than the bathymetric barrier of the Sicilian Ridge that really prevents the expelled taxa from recolonising their former territories? Here it is difficult to be explicit but in default of direct evidence a caveat seems warranted. Firstly, the relationship between dissolved nutrients and ostracod food is debatable in itself; a necessary element for primary production, it is difficult to see how heterotrophic organisms like ostracods could assimilate them. Correlations between dissolved nutrients and ostracods such as those found by Peypouquet (1977) are probably remote and dependent on the nature of local trophic pathways. Little seems to be known about the energy flux towards deep benthic communities in general and those of the Mediterranean in particular. Secondly, food available for benthic ostracods might conceivably correlate with organic carbon. Though there is internal variation, the organic carbon content of the bottom sediment is on an average about the same in the two Mediterranean basins (Emelyanov, 1972); of major inter-basin differences in food conditions there seems to be no evidence here. Our last argument is again concerned with ostracod size: relative size in Recent *Argilloecia acuminata* off Alexandria certainly does not point to food shortage with respect to the western basin (Table 7). However, these data come from only two small samples which, moreover, represent cores taken close to the edge of the Nile submarine delta. According to Emelyanov (1972), these surroundings are among the richest in organic carbon in the entire Mediterranean.

CONCLUSIONS

We associate the local extinction of several eastern Mediterranean deep-sea ostracods with bottom-water anoxy related to Early Holocene S-1 sapropel formation. This anoxy does not seem to have affected the shallow-water ostracods. S-1 minimum depth of occurrence is often quoted as considerably greater than the level of the bathymetric boundary that separates shallow-water from deep-sea ostracod assemblages in the Mediterranean. We conclude, however, that oxygen depletion already prevailed at much smaller depths than that at which the greater part of actual sapropel formation took place and that the anoxic ceiling must have coincided approximately with the faunal divide. Full anoxy may not have occurred in all the deep sub-basins, thus enabling *Bythocypris obtusata* to survive in the eastern Mediterranean.

The onset of anoxy was preceded by a period of declining oxygen content and increased food supply. So far, there is no conclusive evidence that food conditions are playing a major role in preventing the deep-sea ostracods from recolonising their former eastern territories. Their return may however well be hampered by the high stand of the sill of the Sicilian Ridge and the associated high water temperatures. Anyway, the deep-sea ostracod fauna of the Eastern Mediterranean has not yet recovered from partial annihilation in the Early Holocene and its present poor state can be considered a direct legacy of the S-1 anoxic event.

ACKNOWLEDGEMENTS

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DISCUSSION

De Deckker: Do you think that the size differences you have for *Bathycythere vanstraateni* and *Argilloecia acuminata* for pre- and post-sapropel events could simply be due to temperature rather than food availability? Temperature, of course, would have an effect on food supply. If temperature was the *major* controlling factor, then you could perhaps say something about temperature changes.

Van Harten: I was merely quoting Peypouquet's view on what primarily causes size differences. Also, I would think that the increase of size with depth we observed within single transects supports Peypouquet's ideas.

Krstic: I agree with the opinion of De Deckker. The other thing that I would like to mention is that there was something like a salinity crisis just at the beginning of the Holocene; I have some unpublished records from the Aegean basin.

Van Harten: There may well have been. However, we only have evidence of the oxygen crisis leading to the deposition of sapropel.

Schweitzer: I think that your explanation of the change in ostracod faunas should be based on the change in benthonic foraminifers as well, and especially on the benthonic foraminifera stable isotopes. You might model such a study after the paper by Curry and Lohmann (in *Nature*) that you heard at the recent meeting in Kiel.

Van Harten: Our explanation of the change that we see in the ostracods is based on what we see in the lithology. I don't see why we should base this on foraminifers or isotopes. There is a change in the foraminifers across the sapropel which is comparable to that in the ostracods.

Henning Uffenorde: Can you identify specifically the "*Polycope* spp." that are characteristic of deep water? I found rich *Polycope* associations in the Limski Kanal in Yugoslavia and they have nothing to do with a *deep water* environment.

Van Harten: Many *Polycope* species seem to have extremely broad depth ranges, even those which are common in shallow water. *Polycope* spp. also include some new species which we, together with Bonaduce, intend to describe in the near future.

Pandemic and Endemic Distribution Patterns in Quaternary Deep-Sea Ostracoda

ROBIN C. WHATLEY AND MICHAEL AYRESS
University College of Wales, Aberystwyth, Wales

ABSTRACT

From an analysis of 214 deep sea Quaternary samples from the Southwest Pacific, Indian and North Atlantic oceans, a total of 382 species have been recovered. This total does does not include numerous species of *krithe,* which for reasons stated below, have not been considered in this study. Sixty-five of the species (17%) have been encountered in the Quaternary of all three oceans and 61 (16%) occur in two oceans. In all, 33% (126) of the species studied occur in more than one ocean. This is a much higher number and percentage than previous literature would suggest. Of the species recorded here, only approximately 10 (3%) have been recorded hitherto from more than one ocean. The diversity of Quaternary deep sea Ostracoda is shown to be highest in the Pacific and lowest in the Atlantic, with the Indian Ocean in an intermediate position. Most of the 65 cosmopolitan species have their oldest geological record in the Pacific and are shown to have migrated down the diversity gradient to the Atlantic via the Indian Ocean. The Tethys is not thought to have been of major importance in this migration. Much of this migration took place in the Pliocene although it was initiated in the Miocene and, for some species, in the Oligocene or earlier. The number of endemic species is fairly high but endemic genera are few. Ostracods are shown not to be unique in their pan-abyssal distribution; they conform to that of many deep-sea invertebrates.

INTRODUCTION

This study represents part of a much larger research project on Tertiary to Recent deep sea Ostracoda being carried out at Aberystwyth. This work was initiated in the Southwest Pacific but has now spread to the Indian Ocean, the area of the Southern Ocean, south of the South Atlantic and the North Atlantic. The longterm objectives of the project are to document the total faunas of these oceans during the interval studied, to discover their origins, their history of evolution and environmental adaptation and patterns of migration. The present study is principally concerned with the latter facet of the research.

The project to date has revealed that:

a) Deep sea ostracod faunas are much more diverse than they were previously thought to be (Whatley, 1983, and in prep.).
b) An important locus of induction into the deep sea is centred on the area between Australia and New Zealand (Whatley, 1983, 1985; Whatley *et al.,* 1982, 1983, 1984).
c) A major post-Miocene invasion of the abyss took place in the S. W. Pacific (Whatley, 1983); the

consequences of this can now be demonstrated in the North Atlantic (Whatley and Coles, in press) and form the basis of the present paper.

d) Many species which entered the deep sea in the Australian-New Zealand region have subsequently migrated outwards via abyssal pathways to other areas of the world's oceans (Whatley, 1983; Whatley *et al.*, 1982, 1983, 1984). Another important centre of induction into the deep sea was the Caribbean/Gulf of Mexico region. Many of the taxa recorded by Steineck *et al.* (1984) have now been found in the North Atlantic (Whatley and Coles, in press).

The present paper it designed to demonstrate:

e) That many more ostracods, both genera and species, are pan-abyssal in their distribution than has been previously thought.

THE DATA BASE FOR THE PRESENT STUDY

Although much of the migrationary activity outwards from various loci seems to have taken place during the late Micoene and Pliocene, as will be discussed later, the data on which this paper is based is largely confined to the Quaternary. This is both for reasons of space and also because it is in the Quaternery that the end product of Neogene migrations is most clearly revealed.

The study is based primarily on samples from a number of DSDP sites in the North Atlantic, Indian Ocean and S. W. Pacific. It also uses piston core samples collected under a NATO program by hydrographic survey vessels of the Royal and Royal Dutch Navies and box cores collected in the area of the Rockall Trough during various cruises of RRS *Challenger* and *Shackleton.*

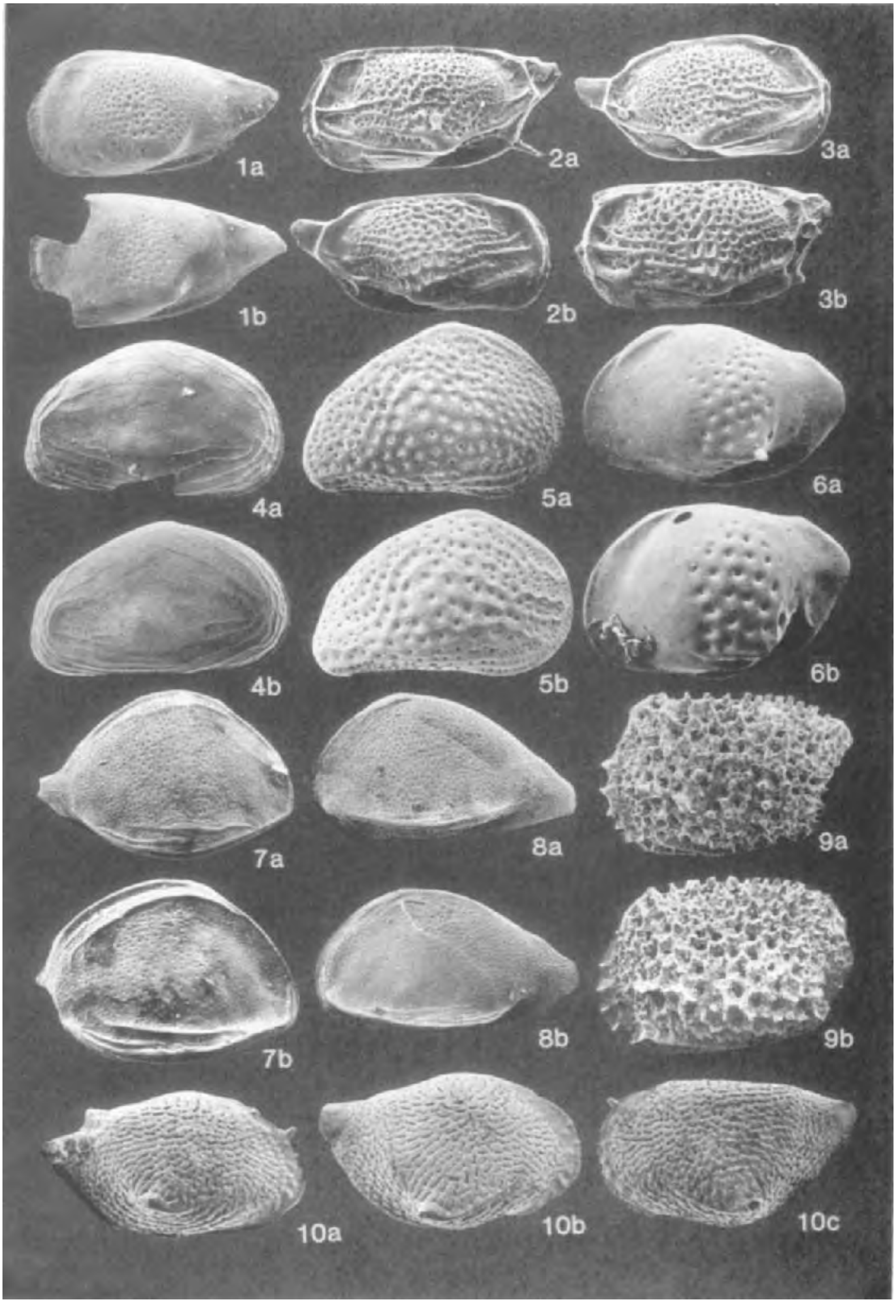
Table 1 gives the number of sites sampled, samples studied and species recovered from each of the three areas studied. The coordinates of the sites and the depth below the surface of the samples, etc. is given in Appendix 1.

TABLE 1—THE NUMERICAL DISTRIBUTION OF QUATERNARY SITES AND SAMPLES STUDIED AND THE NUMBER OF SPECIES RECOVERED (KRITHE OMITTED).

	North Atlantic	Indian Ocean	S.W. Pacific
Sites	75	7	13
Samples	124	34	56
Species	130	190	253

PLATE 1—All specimens of Quaternary age.

Figs. 1a,b. *Monoceratina*? sp. 1a, LV, North Atlantic, NATO Core, P2/A ×123, 1b, LV, A-1, Indian Ocean, DSDP, Site 259/1/5 ×130. Figs. 2a,b,3a,b. *Rostrocythere*? sp. 2a, LV, North Atlantic, NATO Core L5/A ×104. 2b, RV, Indian Ocean, DSDP, Site 254/1/3 ×123. 3a, RV, North Atlantic, NATO Core L5/A ×108. 3b, LV, Indian Ocean, DSDP, Site 254/1/3 ×147. Figs. 4a,b. *Eucythere parapubera* Whatley and Downing, 1983. 4a, RV,♀, North Atlantic, DSDP, Leg 94, Site 607/16 c.c. ×114. 4b, RV,♀, Indian Ocean, DSDP, Site 259/1/5 ×125. Figs. 5a,b. *Eucythere* sp.3 5a,RV,♂ North Atlantic, DSDP, Leg 94, Site 608A/13 c.c. ×144. 5b, RV, ♂ Indian Ocean, DSDP, Site 264/1/3 ×125. Figs. 6a,b. *Cytheropteron* sp.1. 6a, LV, North Atlantic, DSDP, Leg 94, Site 609/9 c.c. ×107. 6b, LV, Pacific Ocean, DSDP, Site 209/2/6 ×102. Figs. 7a,b, 8a,b. *Cytheropteron testudo* Sars 1869. 7a, RV, North Atlantic, NATO Core, R4/C. ×141. 7b, RV, Pacific Ocean, DSDP, Site 262/36/6. ×123. 8a, LV, North Atlantic, NATO Core R4/C. ×129. 8b, LV, Pacific Ocean, DSDP, Site 209/1/1 ×134. Figs. 9a,b. *Eucytherura calabra* (Colalongo and Pasini 1980). 9a, LV, North Atlantic, NATO Core N3/B ×115. 9b, LV, Pacific Ocean, DSDP, Site 209/1/5 ×115. Figs. 10a,b,c. Gen. nov. A. *longipunctata* (Breman 1975). 10a, RV, North Atlantic, NATO Core R5/A ×128. 10b, RV, Indian Ocean, DSDP, Site 259/1/3 ×103; 10c, LV, Pacific Ocean, DSDP, Site 208/5/6 ×130.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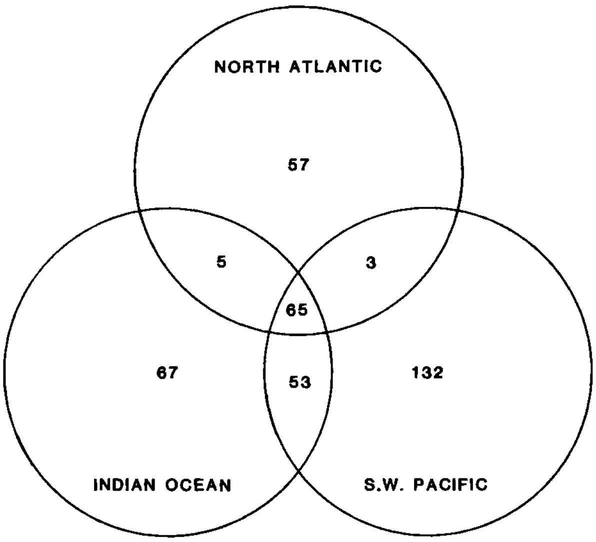


TEXT-FIG. 1—Venn Diagram showing (in the context of this study) the number of species apparently confined to each of the three oceans; the number of species common to two oceans and the number of species common to three oceans, in the Quaternary.

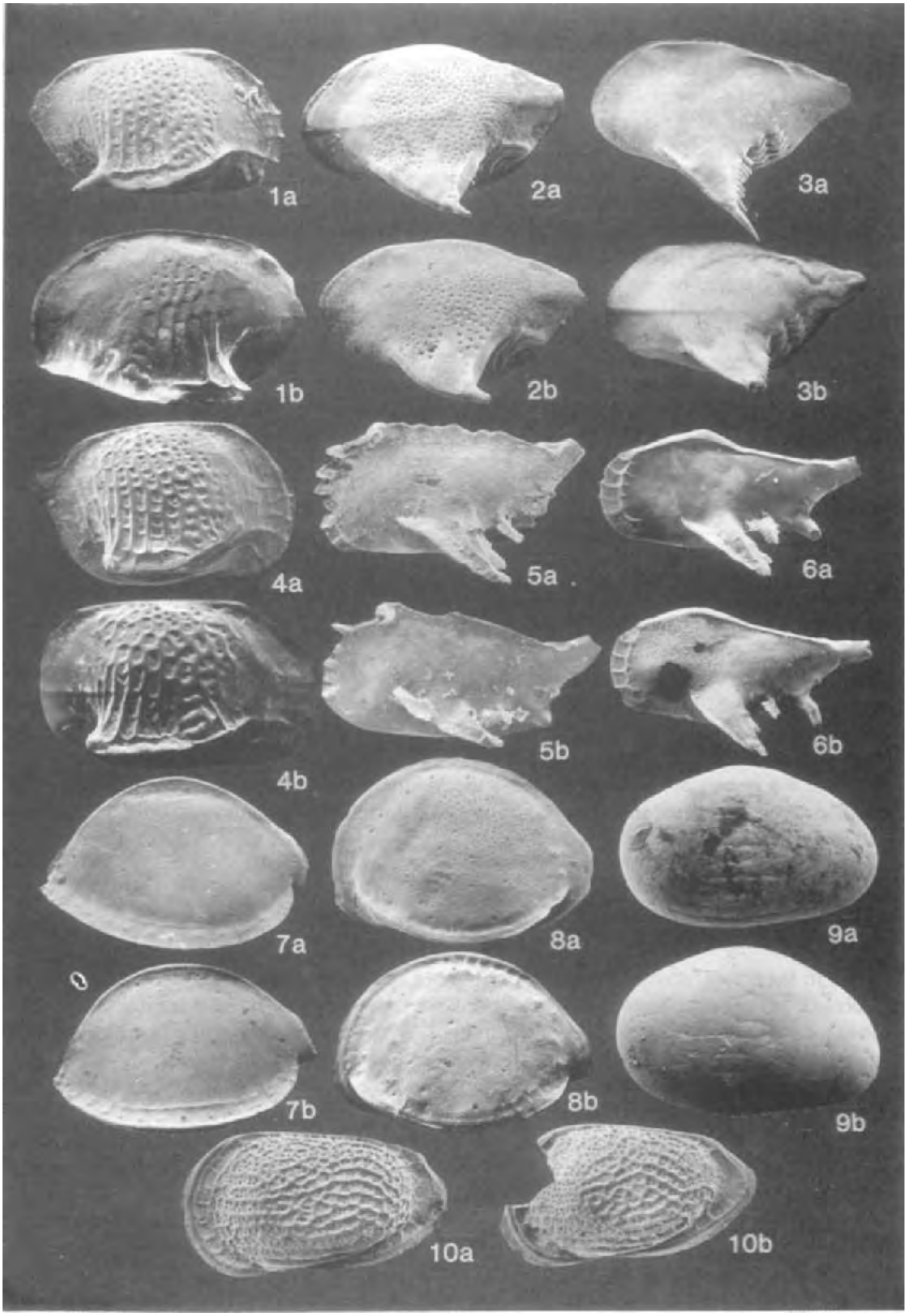
Although the number of sites and samples studied from the North Atlantic considerably exceeds those from the Indo-Pacific, the least number of ostracods were recorded from the former region. It is not intended to imply that the figures recorded in Table 1 represent the total number of species from the Quaternary of these areas. They simply represent the number of species recovered from the samples studied. *Krithe,* the most abundant genus in all the samples studied and frequently the most diverse, is *not* incorporated in these figures, nor elsewhere in the study. *Krithe* is a genus in which the recognition of species is extremely difficult.

Although a detailed study of the *Krithe* faunas of the three areas is underway, it is not complete enough to incorporate the results into the present study. Some *Krithe* species will, however, be subsequently demonstrated to be pan-oceanic in their distribution.

Text-fig. 1 is a Venn Diagram which numerically illustrates the following:

1) The number of species which are (in the context of this study) apparently confined to each of the three oceans in the Quaternary.
2) The number of species which are common to two oceans.

PLATE 2—Figs. 1a,b. *Aversovalva* sp. 2. 1a, RV, North Atlantic, DSDP, Leg. 94, Site 608/9 c.c. ×113. 1b, LV, Pacific Ocean, DSDP, Site 209/2/2 ×121. Figs. 2a,b. *Cytheropteron branchium* Whatley and Ayress in press. 2a, LV, North Atlantic, NATO Core, S3/A ×131. 2b, LV, Pacific Ocean, DSDP, Site 208/4/4 ×141. Figs. 3a,b. *Cytheropteron pherozigzag* Whatley and Ayress in press. 3a, LV, North Atlantic, NATO Core, R3/A ×124. 3b, LV, Pacific Ocean, DSDP, Site 209/1/1 ×133. Figs. 4a,b. *Aversovalva* sp. 1. 4a, RV, North Atlantic, DSDP, Leg 94, Site 607/1c.c. ×102. 4b, RV, Pacific Ocean, DSDP, Site 209/2/2 ×120. Figs. 5a,b. *Pedicythere phryne* Bonaduce *et al.*, 1975. 5a, LV, North Atlantic, NATO Core P2/A ×109. 5b, LV, Pacific Ocean, DSDP, Site 209/1/5 ×128. Figs. 6a,b. *Pedicythere polita* Colalongo and Pasini, 1980. 6a, LV, Indian Ocean, DSDP, Site 254/1/3 ×100. 6b, LV, Pacific Ocean, DSDP, Site 208/4/2 ×109. Figs. 7a,b. *Pelecocythere sylvesterbradleyi* Athersuch, 1979. 7a, LV, North Atlantic, DSDP, Leg. 94, Site 607/26 c.c. ×35. 7b, LV, Pacific Ocean, DSDP, Site 208/3/3 ×36. Figs. 8a,b. *Pelecocythere* sp. 8a, Lv, Indian Ocean, DSDP, Site 264/1/3 ×67. 8b, LV, Pacific Ocean, DSDP, Site 209/2/6 ×65. Figs. 9a,b. *Xestoleberis* sp. 1. 9a, RV, North Atlantic, NATO Core P2/A ×103. 9b, RV, Pacific Ocean, DSDP, Site 284/1/2 ×126. Figs. 10a,b. *Palmoconcha*? sp. 2. 10a, LV, North Atlantic, DSDP, Leg 94, Site 607/12 c.c. ×80. 10b, LV, Indian Ocean, DSDP, Site 259/1/5 ×85.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10a
10b

3) The number of species which are common to three oceans.

Although a large number of species are common only to the Indian Ocean and Southwest Pacific, many fewer species are common only to the North Atlantic/Pacific and North Atlantic/Indian Ocean. The 65 species encountered to date in all three oceans represent a much higher number than previous records of the distribution of Ostracoda in the deep sea would suggest. The percentage of endemic and pandemic species is given in Table 2.

The authors are confident that in due course, others among the endemic species will prove to be more widely distributed. For example, the three species whose present known distribution is the S. W. Pacific and North Atlantic only, almost certainly also occur in the Indian Ocean and await discovery there, unless they are migrants into the Atlantic via the Straits of Panama and the Caribbean.

TABLE 2—THE PERCENTGE OF SPECIES FOR EACH OF THE REGIONS STUDIED IN THE QUATERNARY WHICH ARE ENDEMIC, WHICH OCCUR ONLY IN TWO OCEANS AND WHICH OCCUR IN ALL THREE OCEANS.

	North Atlantic	Indian Ocean	S.W. Pacific
% Endemic	43.8	35.3	52.2
% One other ocean	6.2	30.5	22.1
% Two other oceans	50.0	34.2	25.7

DISTRIBUTION OF THE SPECIES

Many of the species and genera in the following lists are new and will eventually be described elsewhere. They are listed as *nomina aperta* species, although they have unpublished manuscript names in various theses (Smith, 1983 MS.; Dainty, 1984 MS.; Porter, 1984 MS.; Davies, 1981; Ainsworth, 1982 MS.).

Some of the species are also known from the Mediterranean. These are prefixed with an *"M"*. Pandemic species are listed in a more comprehensive form than endemics and only the former are illustrated in Pls. 1 and 2

DISCUSSION

Prior to the present study, only some 10 deep sea species can be seen from the literature to be pan-oceanic in their distribution. As Text-fig. 1 illustrates, many more species are much more widely distributed in the deep sea than previously thought. With 65 species occurring in (at least parts of) three oceans and 61 other species now known from two oceans in the Quaternary, the potential for finding even more pandemic species is high, especially given the relatively small areal extent of the samples studied here.

Of the 382 species recovered in the project, no less than 126 or 33% occur in more than one ocean; 17% occur in 3 oceans and 16% in two oceans. Of the 382 species, only approximately 3% have been recorded from more than one ocean prior to the present study.

An analysis of Tables 1 and 2 and Text-fig. 1 reveals a number of important phenomena:

1) Despite the greater numbers of samples studied there, the Quaternary deep sea fauna of the North Atlantic is less diverse than that of the Indian or S. W. Pacific Oceans. The lower diversity of Indian Ocean faunas compared to the Pacific may possibly be a reflection of sampling incidence,

TEXT-FIG. 2—Diagram to illustrate the stratigraphical distribution of the ostracod species common to three oceans.

S.W. Pacific			Indian Ocean			N. Atlantic			
M	P	Q	M	P	Q	M	P	Q	
	×	×			×			×	*Bairdoppilata* cf. *B. hirsuta*
×	×	×	×	×	×			×	*Bythocypris* cf. *B. mozambiquensis*
×		×			×			×	*Australoecia micra*
×	×	×	×		×	×	×	×	*Abyssocypris atlantica*
×	×	×			×			×	*Aratrocypris retoporrectus*
		×	×		×			×	*Saida* sp. 1
		×			×			×	*Chejudocythere* sp. 1
×	×	×	×	×	×	×	×	×	*Bosquetina mucronalatum*
	×	×			×		×	×	*Bythocythere* sp. 1
		×			×			×	*Ruggieriella* sp. 1
×	×	×			×			×	*Bythoceratina scaberrima*
		×			×			×	Indet. gen. (bythocytherid) sp. 1
	×	×			×			×	*Pseudocythere caudata*
×	×	×	×	×	×		×	×	*Eucythere parapubera*
×	×	×		×	×	×	×	×	*Eucythere* sp. 1
×	×	×			×	×	×	×	*Eucythere* sp. 2
	×	×			×		×	×	*Eucythere* sp. 3
	×	×			×			×	*Cytheropteron hamatum*
	×	×			×			×	*Cytheropteron garganicum*
×	×	×	×	×	×		×	×	*Cytheropteron testudo*
×	×	×		×	×		×	×	*Cytheropteron* cf. *C. testudo*
	×	×			×			×	*Cytheropteron branchium*
	×	×			×			×	*Cytheropteron pherozigzag*
		×			×	×	×	×	*Cytheropteron* sp. 1
	×	×	×	×	×			×	*Cytheropteron* sp. 2
×	×	×	×		×			×	*Cytheropteron* sp. 3
	×	×			×			×	*Cytheropteron* sp. 4
	×	×			×			×	*Cytheropteron* sp. 5
		×			×	×	×	×	*Pelecocythere sylvesterbradleyi*
×	×	×	×	×	×			×	*Peleocythere* sp. 1
×	×	×	×	×	×			×	*Pedicythere phryne*
	×	×			×			×	*Pedicythere polita*
	×	×	×		×			×	*Semicytherura*? sp. 1
	×	×		×	×		×	×	Gen. nov. A. *longipunctata*
		×	×		×			×	*Aversovalva* sp. 1
	×	×			×	×	×	×	*Aversovalva* sp. 2
		×			×			×	*Aversovalva* sp. 3
×	×	×			×		×	×	*Eucytherura calabra*
×	×	×			×		×	×	*Eucytherura* sp. 1
×	×	×			×			×	*Eucytherura* sp. 2
×	×	×			×	×	×	×	*Eucytherura* sp. 3
	×	×			×			×	*Heinia* sp. 1
	×	×			×		×	×	*Heinia* sp. 2
		×			×			×	*Microcythere* sp. 1
×	×	×	×		×		×	×	*Abyssocythereis sulcatoperforata*
	×	×			×			×	*Paijenborchella malaiensis cymbala*
		×			×			×	*Bathycythere vanstraateni*
×	×	×	×	×	×	×	×	×	"*Suhmicythere*" *suhmi*
	×	×			×			×	"*Hyphalocythere*" sp. 1
	×	×			×	×	×	×	*Agrenocythere* hazelae
×	×	×	×	×	×	×	×	×	*Henryhowella* aff. *H. asperrima*
	×	×			×		×	×	*Henryhowella* cf. *H. asperrima*
×	×	×	×	×	×	×	×	×	*Henryhowella dasyderma*
×	×	×		×	×	×	×	×	"*Oxycythereis*" *dorsoserrata*
		×			×			×	"*Oxycythereis*" sp.1
×	×	×		×	×	×	×	×	"*Thalassocythere*" *acanthoderma*
×	×	×	×	×	×	×	×	×	*Bradleya dictyon*
×	×	×			×			×	*Bradleya pygmaea*

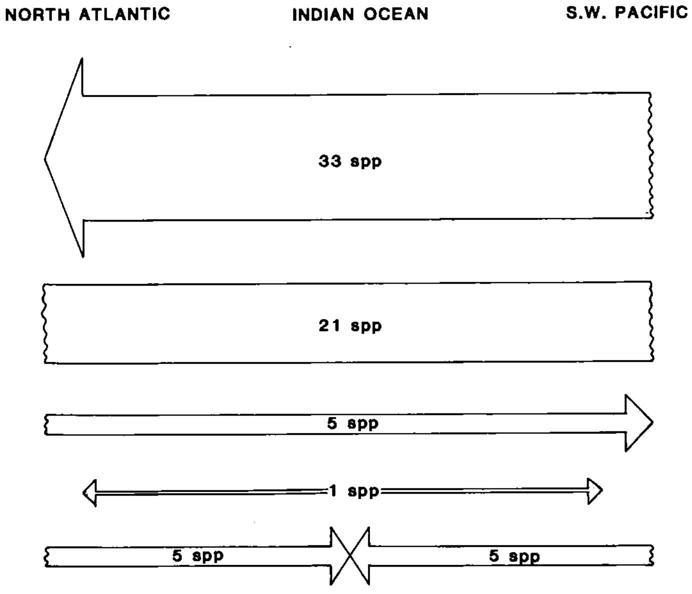
(*Continued*)

TEXT-FIG. 2—*continued.*

S.W. Pacific			Indian Occean			N. Atlantic			
		×			×			×	*Bradleya normani*
×	×	×	×	×	×	×	×	×	*Poseidnamicus major*
×	×	×			×			×	*Poseidnamicus minor*
	×	×	×	×	×	×	×	×	*Poseidonamicus praenudus*
		×			×			×	*Poseidonamicus nudus*
	×	×			×			×	*Phacorhabdotus* sp. 1
×	×	×	×		×		×	×	*Xestoleberis* sp. 1

but other evidence available to the authors suggests that the mean diversity per sample in the Pacific is higher than in the Indian Ocean. There is, therefore, a distinct diversity gradient from the Atlantic to the Indian Ocean and (but less distinct) from the Indian Ocean to the Pacific. This is not a phenomenon unique to the deep sea Quaternary Ostracoda. For example, Titterton and Whatley (this volume) demonstrate in shallow water ostracod faunas, a similar diversity gradient with an increase in numbers of species towards the Indonesian region across the Indian and Pacific Oceans. This phenomenon is apparently common to most marine crustacea, in that overall crustacean diversity is lower in the Atlantic and Eastern Pacific than it is in the Indo-Pacific (Abele, 1982).

2) Because they are entering an envinonment of less biological competition, it is easier for species to migrate down a diversity gradient than the reverse. Therefore, from first principles one would expect that those species in the deep sea Quaternary of the Atlantic which are also known from the Pacific, would have migrated there from the Pacific at some stage in the past via the Indian Ocean. The majority of these 68 species do seem to have their origins in the Pacific as do the 53 species common to the Pacific and Indian Oceans.



TEXT-FIG. 3—Diagram illustrating the inferred migration routes of Cainozoic deep sea Ostracoda.

TEXT-FIG. 4—Digram to illustrate the stratigraphical distribution of those ostracod species common to the Indian and Pacific Oceans.

S. W. Pacific			Indian Ocean			
M	**P**	**Q**	**M**	**P**	**Q**	
		×	×		×	*Bythocypris* aff. *B. madagascarensis*
		×			×	*Bairdoppilata* sp. 1
	×	×			×	*Zabythocypris* sp. 1
	×	×			×	*Zabythocypris ancipita*
	×	×			×	*Pontocypris* sp. 1
	×	×			×	*Abyssocypris* sp. 1
		×			×	*Australoecia* sp. 1
	×	×			×	*Argilloecia* sp. 1
	×	×			×	*Argilloecia* sp. 2
	×	×			×	*Argilloecia* sp. 3
	×	×	×	×	×	*Argilloecia* sp. 4
	×	×			×	*Argilloecia* sp. 5
		×			×	*Argilloecia* sp. 6
		×			×	*Argilloecia* sp. 7
		×			×	*Pseudocythere* sp. 1
×	×	×			×	*Monoceratina* sp. 2
		×			×	*Velibythere* sp. 1
		×			×	*Eucythere* sp. 4
		×			×	*Eucythere* sp. 5
		×			×	*Cytheropteron higashikawai*
	×	×			×	*Cytheropteron* sp. 7
	×	×			×	*Cytheropteron* sp. 8
	×	×			×	*Cytheropteron* sp. 9
		×			×	*Cytheropteron* sp. 10
		×			×	*Cytheropteron* sp. 11
	×	×			×	*Cytheropteron* sp. 12
×	×	×			×	*Cytheropteron* sp. 13
×	×	×			×	*Cytheropteron* sp. 14
		×			×	*Pedicythere* sp. 1
		×			×	*Swainocythere* sp. 1
		×			×	Gen. nov. A. sp. 1
		×			×	*Aversovalva*? *pinarense*
	×	×			×	*Aversovalva* sp. 4
×	×	×			×	*Aversovalva* sp. 5
		×			×	*Aversovalva* sp. 6
	×	×			×	*Aversovalva* sp. 7
	×	×			×	*Heinia semistriata*
	×	×			×	*Heinia* sp. 3
		×			×	*Gibboborchella*? sp. 1
		×			×	*Rockallia inceptiocelata*
		×			×	*Xiphichilus*? *gracilis*
		×			×	*Xiphichilus* sp. 1
×		×			×	"*Trachyleberis*" sp. 1
		×			×	"*Oxycythereis*" sp. 2
	×	×	×	×	×	"*Oxycythereis*" sp. 3
		×	×	×	×	*Ambocythere* sp. 1
		×			×	*Poseidonamicus punctatus*
		×			×	*Henryhowella* sp. 1
		×			×	*Xestoleberis* sp. 2
		×			×	*Xestoleberis* sp. 3

The gross Neogene and Quaternary stratigraphical distribution of the 65 cosmopolitan species in each of the three areas studied is given in Text-fig. 2. These geographical and stratigraphical records are based solely on our own studies or from manuscripts and published records from within the Aberystwyth Department. An analysis of the distributional data for the 65 species reveals the following:

a) Thirty-three species (50.7%) have their oldest record in the Pacific and have subsequently migrated (often demonstrably via the Indian Ocean) to the Atlantic.
b) Twenty-one species (32.3%) appear in each of the three oceans at the same time.
c) Five species (7.6%) seem to have originated in the Atlantic and subsequently migrated to the Pacific.
d) One species (1.5%) seems to have originated in the Indian Ocean and subsequently migrated to both the Atlantic and Pacific Oceans.
e) Five species (7.6%) seem to have originated in either the Atlantic or Pacific Oceans and subsequently migrated to the Indian Ocean.

Subsequent collecting may somewhat alter these figures, but the authors are confident that they are able to demonstrate a large scale migration during the Neogene-Quaternary interval outwards from the Southwest Pacific. This has previously been suggested by Whatley *et al.*, 1982, 1983, 1984 and Whatley 1983. The data on migrations is summarised in Text-fig. 3.

The data on the stratigraphical and geographical distribution of the 53 Quaternary species common to the Indian and S. W. Pacific Oceans is given in Text-fig. 4. The largest number of species have the same stratigraphical distribution in both oceans (24 spp., 45.2%). However, 21 species (39.6%) have their oldest record in the S. W. Pacific and seem subsequently to have migrated to the Indian Ocean. In the case of only 4 species (7.5%) does their origin seem to have been in the Indian Ocean from whence they have migrated to the Pacific.

3) Although many species are endemic to each of the three areas studied, the number of endemic genera in the deep sea is relatively low. To list these is fraught with controversy. In due course most of them will probably be recorded elsewhere. In our studies we have often initially thought that a genus was confined to a particular ocean or part of an ocean only to subsequently encounter it elsewhere. Two good examples are *Rockallia* and *Aratrocypris*. The former genus was originally described on the basis of a single species from Quaternary and Recent sediments from the Rockall Trough area of the N. E. Atlantic by Whatley, Frame and Whittaker (1978) and was thought to be confined there. Whatley *et al.* (1982) subsequently discovered that the genus dates from at least the Eocene in the S. W. Pacific and described a further five species from there and from Europe. Whatley and Coles (in press) have now encountered *Rockallia* at most sites in DSDP Leg 94 in the North Atlantic in the Miocene-Quaternary interval and Ayress has now found the genus in the Quaternary of the Indian Ocean.

Aratrocypris (Whatley *et al.*, in press) was first encountered in the Eocene to Quaternary of the S. W. Pacific and the Quaternary of the Indian Ocean. It was subsequently encountered by Cronin (1983) in the N. W. Atlantic and by Whatley and Coles (in press) in the Pliocene of Leg 94. Both these genera are known in much older strata in the Pacific than in the Atlantic and furnish good examples of migration from the former to the latter Ocean. This has also been the case with many species, one example being two unusual species of *Cytheropteron* with strange gill-like slits beneath and behind the alar process (Whatley and Ayress, 1986).

Unquestionably, not all ostracods entered the deep sea in the S. W. Pacific. *Buntonia*, although recorded from the Indian Ocean (Benson, 1972) is always more common in the Atlantic and *Agrenocythere* was a relatively late arrival in the Pacific where it is confined to abyssal depths (Whatley *et al.*, 1983). We have not encountered deep water species of *Nannocythere* outside the Atlantic where it occurs in both the North Atlantic (Porter, 1984 MS.) and in the South Atlantic/Southern Ocean (Coxill, 1985 MS.). The single species of *Muellerina* to have invaded deep water in the North Atlantic is clearly derived from adjacent stocks on the N. W. Europen continental shelf.

Space precludes a more detailed discussion of endemic taxa here. They can be established from Tables 3–9. However, these tables are somewhat misleading since they are concerned only with

TABLE 3—SPECIES ENCOUNTERED IN THE QUATERNARY OF ALL 3 OCEANS: NORTH ATLANTIC, INDIAN AND S. W. PACIFIC (M = also recorded in Mediterranean).

Bairdoppilata cf. *B. hirsuta* (BRADY, 1880)
Bythocypris cf. *B. mozambiquensis* Maddocks, 1969
M Australoecia micra (Bonaduce *et al.*, 1975)
Abyssocypris atlantica (Maddocks, 1977)
Aratrocypris rectoporrectus (Whatley *et al.*, 1985)
M Saida sp. 1
Chejudocythere sp. 1
Bosquetina mucronalatum (Brady, 1880)
Bythocythere sp. 1
M Ruggieriella sp. 1
M Bythoceratina scaberrima (Brady, 1886)
Indet. Gen. (bythocytherid) sp. 1
M Pseudocythere caudata Sars, 1866
Eucythere parapubera Whatley & Downing, 1983
Eucythere sp. 1
Eucythere sp. 2
Eucythere sp. 3
Cytheropeteron hamatum Sars, 1869
M Cytheropteron garganicum Bonaduce *et al.*, 1975
M Cytheropteron testudo Sars, 1869
Cytheropteron cf. *C. testudo* Sars, 1869
Cytheropteron branchium Whatley & Ayress, 1986
Cytheropteron pherozigzag Whatley & Ayress, 1986
Cytheropteron sp. 1
Cytheropteron sp. 2
Cytheropteron sp. 3
Cytheropteron sp. 4
Cytheropteron sp. 5
Pelecocythere sylvesterbradleyi Athersuch
Pleocythere sp. 1
M Pedicythere phryne Bonaduce *et al.*, 1975
M Pedicythere polita Colalongo & Pasini, 1980
M Semicytherura? sp. 1
M Gen. nov. A. *longipunctata* Breman, 1975
Aversovalva sp. 1
Aversovalva sp. 2
Aversovalva sp. 3
M Eucytherura calabra Colalongo and Pasini, 1980
M Eucytherura sp. 1
Eucytherura sp. 2
Eucytherura sp. 3
Heinia sp. 1
Heinia sp. 2
Microcythere sp. 1
Abyssocythereis sulcatoperforata (Brady, 1880)
M Paijenborchella malaiensis cymbula Ruggieri, 1950
M Bathycythere vanstraateni Sissingh, 1974
"*Suhmicythere*" *suhmi* (Brady, 1880)
M "*Hyphalocythere*" sp. 1
Agrenocythere hazelae (Bold, 1946)
Henryhowella aff. *H. asperrima* (Reuss, 1850)
Henryhowella cf. *H. asperrima* (Reuss, 1850)
Henryhowella dasyderma (Brady, 1880)
"*Oxycythereis*" *dorsoserrata* (Brady, 1880)
"*Oxycythereis*" sp. 1
"*Thalassocythere acanthoderma* (Brady, 1880)
Bradleya dictyon (Brady, 1880)
Bradleya pygmaea Whatley *et al.*, 1983
Bradleya normani (Brady, 1865)
Poseidonamicus major Benson, 1972
Poseidonamicus minor Benson, 1972
Poseidonamicus nudus Benson, 1972
Poseidonamicus praenudus Whatley *et al.*, 1983
Phacorhabdotus sp. 1
Xestoleberis, sp. 1

TABLE 4—SPECIES ENCOUNTERED IN THE QUATERNARY OF THE ATLANTIC AND INDIAN OCEANS, BUT NOT THE PACIFIC.

Heinia? sp. 1
Poseidonamicus pintoi Benson, 1972
Anchistroches cf. *antemacela* Maddocks, 1969
Rockallia enigmatica Whatley *et al.*, 1978
Argilloecia sp. 1.

TABLE 5—SPECIES ENCOUNTERED IN THE QUATERNARY OF THE ATLANTIC AND PACIFIC OCEANS BUT NOT IN THE INDIAN OCEAN.

Monoceratina sp. 1
Cytheropteron sp. 6
Rostrocythere? sp. 1

TABLE 6—SPECIES ENCOUNTERED IN THE QUATERNARY OF THE INDIAN AND PACIFIC OCEANS, BUT NOT IN THE ATLANTIC.

Bythocypris aff. *madagascarensis* Maddocks, 1969
Bairdoppilata sp. 1
Zabythocypris ancipita Maddocks, 1969
Zabythocypris sp. 1
Pontocypris sp. 1
Abyssocypris sp. 1
Australoecja sp. 1
Argilloecia sp. 1
Argilloecia sp. 2
Argilloecia sp. 3
Argilloecia sp. 4
Argilloecia sp. 5
Argilloecia sp. 6
Argilloecia sp. 7
Pseudocythere sp. 1
Monoceratina sp. 2
Velibythere sp. 1
Eucythere sp. 4

(*Continued*)

TABLE 6—*Continued.*

Eucythere sp. 5
Cytheropteron higashikawai Ishizaki, 1981
Cytheropteron sp. 7
Cytheropteron sp. 8
Cytheropteron sp. 9
Cytheropteron sp. 10
Cytheropteron sp. 11
Cytheropteron sp. 12
Cytheropteron sp. 13
Cytheropteron sp. 14
Pedicythere sp. 1
Swainocythere sp. 1
Gen. nov. A. sp. 1
M? Aversovalva? pinarense Bold, 1973
Aversovalva sp. 4
Aversovalva sp. 5
Aversovalva sp. 6
Aversovalva sp. 7
Eucytherura sp. 4
Eucytherura sp. 5
Cluthia sp. 1
Palmoconcha? semistriata Kingma, 1948
Palmoconcha sp. 3
Gibboborchella? sp. 1
Rockallia inveptiovelata Whatley *et al.*
Xiphichilus? gracilis (Neale, 1967)
Xiphichilus? sp. 1
"*Trachyleberis*" sp. 1
"*Oxycythereis*" sp. 2
"*Oxycythereis*" sp. 3
Ambocythere sp. 1
Poseidonamicus punctatus Whatley *et al.*, 1983
Henryhowella sp. 1
Xestoleberis sp. 2
Xestoleberis sp. 3

TABLE 7—LIST OF GENERA AND NUMBERS OF SPECIES ENCOUNTERED ONLY IN THE NORTH ATLANTIC QUATERNARY.

	No. species		No. species
Bairdoppilata	1	*Swainocythere*	1
Neonesidea	1	*Muellerina*	1
Bythocypris	4	*Loxoconcha*	1
Macrocypris	3	*Nannocythere*	1
Argilloecia	8	*Echinocythereis*	1
Propontocypris	1	*Ambocythere*	2
Bythocythere	2	*Abyssocythere*	1
Pseudocythere	2	*Buntonia*	2
Eucythere	3	*Agrenocythere*	1
Parakrithe	2	*Cytherella*	1
Cytheropteron	11	*Polycope*	5
Eucytherura	2		

Many of the samples studied by Porter and Davies were heavily contaminated by allochthonous material; these amounting to some 40 species, have not been included in this table. Some few shallow water contaminants were also encountered in Leg 94; these were probably ice rafted.

TABLE 8—LIST OF GENERA AND NUMBERS OF SPECIES ENCOUNTERED ONLY IN THE INDIAN OCEAN QUATERNARY.

	No. species		No. species
Neonesidea	2	*Eucythere*	4
Macrocypris	3	*Typhlocythere*	1
Pontocypris	1	*Tuberculocythere*	1
Maddocksella	2	*Cluthia?*	1
Argilloecia	6	*Abyssocythere*	1
Saida	1	*Limburgina?*	1
Pseudocythere	2	*Henryhowella*	1
Vijtjasiella	1	*Ambocythere*	1
Rhombocythere	2	"*Trachyleberis*"	1
Eucythere	6	"*Oxycythereis*"	1
Cytheropteron	15	*Bradleya*	2
Pedicythere	4	*Cytherella*	4
Aversovalva	3		

TABLE 9—LIST OF GENERA AND NUMBERS OF SPECIES ENCOUNTERED ONLY IN THE PACIFIC OCEAN QUATERNARY.

	No. species		No. species
Bairdoppilata	2	*Eucytherura*	6
Neonesidea	1	*Cluthia*	1
Anchistrocheles	2	*Abyssocythere*	3
Macrocypris	2	*Acanthocythereis*?	1
Macrocyprina	1	*Actinocythereis*?	2
Bythocypris	2	*Ambocythere*	2
Zabythocypris	1	*Cletocythereis*	1
Paracypris	1	"*Trachyleberis*"	2
Australoecia	6	"*Oxycythereis*"	4
Aratrocypris	1	Trachyleberid Indet. gen. Z.	1
Argilloecia	15	Trachyleberid Indet. gen. E.	2
Propontocypris	2	*Bradleya*	6
Bythoceratina	2	*Poseidonamicus*	4
Pseudocythere	1	*Agrenocythere*	1
Bythocythere	2	*Henryhowella*	2
Parakrithe	2	"*Thallassocythere*"	4
Eucythere	12	"*Suhmicythere*"?	1
Copytus	1	Trachyleberid Indet. gen. A.	2
Cytheropteron	24	Trachyleberid Indet. gen. B.	1
Hemicytherura	1	*Paijenborchella*	2
Gen. nov. A.	1	*Xestoleberis*	2
Indet. gen. F.	1	*Cytherella*	3
Aversovalva	4	*Polycope*	2

Quaternary records. A more detailed account of the evolution of pandemic distribution from original endemic ostracod faunas will be the subject of a future paper.

CONCLUSIONS

Clearly demonstrated in the present paper is the cosmopolitan character of deep sea Ostracoda in the Quaternary. This is by no means unique to ostracods. Many invertebrate groups are, in the deep sea, similarly pandemic in their distribution. For example, Marshall (1979) comments on the widespread distribution of many species of sponges, coelenterates, bivalves, polychaetes, isopods, decapods, brachiopods, and various members of the Echinodermata. Certain benthonic Foraminifera are also cosmopolitan (Gooday, pers. comm., 1985) as are some benthonic fishes, particularly tripod-fish (Marshall, 1979).

Most of these, however, have pelagic larval stages which obviously facilitiate their dispersal. Despite their lack of pelagic larvae the podocopid and platycopid ostracods discussed here are capable of extremely widespread distribution. To what extent this sub-ubiquitous to ubiquitous distribution has been achieved by active migration is debatable and beyond the scope of the present study. However, a brief glance at a map of the circulation patterns of currents in the deep oceans demonstrates no series of such currents which would, in an overall sense, facilitate the passive migration of ostracods from the S. W. Pacific via the Indian Ocean to the North Atlantic. If, however, the trend of migration was eastwards across the Pacific, then deep ocean bottom currents could assist migration through the Drake Passage into the Atlantic. Currently, we have no good data from the S. E. Pacific to test this possibility although it is hoped to rectify this in the near future. Given the data in hand as synthesized in Text-fig. 1, we are obliged to postulate that the major component of migration was westwards across the Indian Ocean to the Atlantic and this contention is supported by the diversity gradient outlined in Table 1.

Because of its essentially thermospheric character (Benson, 1971), the Tethys was probably not of major consequence as a migration route for most of the ostracods studied here. However, evidence that it played some part is provided by the fact that 16 of the 65 species to occur in the Quaternary of the Pacific, Indian and Atlantic Oceans are also known from the Mediterranean.

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APPENDIX 1—THE LOCATION OF THE SAMPLES USED IN THIS STUDY.

a) Atlantic

NATO Cores (Porter, 1984 MS.)

Cores No.	*Position*		*Water Depth* (m)	*Sample below seabed* (cm)
L4	Lat. 43°03'N;	Long. 23°16'W.	3422	75–79
L5	Lat. 43°01'N;	Long. 17°14'W.	4566	7.5–15.5
				50–55
				100–105
N3	Lat. 48°40'N;	Long. 24°31'W.	4096	9.5–14.5
				70–75
N4	Lat. 48°55'N;	Long. 17°12'W.	4780	21–25
				70–75
01	Lat. 52°01'N;	Long. 12°40'W	938	7.5–11.5
				55–60
				105–110
				155–160
				205–210
				255–260
02	Lat. 52°00'N.	Long. 17°50'W.	4530	10–15
				60–65
				93–96
P2	Lat. 55°09'N;	Long. 22°45'W.	2931	65–70
				115–120
				158–162.5
R2	Lat. 60°54'N;	Long. 13°05'W.	1678	50–55
				100–105
				155–160
R3	Lat. 60°58'N;	Long. 20°58'W.	2177	50–55
				100–105
				155–160
R4	Lat. 61°04'N;	Long. 32°20'W.	2747	25–29
				75–79
				125–129
				143.5–148.5
R5	Lat. 61°02'N;	Long. 39°00'W.	2743	26.5–30.5
				30–40
				75–79
				135–140
S1	Lat. 64°00'N;	Long. 02°00'W.	2701	50–55
				100–105
S3	Lat. 64°02'N;	Long. 28°57'W.	1690	4.5–90
				59–62
T2	Lat. 68°28'N;	Long. 00°56'W.	2853	40–45
				140–145
				155–159
T3	Lat. 68°36'N;	Long. 06°55'W.	3006	21.5–26.5
				70–75
				130–135
T4	Lat. 68°37'N;	Long. 18°21'W.	1200	5–9.5
				100–105

(*Continued*)

Appendex 1—*Continued.*

Station	*Position*			*Water Depth*(m)
RRS *Challenger* Box Cores. Cruise 10/76 (Davies, 1981 MS).				
3	Lat. 59°37.10'N;	Long. 07°00.10'W.		1040
4A1	Lat. 60°09.60'N;	Long. 08°12.50'W.		912
4A2	Lat. 60°10.64'N;	Long. 08°12.40'W.		901
8	Lat. 60°04.70'N;	Long. 05°55.70'W.		1065
12A	Lat. 60°12.80'N;	Long. 09°38.50'W.		928
13	Lat. 60°00.80'N;	Long. 10°37.39'W.		1148
15	Lat. 59°02.60'N;	Long. 11°05.10'W.		1963
16	Lat. 58°24.00'N;	Long. 12°34.00'W.		1585
RRS *Challenger* Cruise 16/76				
A2	Lat. 55°02.55'N;	Long. 12°05.76'W.		2880
1	Lat. 54°40.94'N;	Long. 15°10;89'W.		2500
2	Lat. 54°52.50'N;	Long. 15°34.16'W.		2200
4	Lat. 55°17.41'M;	Long. 15°53.23'W.		1500
12	Lat. 57°07.37'N;	Long. 12°18.67'W.		2000
14	Lat. 56°27.14'N;	Long. 10°22.89'W.		1000
RRS *Challenger* Cruise 7/77				
A2	Lat. 55°01.55'N;	Long. 12°05.76'W.		2880
3	Lat. 56°32.30'N;	Long. 09°17.30'W.		1036
4	Lat. 56°32.00'N;	Long. 09°28.00'W.		1260
5	Lat. 56°36.40'N;	Long. 09°40.10'W.		1650
6	Lat. 56°42.70'N;	Long. 09°42.70'W.		1750
7	Lat. 56°54.00'N;	Long. 09°54.30'W.		2000
8	Lat. 56°55.20'N;	Long. 10°29.80'W.		2250
RRS *Challenger* Cruise 12/77				
A2	Lat. 55°03.40'N;	Long. 12°02.40'W.		2880
1	Lat. 53°47.00'N;	Long. 14°59.00'W.		3000
2	Lat. 52°37.90'N;	Long. 16°29.50'W.		3500
3	Lat. 52°12.30'N;	Long. 16°51.30'W.		4000
A1	Lat. 49°30.20'N;	Long. 16°30.30'W.		4820
P1	Lat. 49°51.50'N;	Long. 15°06.60'W.		4500
P2	Lat. 50°03.10'N;	Long. 14°22.20'W.		4000
P4	Lat. 50°34.80'N;	Long. 13°28.20'W.		2600
P6	Lat. 51°19.60'N;	Long. 13°08.40'W.		1500
P7	Lat. 51°54.70'N;	Long. 12°46.70'W.		1000
RRS *Challenger* Cruise 6/73				
4	Lat. 66°52'N;	Long. 10°01'W.		1993
6	Lat. 55°03'N;	Long. 12°29'W.		2900
10	Lat. 56°37'N;	Long. 11°04'W.		2540
RRS *Shackeleton* Cruise				
F	Lat. 59°06'N;	Long. 10°07'W.		1150
G	Lat. 59 03'N;	Long. 10°08'W.		1150
H	Lat. 59 12'N;	Long. 10°09'W.		900
DSDP Leg. 94. (Whatley and Coles, in press)				
Site/Hole	*Position*		*Core* c.c.	*PDWD*(m)
606	Lat. 37°20.32'N;	Long. 35°29.99'W.	1–5	3022
607	Lat. 41°00.07'N;	Long. 32°57.44'W	1, 3, 5	3427
608	Lat. 42°50.21'N;	Long. 23°05.25'W.	1, 3, 5	3526
608A			1, 3, 5	
609	Lat. 49°52.67'N;	Long. 24°14.29'W	7, 9, 11, 13, 15	3884
609A			1, 2	
609C			1	

(*Continued*)

Appendix 1—*Continued.*

Station	*Position*			*Water Depth*(m)
609B			1–3, 5, 7, 9, 11, 13, 15	
610	Lat. 53°13.30′N;	Long. 18°53.21′W.	1–5	2417
610C			2–4	
611D	Lat. 52°50.47′N;	Long. 30°19.58′W.	1	3195

b) Indian Ocean DSDP

Site	*Position*		*Core*	*Section*	*PDWD* (m)
254	Lat. 30°58.15′S;	Long. 87°53.72′E.	1	2, 3	1253
			2	1	
253	Lat. 24°52.65′S.	Long. 87°21.97′E.	1	1–5	1962
214	Lat. 11°20.21′S;	Long. 88°43.08′E.	1	1, 3, 5	1665
			2	1, 3, 5	
			3	1, 3	
264	Let. 34°58.13′S;	Long. 112°02.68′E.	1	1, 3, 5, 6	2876
258	Lat. 33°47.69′S;	Long. 112°28.4′E.	1	1, 3, 5	2793
			2	2, 3	
			3	1	
259	Lat. 29°37.05′S;	Long. 112°41.78′E.	1	2–5	4696

c) Pacific DSDP

203	Lat. 22°09.22′S;	Long. 177°32.77′W.	1	1, 4	
			2	1	
			3	5	
			4	1, 2	
200	Lat. 12°50.20′N;	Long. 156°47.00′E.	1	1–6	
			2	1	
282	Lat. 42°14.76′S;	Long. 143°29.18′E.	1	1, 2, 4	4202
281	Lat. 47°59.84′S;	Long. 147°45.85′E.	2	1–4	1591
277	Lat. 53°13.43′S;	Long. 166°11.48′E.	1	2	1214
279/A	Lat. 51°20.14′S;	Long. 162°38.10′E.	1	1–3	3341
284	Lat. 40°30.48′S;	Long. 167°40.81′E.	1	2, 3, 5	1066
			3	1, 5	
208	Lat. 26°06.61′S;	Long. 161°13.27′E.	1	3	1545
			2	3	
			3	3	
			4	2	
207	Lat. 36°57.75′S;	Long. 165°26.06′E.	1	2	1389
			2	2	
			3	2	
			4	1	
206	Lat. 32°00.75′S;	Long. 165°25.15′E.	1	1	3196
			4	3	
			6	2	
			8	2, 6	
			10	1	
			11	3	

VIII

Biogeography and Palaeobiogeography

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The Provincial Distribution of Shallow Water Indo-Pacific Marine Ostracoda: Origins, Antiquity, Dispersal Routes and Mechanisms

ROSEMARY TITTERTON AND ROBIN C. WHATLEY
Robertson Research International, Llandudno and
University College of Wales, Aberystwyth, Wales

ABSTRACT

The geographical distribution of Indo-Pacific and Southern Ocean shallow marine podocopid and platycopid ostracods of Tertiary to Recent age is recorded. Some 285 publications were consulted and the 2,599 species are shown to fall into 13 zoogeographical provinces. These range considerably both in areal extent and the degree of endemism of their faunas. The provinces are: East African, Arabian, Bengalian, East Indian, Kymerian, Japanese, Australian, New Zealand, Southern and Southwestern Pacific, Western-North and Central American, Western South American, and Southern Ocean. A series of link diagrams and tables demonstrate both the endemism and the affinities, at the species level, of the faunas of the various provinces. The overall level of endemism is high. Less than 20% of the faunas of any province occur outside that province; the mean for all provinces is only 8%. Faunal relationships between provinces and the age of occurrences of various species are used to demonstrate that the East Indian, Southwest Pacific region was a locus from which ostracods have, since the Miocene, migrated out, particularly westwards around the Indian Ocean to the Bengalian, Arabian and East African Provinces. A northward and southward migration from this locus is also demonstrated. A limited eastward migration is also shown. Sixteen species which occur as fossils in the Solomon Islands are used to document this migration, which seems to have taken place post the closure of the Tethys, from which time the 13 provinces also date. Various mechanisms by which shallow marine ostracods can migrate over the very large distances involved in the Indo-Pacific are discussed. It is concluded that probably the major factor is passive migration by ocean currents.

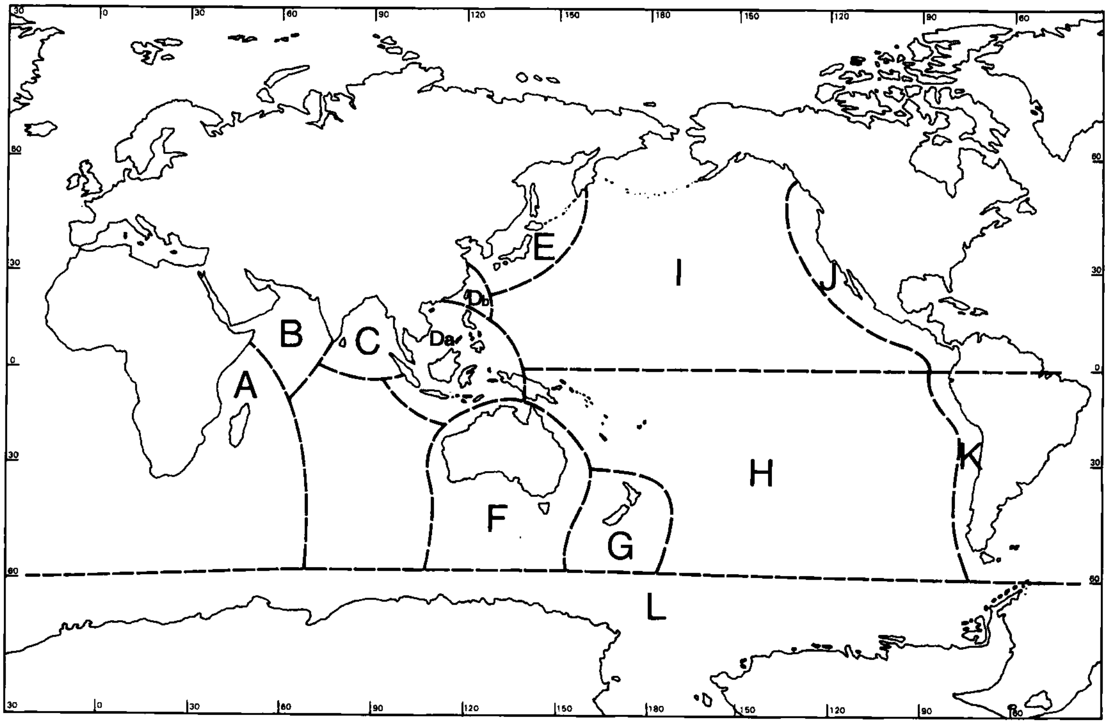
INTRODUCTION

The present paper arose from a doctoral study of Recent, shelf and littoral Ostracoda of the Solomon Islands carried out by Titterton at Aberystwyth under the supervision of Whatley. This study, in which 152 species belonging to 55 genera (of which 69 species and 3 genera are new) were described will be published elsewhere.

One of the objects of the study of the Solomon Islands fauna was to attempt to determine its origins and closest affinities. To this end, all published literature on Tertiary to Recent Ostracods from the Indo-Pacific and adjacent southern ocean has been analysed. This includes studies from adjacent coastal areas such as East Africa and the Western seaboard of North and South America, etc. Since the study of the Solomon Islands fauna was restricted to the Podocopid and Platycopina, only data on these groups is presented here. For similar reasons, only data on littoral and shelf species is included.

The number of papers analysed was 285 and the study is up to date to April 1985. A total of 2599 species were recorded and their geological and geographical distribution noted. Space precludes the listing of the various species here. They can be found in Titterton (1984 MS.). The present study, therefore, is based on a numerical analysis of the species.

Although we encountered some species which are very widespread geographically and fairly long ranging, the vast majority are very restricted both geographically and in time. Approximately 70% of the species are recorded only from very limited geographical areas.



TEXT-FIG. 1—Map showing the 13 zoogeographical provinces in the Indo-Pacific region, based on Ostracoda.

THE PROVINCIAL DISTRIBUTION OF SHALLOW WATER INDO-PACIFIC OSTRACODA

Compared to our knowledge of the Tertiary to Recent ostracoda of Europe and North America, we know relatively little of Indo-Pacific faunas. Although studies in the region began as early as 1850, only 85 papers on fossil and Recent ostracods were published prior to 1945. Since that date, approximately 200 papers have been written, reflecting the growing interest in this extensive region. Many of these works have been concerned with faunas of a limited area. The faunas of some areas within the Indo-Pacific are relatively well known; *viz* Japan, the west coast of North America and, to a lesser extent, Australia, Indonesia and South Africa. However, large areas have been substantially neglected, particularly the Pacific Islands and the northwestern coast of South America. Subsequent studies in these and other areas may alter some of the details of the present study, but the major features are not likely to change.

The reasons for endemism are well known being principally due to physical barriers. Latitude and the deep oceans are the principal barriers to the distribution of Indo-Pacific shallow water ostracods. In the present study, the Ostracoda of the Indo-Pacific fall into 13 zoogeographical provinces. These vary considerably in the geographical areas they encompass and in the total number of species recorded from them (Table 3). Those taxa which typify the various provinces are given in Titterton (1984 MS.) and will be eventually published elsewhere. Space requirements preclude their inclusion here. The 13 provinces are shown in Text-fig. 1.

Although Benson's (1964) paper on the provincial distribution of the Pacific has been considered, the Pacific provinces proposed in the present study are not based on this work. Benson recognized 11 realms in the Pacific. He comments (p. 3880, that "The effects of temperature, salinity, bottom sediment, depth, and immigration history are strongly suggested within the distribution of the 465 species thus far identified or described". The present study concentrates on the immigrant history of the various faunas in an attempt to elucidate the origins of the Recent Indo-Pacific Ostracoda as a whole.,

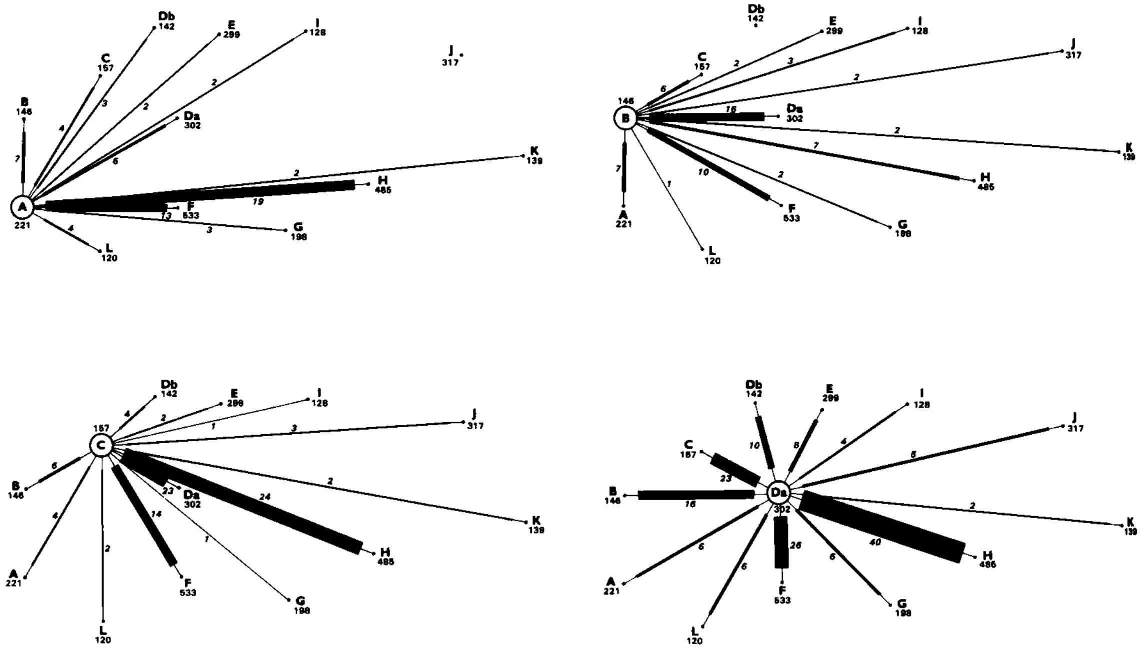
A SYNPOSIS OF THE NATURE OF THE 13 PROVINCES

The following observations have been made on the provinciality of the faunas of the various provinces and of the degree of affinity between provinces.

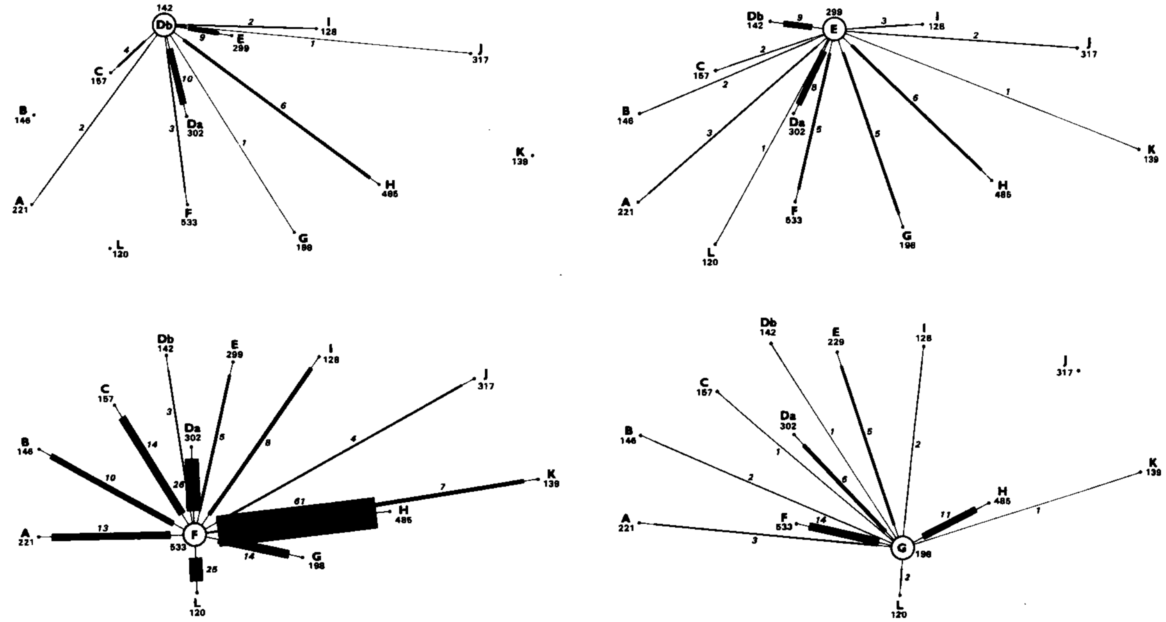
The Recent marine fauna of the Eastern African Province (Province A) is comparatively poorly known, the most extensive work being by Hartmann (1974). Other authors have studied species from 1 or 2 localities or have concentrated on a single taxonomic group from scattered localities. A total of 221 species have been recorded from this province. The provinciality of the fauna of this province is relatively poor (Text-fig. 2a). The fauna shows strongest affinity with that of the Southern and Southwestern Pacific (Province H), with 19 common species. The fauna also shows strong affinities with that of the Australian Province (Province F) with 13 species being common. However, no species were common with the Western North and Central American Province (Province J).

The provinciality of the fauna of the Arabian province (Province B) is strong; however, relatively few species (146) have been recorded from this region and the ostracods have not been comprehensively studied (Text-fig. 2b). The fauna displays strongest affinity with that of the East Indian (Province Da), 16 species being common to both. No species are common with Provinces B and Db (Khymerian).

Similarly, the Recent faunas of the Bengalian Province (Province C) are poorly known, the



Text-fig. 2—Link diagrams illustrating the number of endemic species and number of species common with other provinces for four zoogeographical provinces. 2a, East African Province; 2b, Arabian Province; 2c, Bengalian Province; 2d, East Indian Province.



Text-fig. 3—Link diagrams illustrating the number of endemic species and number of species common with other provinces for four zoogeographical provinces. 3a, Kymerian Province; 3b, Japanese Province; 3c, Australian Province; 3d, New Zealand Province.

majority of the 157 species being recorded by Brady (1866) and Scott (1905) from around Ceylon. The fauna of this province shows a comparatively strong connection with that of the East Indian (Province Da) with 23 species common and the Southern and Southwestern Pacific (Province H) with 24 common species (Text-fig. 2c).

The Neogene and Recent faunas of the East Indian Province (Province Da) are comparatively well documented. The provinciality of the fauna is poor; only 126 species of the 302 recorded in this province are endemic. The fauna displays strongest links with that of the Southern and Southwestern Pacific (Province H) as 40 species have been recorded in both (Text-fig. 2d). Affinity is also strong with the fauna of the Bengalian (Province C) with 23 common species, Australian (Province F) with 26 common species and the Khymerian (Province Db) with 10 common species.

The study by Kingma (1948) paved the way for the re-evaluation of the taxonomy of the ostracods of the Indo-Pacific. This work has been continued more recently in this region by Keij (1966–1979) and two further studies are currently being undertaken at Aberystwyth.

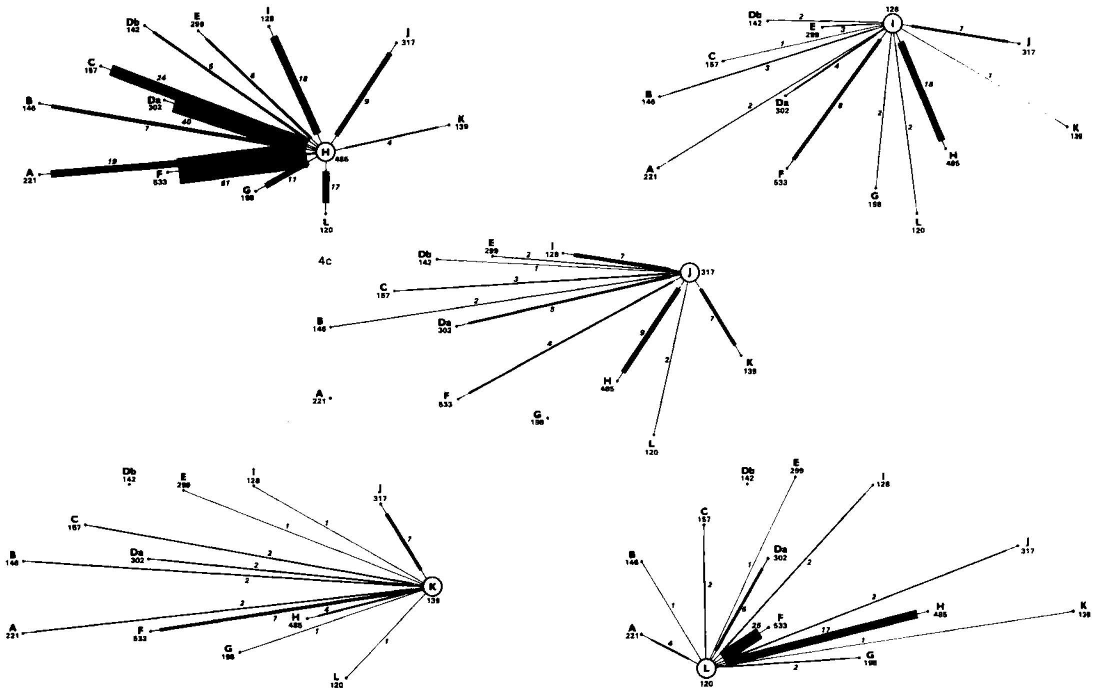
The majority of work in the Khymerian (Province Db) is comparatively recent, initiated by studies on faunas from Vietnam by Schneider (1971) and Herrig (1975–1978) and on the faunas of Taiwan by Hu and others (1975–1977) and Malz (1980). The provinciality of the fauna of this province is strong; 96 of the 142 recorded species appear to be endemic. The fauna demonstrates strongest connections with that of the adjacent provinces: Da (East Indian) to the south has 10 species in common and E (Japan) to the north has 9 species in common (Text-fig. 3a). No common species occur between this province and provinces B (Arabia), K (Western South American) and L (Southern Ocean).

The Neogene and Recent faunas of Japan (Province E) are very well documented. Of the 299 species recorded in this province, 244 appear to be endemic. The fauna shows strongest and equal affinity with that of Da (East Indian) and Db (Khymerian) with 9 species being common in each case (Text-fig. 3b). Six species are common with the Southern and Southwestern Pacific (Province H). The majority of species in this province have been recorded by Hanai (1957–1961) and Ishizaki (1963–1977).

The greatest number of species listed (533) have been recorded in and around Australia (Province F) from the Tertiary and Recent; the majority of Recent species being recorded by Hartmann (1978–1982). The provinciality of the fauna appears to be poor and the fauna shows strong affinities with 6 other provinces. The strongest links are with the fauna of the adjacent province H (Southern and Southwestern Pacific) to the north-east with 61 common species (Text-fig. 3c). Twenty-six species are common to Province Da (East Indian), which is also adjacent to the north-west. The connection with the faunas of the Southern Ocean (O) is illustrated by the 25 species that are common and connections to the east with 14 species common to New Zealand (G). Province F also has links with the Indian Ocean region with 13 species common with Eastern Africa (Province A) and 14 with the Bengalian Province (Province C).

The work by Hornibrook (1952) on the ostracods of New Zealand (Province G) was an important contribution to the understanding of Pacific ostracods. The relatively few species in the fauna (198) exhibit strong provinciality; strongest links are with Australia (F) to the west with 14 common species (Text-fig. 3d). There is also a connection to the north and east with 11 species common to the Southern and Southwestern Pacific (Province H). There are no common species with Western North and Central America (Province J).

Province H, Southern and Southwestern Pacific is rather difficult to define on the distribution of species as provinciality of the fauna is poor. This may be a function of our limited knowledge of the ostracods of this region. Of the 485 species recorded in the province, only 182 appear to be endemic. The fauna demonstrates strongest affinity with that of Australia (Province F) to the southwest with 61 common species (Text-fig. 4a). Links are also strong to the northwest with 40 species also



TEXT-FIG. 4—Link diagrams illustrating the number of endemic species and number of species common with other provinces for five zoogeographical provinces. 4a, Southern and Southwestern Pacific Province; 4b, Northern and Central Pacific Province; 4c, Western North and Central American Province; 4d, Western South American Province; 4e, Southern Ocean Province.

occurring in the East Indies (Province Da). Connections with the Indian Ocean region are illustrated by the 24 species common to Province C (Bengalian) and 19 species common to Province A (Eastern African). Connections to the north and south are also indicated as 18 species are shared with Province I (Northern and Central Pacific) and 18 species shared with Province L (Southern Ocean).

The Northern and Central Pacific (Province I) encompasses several isolated localities, mainly from around the islands of the Northern and Western Central Pacific Ocean. The faunas from these scattered localities show little affinity with each other or with other provinces. Affinities of the 128 species recorded from this region are strongest with the Southern and Southwestern Pacific (Province H) with 18 common species (Text-fig. 4b). Links with the faunas of the western coasts of Northern and Central America are indicated by the 7 species common with J. There is also some connection with Australia (F) with 8 common species.

The Recent faunas of Western North and Central America (Province J) are relatively well documented by a variety of authors. The fauna of 317 species, shows relatively poor affinity with the Pacific Ocean as only 7 species also occur in I (Northern and Central Pacific) and 9 in H (Southern and Southwestern Pacific (Text-fig. 4c). There is no connection with the faunas of either Eastern Africa (A) or New Zealand (G).

The ostracods of Western South America (Province K) are poorly known, most of the species being recorded by Hartmann (1962, 1965) and Ohmert (1968, 1971). The provinciality of the fauna of 139 species is strong (Text-fig. 4d). Similarly, the ostracods of Province L (Southern Oceans) are poorly documented, the majority of the 120 species being recorded prior to 1919 (Text-fig. 4e), mainly from south of the Indian Ocean.

THE ENDEMISM OF THE FAUNAS

The degree of endemism (or provinciality) of shallow water Indo-Pacific Cainozoic and Recent ostracods is well illustrated in Text-figs. 2–4. The following tables also illustrate numerically the levels of endemism in these faunas. One means of doing this is to analyse the extent to which species are subsequently recorded in provinces other than those in which they were first recorded. Data based on absolute numbers of species which occur in more than one province is summarized in Table 1.

TABLE 1—NUMBER OF SPECIES WHICH OCCUR IN MORE THAN 1 PROVINCE.

Provinces in which species were first recorded.	A	B	C	Da	Db	E	F	G	H	I	J	K	L	
A	*	5	2	3	2	1	8	5	8	2	0	2	2	40
B	3	*	1	1	0	0	2	0	2	2	0	0	0	11
C	1	5	*	5	0	0	3	0	4	0	1	0	0	19
Da	3	15	18	*	2	8	13	4	18	2	2	0	2	87
Db	0	0	4	8	*	3	3	1	4	1	1	0	0	25
E	2	2	2	0	6	*	3	1	3	3	0	0	2	24
F	5	8	11	13	0	2	*	9	22	7	2	3	13	95
G	0	2	1	2	0	4	5	*	2	1	0	0	1	18
H	11	5	20	22	2	3	39	9	*	15	2	2	10	150
I	0	1	1	1	1	0	1	1	3	*	0	0	1	10
J	0	2	2	3	0	2	2	0	7	7	*	5	0	30
K	0	2	0	2	0	1	4	1	2	1	2	*	1	16
L	2	1	2	4	0	0	11	1	7	1	2	0	*	31
	27	48	64	54	13	24	94	32	82	42	12	12	32	

Number of species subsequently recorded in each province.

In 7 provinces (A, Da, Db, F, H, J, K) the number of species recorded for the first time in the province exceed the number of species first recorded elsewhere but subsequently recorded in the province. In the case of the remaining 6 provinces, (B, C, E, G, I, L), the reverse occurs.

Table 2 shows the number of species common to any two provinces and again can be used to assess the degree of endemism of any one province.

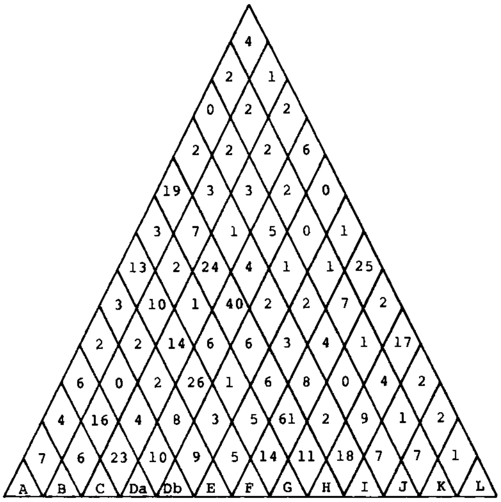
Numerical and percentage data are combined in Table 3 for all 13 provinces. Columns 1 and 2 give the number and percentage of species restricted to each province and the latter is expressed in rank order below:

Only the East Indian, Bengalian, Southern and Southwestern Pacific and the Southern Ocean Provinces have less than 50% endemic species. The level of provincialism in the faunas of the Western North and Central American, Japanese, Western, South American, New Zealand and the Khymerian Provinces is very high with over 60% of the species being endemic and that of the first two provinces being exceptionally high with more than 80% endemism.

Columns 3 and 4 of Table 3 are important guides to the degree of overall endemism of Indo-Pacific shallow water ostracod faunas and to certain provinces in particular. Column 3 gives the number and column 4 the percentage of species which were first recorded only in each of the 13 provinces, but which have subsequently been recorded in other provinces. The percentage of these species is always less than 20% and in only 4 provinces is it more than 10%. It can be seen, therefore, that there is a mean of only 8% of species for all 13 provinces, which once recorded in a province are subsequently recorded elsewhere.

It is the high degree of endemism which enables the recognition of the various provinces considered here. However, it is those species which occur in two or more provinces which make it

Table 2—The Number of Species Common to Two Provinces.



	%
Province J, Western North and Central American	81.7
Province E, Japanese	80.2
Province K, Western South American	72.7
Province G, New Zealand	69.2
Province Db, Khymerian	67.6
Province A, East African	57.9
Province F, Australian	56.4
Province B, Arabian	56.2
Province I, North and Central Pacific	55.5
Province Da, East Indian	39.4
Province C, Bengalian	37.4
Province H, Southern and Southwestern Pacific	36.7
Province L, Southern Ocean	35.0

possible to discuss the relationships between the faunas of various provinces, the nature of faunal migrations between them, and therefore, the possible origins of the faunas.

FAUNAL RELATIONSHIPS BETWEEN PROVINCES THROUGHOUT THE INDO-PACIFIC

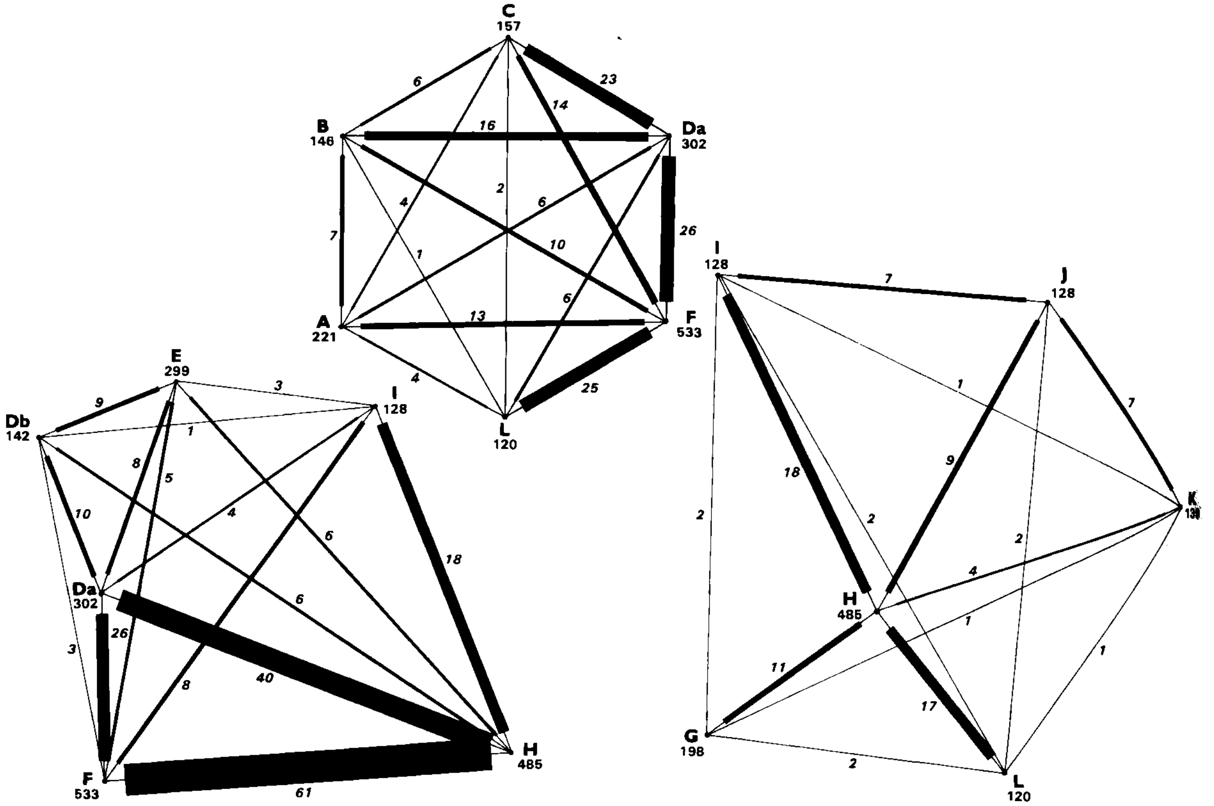
Text-figure 5 is a composite species relationship diagram which brings together the number of species common between all the provinces. Very clearly illustrated in Text-fig. 5 are the following phenomena:

1. More species occur in the Bengalian, East Indian, Australian and S. W. Pacific regions than elsewhere and the number of common species between provinces in these regions is markedly greater than elsewhere. The number of common species between adjacent and near-adjacent provinces in the complex of the East Indies, Bengal, Australia, Southern and Southwestern Pacific area are, with only one exception, the only ones to exceed 20. Trans-Pacific faunal links are very tenuous, even more so than the relatively poor trans-Indian Ocean links. The area of strongest faunal links is also the area where the greatest number of provinces are clustered and also in

Table 3—The Number and Percentage of Various Categories of Species in Each Province

		Provinces												
		A	B	C	Da	Db	E	F	G	H	I	J	K	L
No. of species restricted to province	1)	128	82	59	119	96	240	301	137	178	71	259	101	42
% of species restricted to province	2)	57.9	56.2	37.5	39.4	67.6	80.2	56.4	69.2	36.7	55.5	81.7	72.7	35.0
No. of species originally recorded in province but subsequently also recorded elsewhere	3)	25	5	15	42	8	11	43	11	75	5	16	9	15
% of species originally recorded in province but subsequently also recorded elsewhere	4)	11.3	3.4	9.5	13.9	5.6	3.6	8.1	5.5	15.5	3.9	5.0	6.5	12.5
No. of species simultaneously originally recorded in more than one province	5)	1	1	1	1	2	2	4	2	6	4	0	1	8
Total number of species originally recorded from province (1 + 3 + 5)	6)	154	88	75	162	106	253	348	150	259	80	275	111	65
% of species originally recorded from) province (1 + 3 + 5–10 × 100)	7)	69.7	60.3	47.8	53.6	74.6	84.6	65.3	75.7	53.4	62.5	86.7	79.8	54.1
No. of species in province originally recorded elsewhere (excluding 5)	8)	66	58	82	140	36	46	185	48	226	48	42	28	65
% species in province originally recorded elsewhere (excluding 5)	9)	29.9	39.7	52.2	46.3	25.3	20.1	34.7	24.2	46.6	37.5	13.2	20.1	54.1
Total number of species in province	10)	221	146	157	302	142	299	533	198	485	128	317	139	120

this Bengalian, Indonesian, S. W. Pacific, Australian area, a continuum of shelf environments occurs. The great distance across the Pacific and the interspersion of an abyssal plain, would only allow many western American seaboard ostracods to be common with those of the S. W. Pacific if they could migrate along a shelf continuum via the Aleutians and Japan. The climatic effects of latitude have clearly prevented this from taking place in the Pacific. Also, but to a much lesser extent, in the Indian Ocean, latitude seems to have influenced the migration of species.



Text-fig. 5—Three link diagrams demonstrating the number of species common between various provinces.

The Migration Routes of Indo-Pacific Shallow Water Ostracoda

McKenzie (1967) suggested that during the early Tertiary, the Tethys allowed the rapid dispersal of marine ostracod genera *via* Simpson's (1940) methods of migration.

Simpson's (1940) methods of dispersal, although proposed for land animals, can be applied to marine animals such as benthonic ostracods. Simpson proposed 3 routes by which animals can migrate. The corridor route runs parallel to latitude with little climatic change which allows the active migration of animals, for example across Asia. The filter route requires a narrow channel which also allows active migration, the example for land animals being the Central American isthmus. Finally, the sweepstakes route involves chance dispersal, possibly by rafts, usually *via* small islands.

The Tethys acted as a latitudinal corridor that linked the faunas of the Caribbean, Mediterranean, Indonesian and Australian regions. The Tethys gradually closed during the Neogene, and since that time the respective faunas have developed more or less independently, the Caribbean and Gulf Coast regions no longer being directly linked with the Mediterranean and Europe or Indonesia, Australia and the Western Pacific. The links between these regions was illustrated by McKenzie (1967) by a series of 4 figures showing the Tertiary distribution of the genera *Paracypris, Triebelina, Miocyprideis* (herein considered a junior synonym of *Neocyprideis*) and *Caudites.* He also gave other examples of marine myodocopid and podocopid genera that have achieved their present day distribution *via* the Tethys. McKenzie suggested that the pelagic fauna could have been carried by currents and that the benthonic fauna migrated along the continental shelves.The shallow water benthonic faunas, however, need not necessarily be confined to the shelves. Benson (1979) argues that the Tethys was an ocean, although without a psychrosphere. It had no links with the colder waters of the Polar regions, being fed with thermospheric water from the Pacific Ocean. Consequently, decrease in temperature with increasing depth would not be a limiting factor, although other factors such as increase in pressure may be prohibitive for shallow water faunas.

Although McKenzie (1967) concludes that no single region provided the principal locus for the adaptive radiation of shallow water ostracod genera during the Tertiary, he implies that the dominant movement of migration was from west to east. For example, he states that the fauna of New Zealand is endemic because of its position at the end of a sweepstakes route *via* the island chains of the Western Pacific Ocean. He illustrates that the genera used as examples, only occur in the Recent in the Western Pacific and originate from Europe and/or the Gulf Coast. Since 1967, several more occurrences can be added to the figures given by McKenzie for the distribution of *Paracypirs, Triebelina* and *Neocyprideis.* In particular, Miocene occurrences of *Paracypris* and *Triebelina* at Midway Island (Holden, 1976) and the Quaternary occurrence of *Neocyprideis* in the Solomon Islands (Williams, 1980, MS.). The Tertiary to Recent occurrences of *Caudites,* however, appear to be correct as far as is known. McKenzie also gives examples of genera that may have migrated west wards through the Tethys, for example *Bythoceratina* and *Arcacythere,* although these are in the minority. Overemphasis on Mediterranean faunas in discussions on the Tethys may also have led to the implication that all ostracod taxa originated there. In addition, there is a much greater knowledge of the ostracods of Europe and the Caribbean, both fossil and Recent, than of Indonesia, the Western Pacific and New Zealand.

Some genera may have reached the Pacific coasts of the Americas from the Gulf Region *via* the Panamanian Straits which, prior to the Pliocene, acted as a filter route. Some of these genera are believed to have crossed the Pacific Ocean from east to west, for example *Cushmanidea* and *Munseyella* (McKenzie, 1967). However, the discovery of *Munseyella* and possible ancestral genera in the Upper Cretaceous of Western Australia (Bate, 1972) renders this doubtful.

Benson (1979) proposed that the Tethys was a primary channel for world ocean, deep circulation. Water entered the Tethys from the Pacific to the east, moved west and passed south down the opening South Atlantic and west across the Panamanian Straits to enter the Pacific Ocean again from the east. Insupport of the view that many genera may have originated from the Pacific is the fact that this ocean had probably always been in existence during the Phanerozoic. The occurrence of such "living fossils" as the palaeocopid genera *Puncia* and *Manawa,* for example, still found living off New Zealand and Australia, supports this suggestion, as does the occurrence of *Saipanetta* in the western Pacific.

Since the Tethys closed during the Neogene, barriers to the migration of species, such as temperature and depth, have led to the establishment of provincial faunas. Some species, however, have achieved interoceanic dispersal, at least between the Indian and Pacific Oceans. Text-figure 5, showing the links between faunal provinces, suggests that most species are either moving to or from the Western Pacific. As the Indian Ocean has existed in its present form only since the Tethys closed, it is suggested that the dominant movement of species across this ocean is eastwards from the Western Pacific (including Southern Indonesia, Northern Australia and New Zealand). This does not, however, apply to migration within the Pacific Ocean.

EVIDENCE OF MIGRATION ROUTES FROM INDIVIDUAL SPECIES

The 16 species recorded in the Recent of the Solomon Islands that have also been recorded fossils as there or elsewhere, can be used to trace the direction of movement through geological time.

The earliest fossil record of 4 of these species is in Indonesia or the Phillipines. The oldest record of *Triebelina sertata* Triebel, 1948 (Text-fig. 6) is from the Upper Miocene deposits in the Phillipines (Keij, 1974) and the Lower Pliocene of the Andaman Islands (Guha, 1968) and Northern Sumatra (Kingma, 1948). This species has migrated westwards to occur in the Recent off Madagascar (Maddocks, 1969a), Reunion Island (Keeler, 1981 MS) the Red Sea (Triebel, 1948), Persian Gulf (Keij, 1974), Ethiopia (Keij, 1974) and Cyprus (Keij, 1974) and eastwards to the Solomon Islands, Fiji (Allison and Holden, 1971) and Clipperton Island (Allison and Holden, 1971). The species has also been recorded in the Recent off British Honduras (Teeter, 1973), Venezuela (Bold, 1948) and the Gulf of Mexico (Puri, 1960).

Tanella gracilis Kingma, 1948 (Text-fig. 7) also possibly occurs in the Recent of the Gulf of Mexico (Teeter, 1973). Its oldest record is in Pliocene strata of Northern Sumatra (Kingma, 1948) and it has migrated westwards to occur in the Recent in the Gulf of Manaar (Guha, 1970), around the coast of India (Jain, 1976, 1978), the Gulf of Oman (Paik, 1977), the Persian Gulf (Bate, 1971; Teeter, 1973; Paik, 1977), Gulf of Aden (Teeter, 1973) and Suez Canal (Teeter, 1973) and eastwards to Java (Keij, 1979a), Australia (Hartmann, 1978, 1981) and the Solomon Islands.

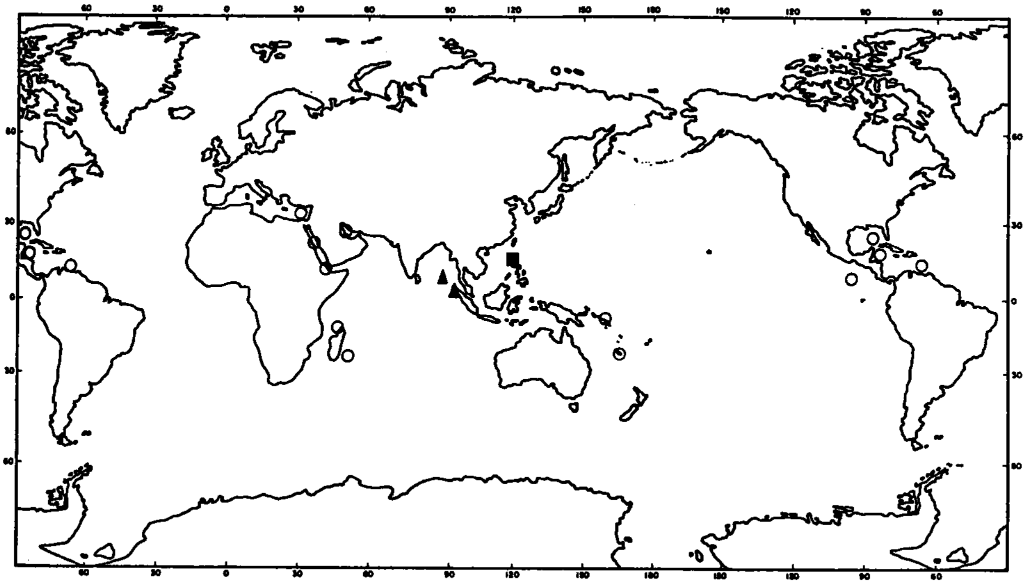
Neocyprideis spinulosa (Brady, 1968) (Text-fig. 8) occurs in the Upper Pliocene of Timor (Fyan, 1916) and the Pliocene–Pleistocene of Southern India (Guha, 1968a). This species has spread westwards to occur in the Recent off Mauritius (Brady, 1868) and Reunion Island (Keeler, 1981, MS.) and north and eastwards to occur in the Quaternary (Williams, 1980 MS.) and the Recent of the Solomon Islands, the Philippines (Keij, 1954), New Caledonia (Brady, 1980), Fiji (Brady, 1890) and the Southeastern Pacific Ocean (Brady, 1880). The fourth species, *Leptocythere foveoreticulata* (McKenzie, 1982) (Fig. 9) occurs in the Late Pliocene of Java (McKenzie, 1982) and the Recent of the Solomon Islands.

These 4 species suggest that migration to achieve their present day distribution has been both westwards and eastwards from the Indonesian Philippine region.

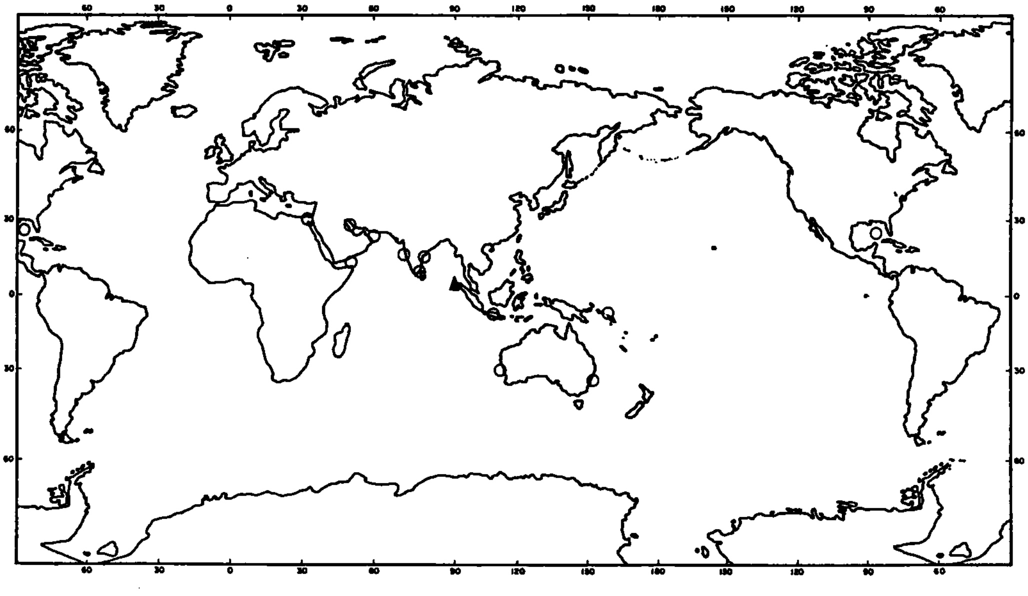
Seven species which have their earliest fossil record in the Solomon Islands also indicate that the dominant direction of movement is outwards from the Southwestern Pacific and Indonesia. *Neocyprideis timorensis* (Fyan, 1916) (Text-fig. 10) occurs in the Miocene (Hughes, 1977 MS.) Quaternary (Williams, 1980 MS.) and Recent of the Solomons, the Upper Pliocene of Timor (Fyan, 1916) and the Recent of the Red Sea (Bonaduce *et al.,* 1976 as *Bishopina mozarti*).

Quadracythere sp. (a new species to be described shortly (Text-fig. 11) also occurs in the Miocene, Quaternary and Recent of the Solomons and has been recorded in the Recent off Madagascar (Maddocks, 1966). *Hemicytheridea* sp. (a new species to be described shortly (Text-fig. 12) was recorded in Quaternary and Recent deposits in the Solomons and at the present day occurs off the Philippines (Keij, 1954), Mozambique (Teeter, 1973) and Reunion Island (Keeler, 1981 MS.). This species also occurs in the Recent off British Honduras and Florida (Teeter, 1973).

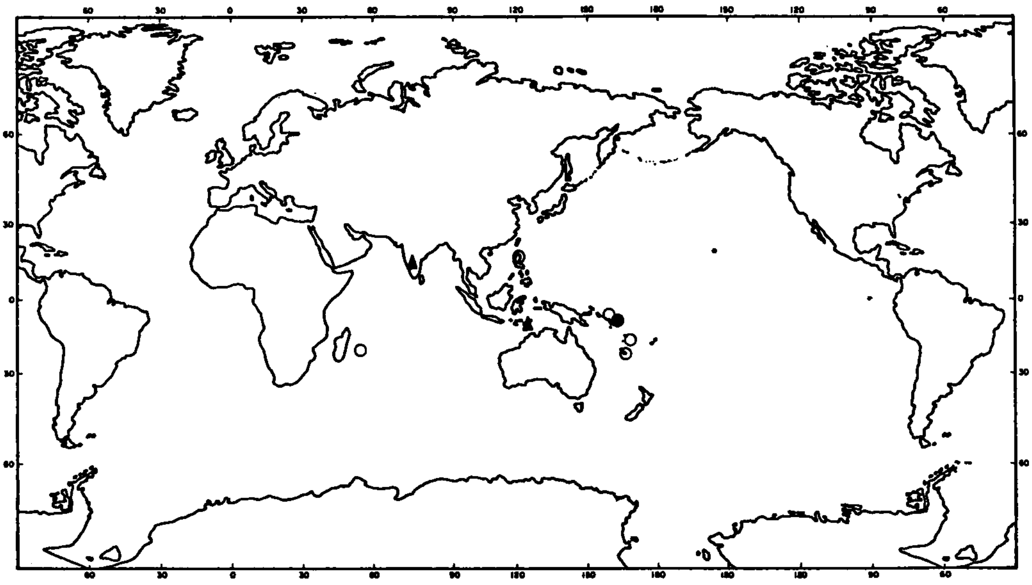
Xestoleberis sp. (Text-fig. 13) occurs in the Quaternary and Recent of the Solomons and in the Recent off Madagascar (Maddocks, 1966). In addition, *Cytherella semitalis* Brady, 1868 (Text-fig. 14) has been recorded in the Lower Miocene of New Zealand (Swanson, 1969), the Miocene of the



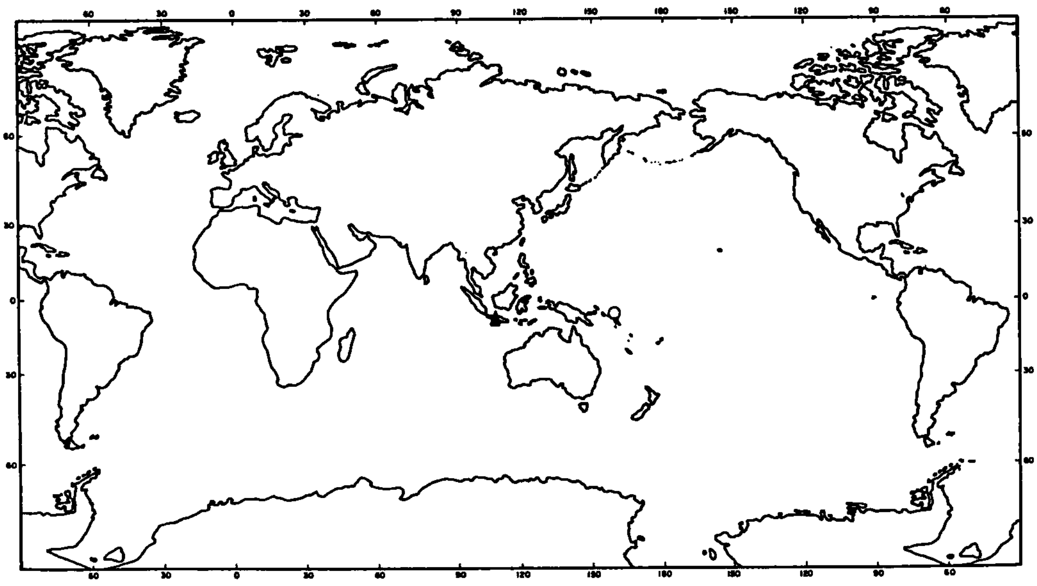
TEXT-FIG. 6—The geographical and stratigraphical distribution of *Triebalina sertata* Triebel.
(Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



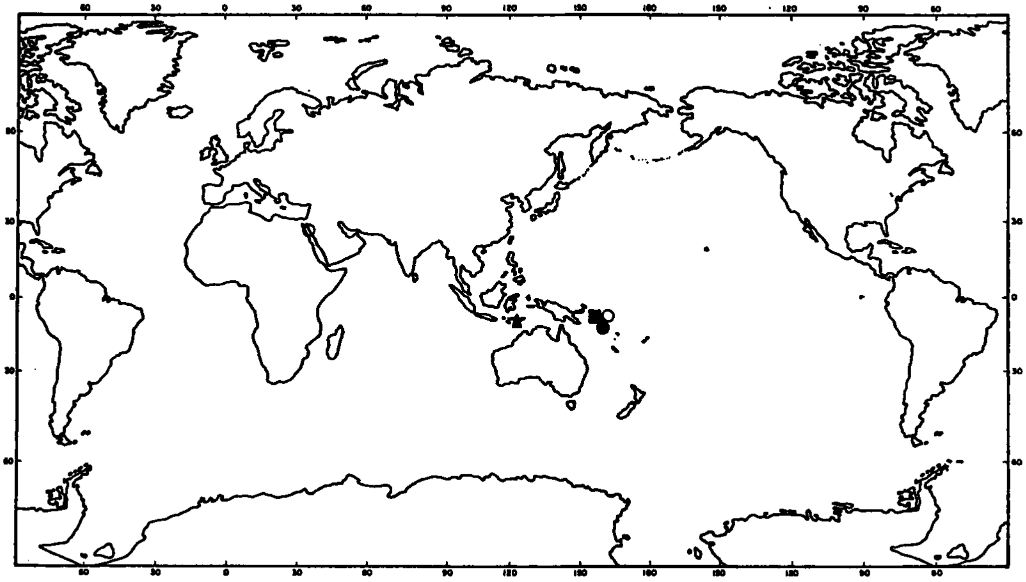
TEXT-FIG. 7—The geographical and stratigraphical distribution of *Tanella gracilis* Kingma.
(Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



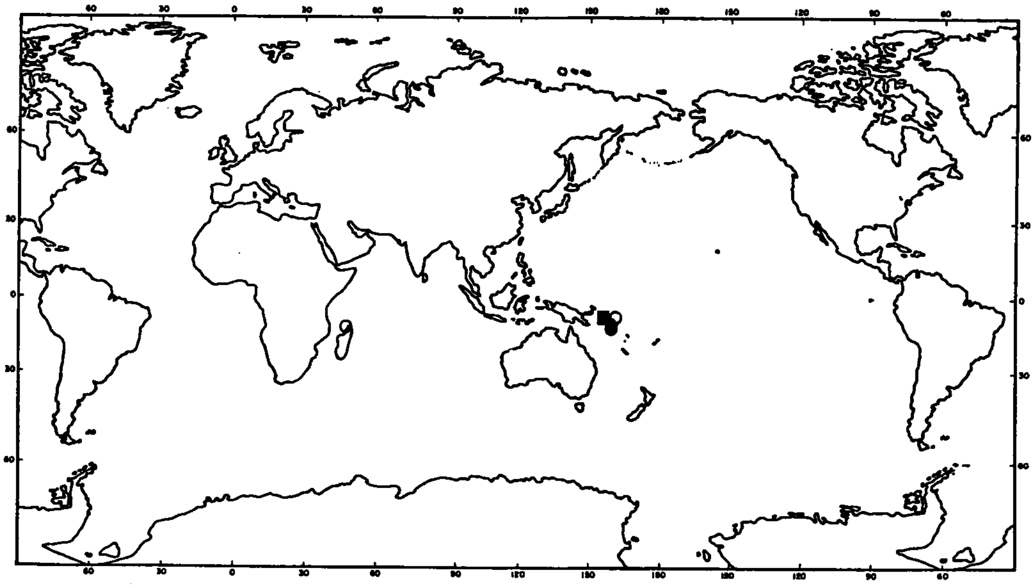
TEXT-FIG. 8—The geographical and stratigraphical distribution of *Neocyprideis spinulosa* (Brady). (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open ciecle = Recent).



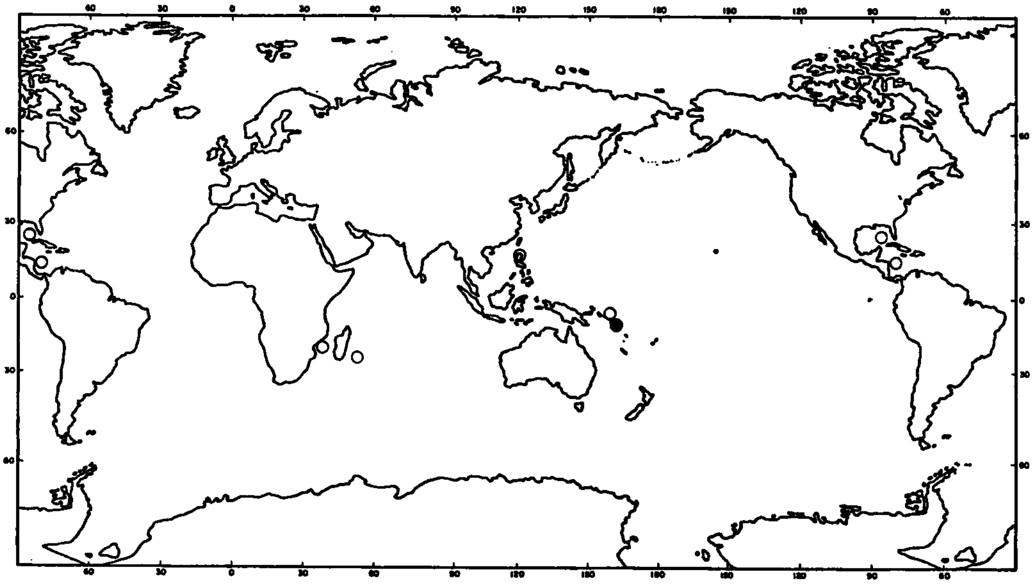
TEXT-FIG. 9—The geographical and stratigraphical distribution of *Leptocythere foveoreticulata* (McKenzie). (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



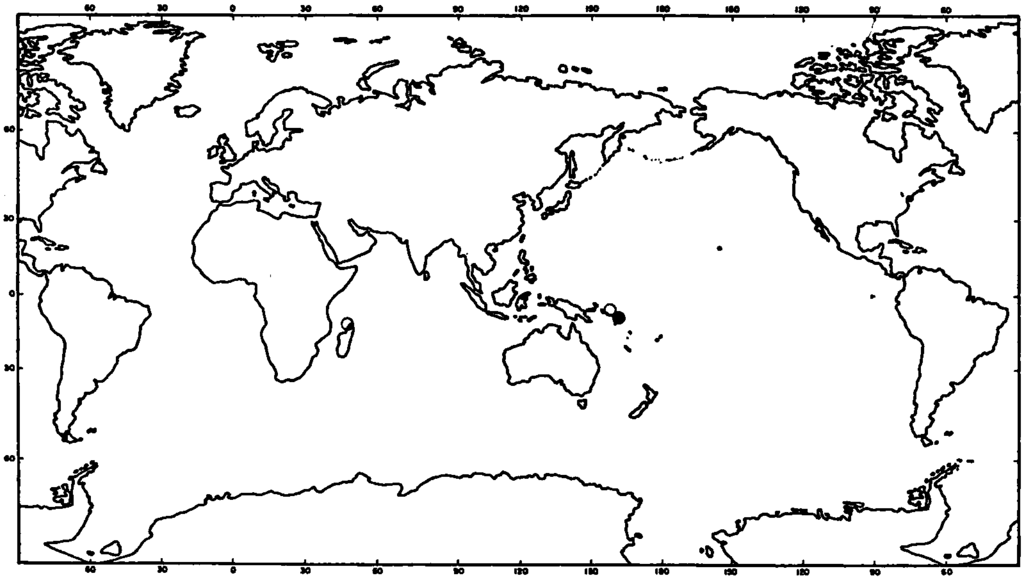
TEXT-FIG. 10—The geographical and stratigraphical distribution of *Neocyprideis timorensis* (Fyan). (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



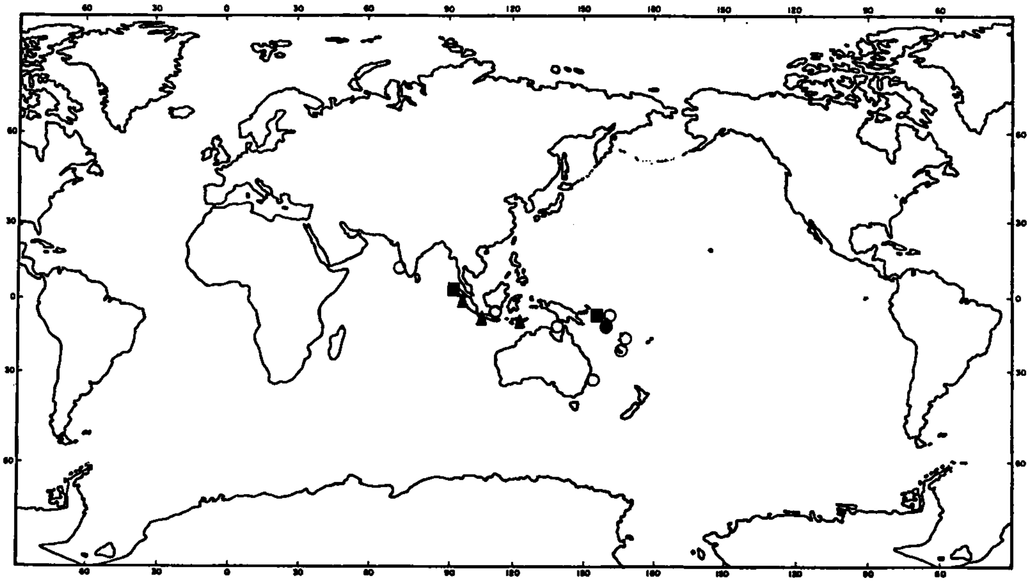
TEXT-FIG. 11—The geographical and stratigraphical distribution of *Quadracythere* sp. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



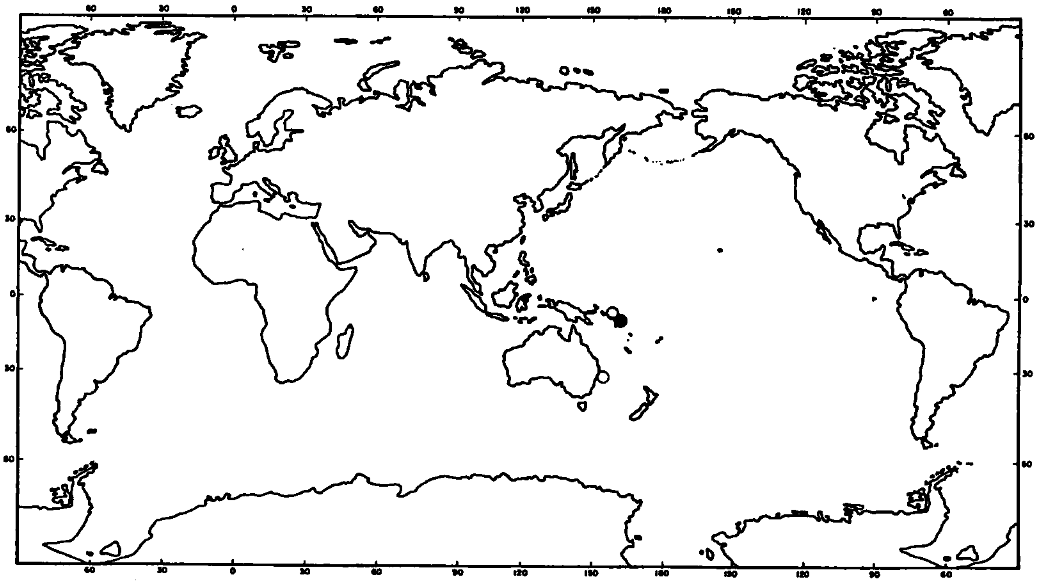
TEXT-FIG. 12—The geographical and stratigraphical distribution of *Hemicytheridea* sp. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



TEXT-FIG. 13—The geographical and stratigraphical distribution of *Xestoleberis* sp. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



TEXT-FIG. 14—The geographical and stratigraphical distribution of *Cytherella semitalis* Brady. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



TEXT-FIG. 15—The geographical and stratigraphical distribution of *Loxoconcha henonislandensis* Hartmann. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).

Solomons (Hughes, 1977 MS.) and Sumatra (Leroy, 1943), the Pliocene of Sumatra (Kingma, 1948), Java (Kingma, 1948), and Timor (Fyan, 1916) and the Quaternary of the Solomons (Williams, 1980 MS.). This species occurs in the Recent around New Caledonia and Fiji (Brady, 1890) and off Eastern (Chapman, 1941) and Northern Australia (Brady, 1880) and off Java (Brady, 1867-1872; Kingma, 1948) and has spread to the western coast of India (Jain, 1978).

The remaining species recorded in Quaternary deposits from the Solomon Islands (Williams, 1980 ms.) appear to have migrated in a more southerly direction. *Loxoconcha heronislandensis* Hartman, 1981 (Text-fig. 15) has spread southwestwards to occur in the Recent along the coast of Eastern Australia (Hartmann, 1981). *Ponticocythereis ichthyoderma* (Brady, 1890) (Text-fig. 16) has also spread to the southwest, occurring in the Recent around the southern coast of Australia (Hartmann, 1981), New Caledonia and Fiji (Brady, 1890; Whatley and Titterton, 1981). Finally, *Cytherelloidea keiji keiji* McKenzie, 1967 (Text-fig. 17) has migrated further south to New Zealand (Bold, 1963) and also occurs in the Recent around the coast of Australa (McKenzie, 1967; Hartmann, 1978, 1979).

Three species recorded in the Recent of the Solomons occur in Miocene–Pleistocene sediments from Midway Island (Holden, 1976). These species have spread in a general westward direction and are not recorded to the east of Midway, except *Kotoracythere inconspicua* (Brady, 1880) (Text-fig. 18). This species has been recorded in the Miocene — Pleistocene of Midway, the Neogene of the Andaman Islands (Guha, 1968b) and the Quaternary of the Solomon Islands (Williams, 1980 MS.). At the present day, it has achieved interoceanic distribution, occurring around Hawaii (Teeter, 1973), Fiji and New Caledonia (Brady, 1890; Holden, 1976), the Solomons, the Philippines (Keij, 1954; Teeter, 1973; Hartmann, 1980, 1981), the Persian Gulf (Teeter, 1973), Reunion Island (Keeler, 1981 MS.), the Bahamas, Florida and in the Caribbean (Teeter, 1973, 1975).

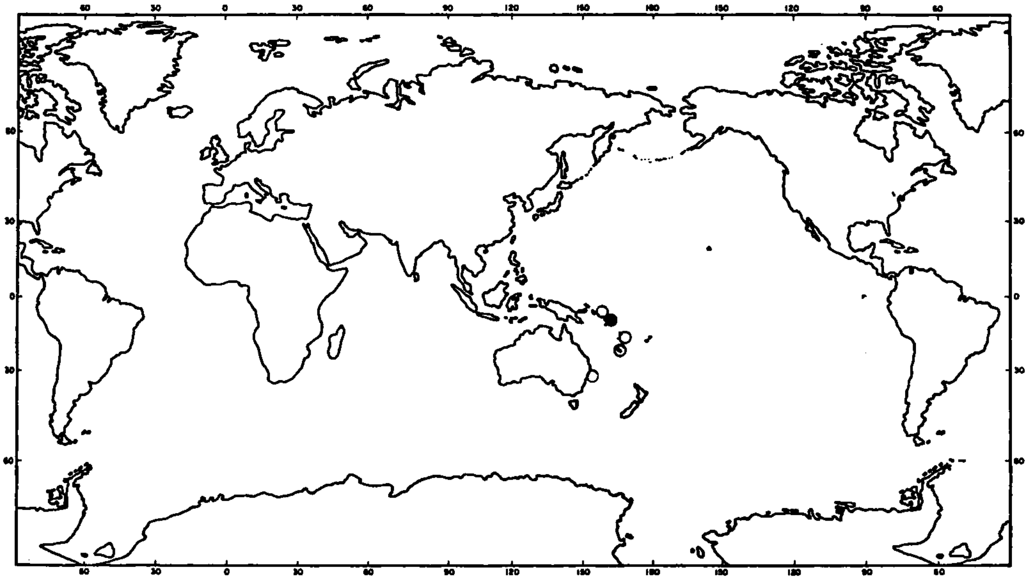
Neonesidea schulzi (Hartmann, 1964) (Text-fig. 19) was recorded in the Miocene of Midway Island and has migrated westwards to occur in the Quaternary (Williams, 1980, unpub. MS.) and Recent of the Solomons and Recent of Madagascar (Maddocks, 1966, 1969a), the eastern coast of Africa (Hartmann, 1974), the Red Sea (Hartmann, 1964) and the Persian Gulf (Bate, 1971; Bonaduce *et al.,* 1976).

Quadracythere insulardaensis Hartmann, 1981 (Text-fig. 20), recorded in the Pleistocene of Midway, occurs in the Quaternary (Williams, 1980 MS.) and Recent deposits from the Solomons and Recent around the eastern coast of Australia (Hartmann, 1981) and off Madagascar (Maddocks, pers. comm., 1980).

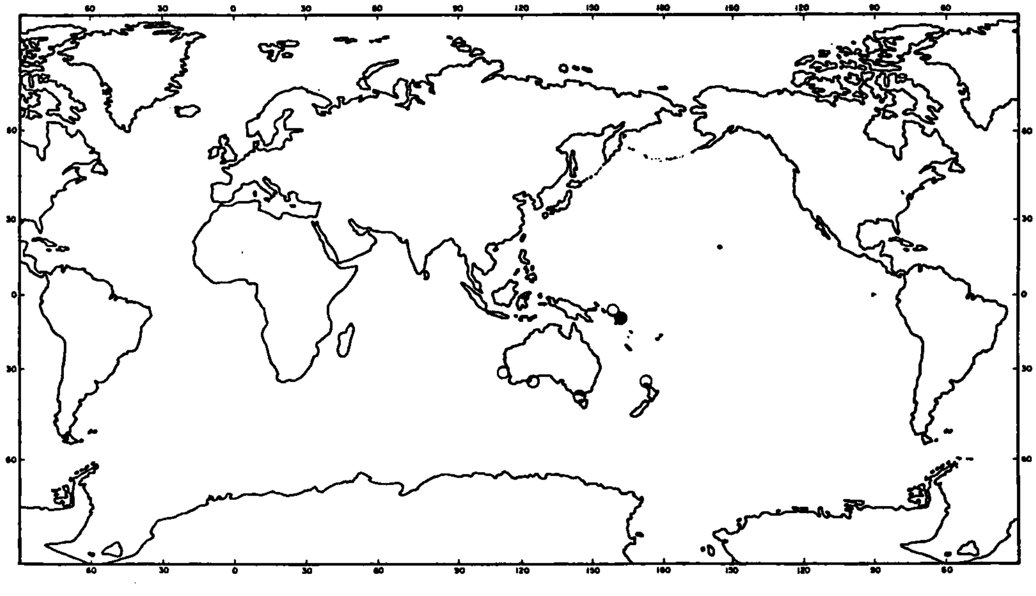
Finally, *Triebelina bradyi* Triebel, 1948 (Text-fig. 21) occurs in Upper Miocene — Lower Pliocene deposits of Fiji (Keij, 1974) and has migrated northwards to occur in Pleistocene deposits of Midway (Holden, 1976) and the Recent of the Gilbert Islands (McKenize and Keij, 1977), the East China Sea (Keij, 1974) and eastwards to Samoa (Brady, 1890). It has also spread westwards, occurring in the Recent around New Caledonia (Brady, 1890), the Solomons, Indonesia (Bold, 1950; Keij, 1953) and off Madagascar (Maddocks, 1969).

Holden (1976) referred to Cole's (1969) observations that the larger foraminifera, both fossil and Holocene, from Midway Island had Indo-Pacific affinities, indicating eastward migration to Midway Island. Holden (1976) observed that the Miocene ostracod fauna of Midway Island showed connections with the Caribbean, but also with Indonesia and India. The Recent fauna, however, has little in common with Caribbean faunas. Midway Island faunas also have affinities with faunas in Japan. Some species of Pliocene-Holocene *Parakrithella* in Japan have been recorded in Midway Island in Late Miocene and younger deposits, possibly indicating westward migration from Midway. Three other Midway species present in Late Miocene and younger sediments, however, appear to have migrated eastwards from Japan.

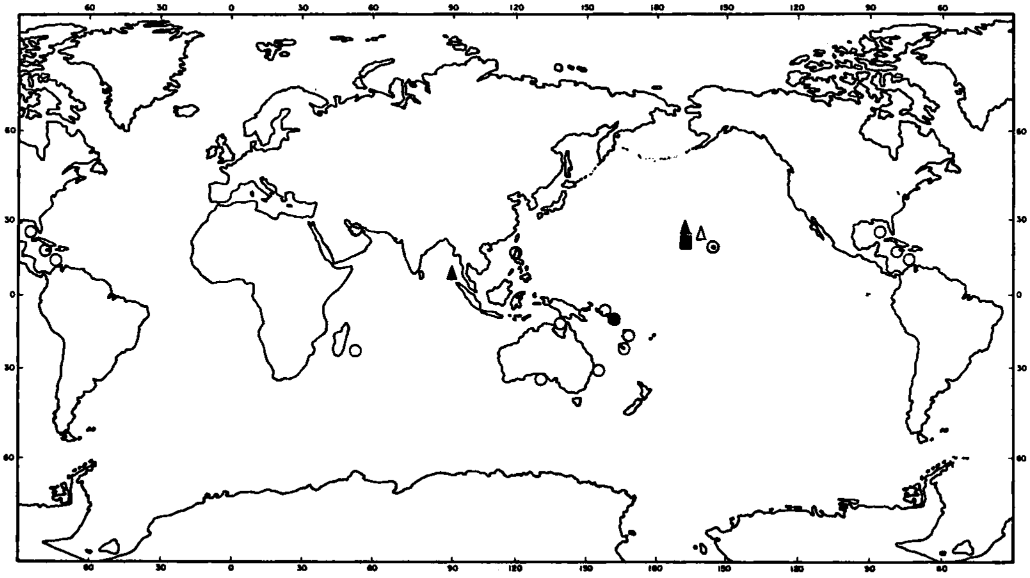
These examples support the view that the Indonesian-Philippine region and the Southwestern Pacific appear to be the major locus from which migration took place. They illustrate also that



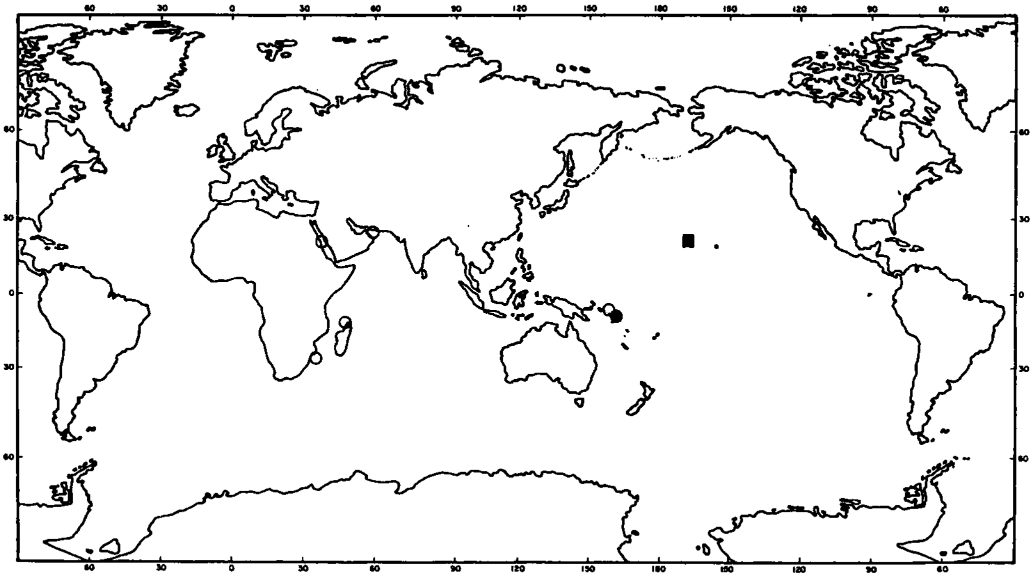
TEXT-FIG. 16—The geographical and stratigraphical distribution of *Ponticocythereis ichthyoderma* (Brady). (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



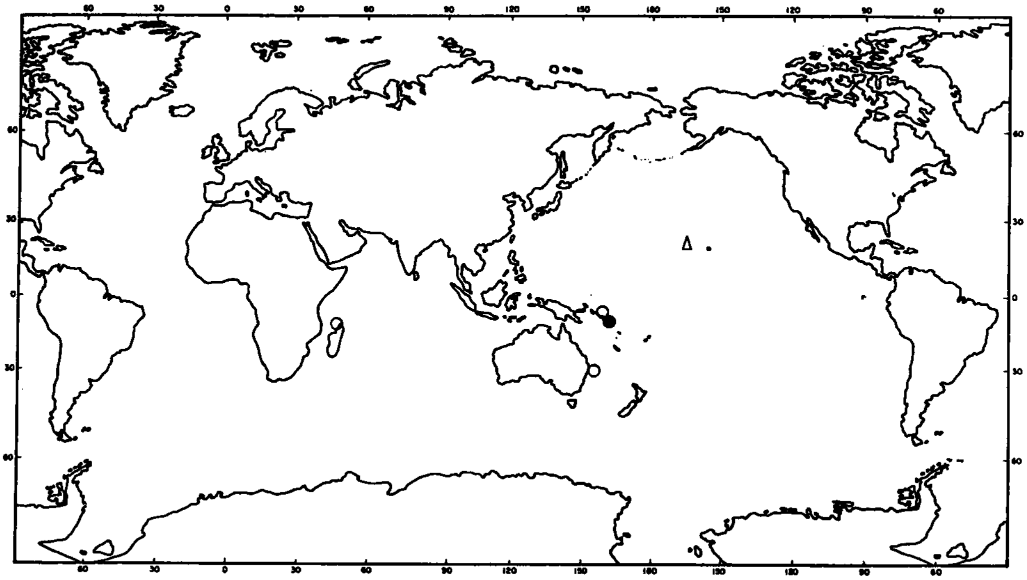
TEXT-FIG. 17—The geographical and stratigraphical distribution of *Cytherelloidea keiji keiji* McKenzie. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



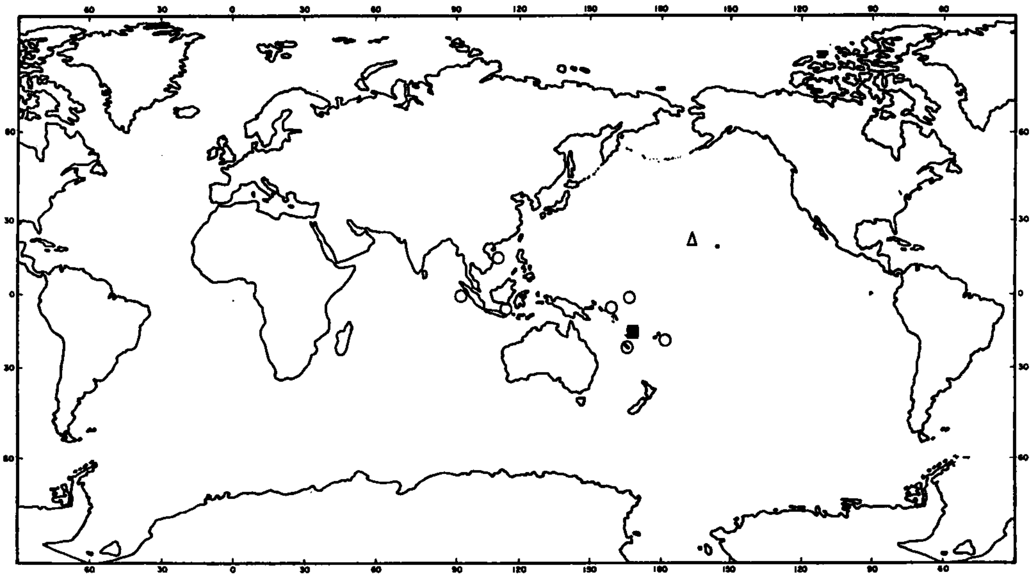
TEXT-FIG. 18—The geographical and stratigraphical distribution of *Kotoracythere inconspicua* (Brady). (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



TEXT-FIG. 19—The geographical and stratigraphical distribution of *Neonesidea schulzi* (Hartmann). (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



Text-fig. 20—The geographical and stratigraphical distribution of *Quadracythere insulardaensis* Hartmann. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).



Text-fig. 21—The geographical and stratigraphical distribution of *Triebelina bradyi* Triebel. (Black square = Miocene; black triangle = Pliocene; black circle = Quaternary; open circle = Recent).

species have crossed the Indian Ocean from east to west. None of the 152 encountered by the authors in the Recent of the Solomon Islands originated in the Indian Ocean or the Eastern Pacific.

Bate (1971) discussed the close affinities between the Neogene fauna of Indonesia and that of the Recent of Abu Dhabi and postulated a westward migration of species from Indonesia.

DISCUSSION

Why some species become transoceanic in their distribution, while others remain confined within narrow geographical limits is probably the function of a number of factors such as relative degrees of environmental tolerance and opportunism. Those species endowed with a high degree of both become successful wanderers, the remainder 'stayed at home'. The 'why' of relative success in migration is beyond the scope of this study, but it is thought appropriate to consider the 'how'.

While it is relatively easy to account for the widespread occurrence of some freshwater cyprids whose encysted eggs are able to resist dessication, freezing and immersion in salt water and which can be dispersed by wind, currents and various animal agencies, no such facility is available to explain pandemic distributions in shallow water marine podocopid Ostracoda. Indeed, the common means of dispersal employed by other marine benthonic invertebrates, pelagic larvae, is denied to them. Ostensibly, since none of them are swimmers, they can only migrate as far as they can 'walk' or be swept by currents, during their lifetime, usually less than one year.

McKenzie and Hussainy (1968) and Klie (1939) have considered the means of dispersal of *Gomphocythere* and *Cyprideis torosa* respectively and the latter author came out in favour of the agency of migrant water birds. Puri (1966) discussed the possible methods of migration available to benthonic marine ostracods. He considered that the wide distribution of some marginal marine species can be attributed to tides, strong winds, storms and currents. He gave examples in which bottom and surface ocean currents were believed to be important in the distribution of ostracods. Teeter (1973) suggested that marine, benthonic ostracods may be transported on floating marine algae carried by currents. He found living ostracods, notably *Hemicytherura cranekeyensis* Puri, 1960 on *Turbanaria* collected off British Honduras and one of us (RCW) has seen live *Paradoxostoma, Xestoleberis, Semicytherura* and a hemicytherid on Sargasso weed from the North Atlantic. Teeter believed that such a method of transport would be restricted by temperature. For tropical species, the colder waters around the tips of the African and American continents would provide barriers to interoceanic dispersal via these routes. (This barrier, however, has only existed since the onset of major Antarctic glaciation (38 m.a.). He suggested, therefore, that interoceanic dispersal achieved by the species he gave as examples, may be the result of man to some extent. Ostracods may be carried in water ballast taken on ships, as is the case through the Panama and Suez Canals, and among weed and barnacles on the hulls.

Interoceanic dispersal has been achieved by relatively few shallow water species. A major limiting factor in determining the extent to which this has taken place is reliance on non-illustrated identifications in the literature.

Most animals and plants tend to spread, actively or passively from their locus of origin to colonise nearby niches. Marine, benthonic ostracods are active to a greater or lesser extent and may migrate actively during life and be passively carried short distances. Longer distances may be achieved by a series of small-scale but rapid saltations. These may be assisted by such passive mechanisms of transport as rafting and currents, local or global. Barriers to such movements would need to be greater than a few miles of unsuitable conditions. Such movements, perhaps, would not explain the interoceanic dispersal achieved by some species. It may, however, contribute to the interoceanic dispersal of genera, small changes in environment in new localities causing allopatric speciation. An analogous example is the invasion and spread of species of *Bradleya* and *Poseidonamicus* into the deep sea of world oceans during the Tertiary from an initial locus in the Southwest Pacific (Whatley, *et al.*, 1983, 1984; Whatley, 1983, and of other deep sea ostracods Whatley and Ayress, this volume).

Notwithstanding this, interoceanic dispersal of certain species is very difficult to account for even with respect to geological time. The present authors are of the opinion that dispersal of certain species of benthonic ostracods between the Indian and Pacific Oceans has been occasioned by a combination of active migration, aided by passive mechanisms, in particular surface ocean currents.

Present day surface ocean currents (Text-fig. 22) may account for some of the links observed between the faunal provinces. The rafting of ostracods on floating weed in these currents could be of great importance. The links between the faunas of Western North and Central America and of of Western South America with those of the Northern and Central Pacific and Southern and Southwestern Pacific may be the result of the North and South Equatorial Currents which move across the Pacific from east to west. In addition, the Equatorial Counter Current may allow west to east movement in the equatorial regions. Allison and Holden (1971) remarked on the Caribbean affinities of the Holocene Clipperton Island ostracods and suggested that Central America was a seaway with surface currents moving from east to west as the North Equatorial Current does today. Bate *et al.* (1981) also observed that the ancestors of some of the Recent species of the Galapagos Islands can be traced back to the Pliocene of North Carolina.

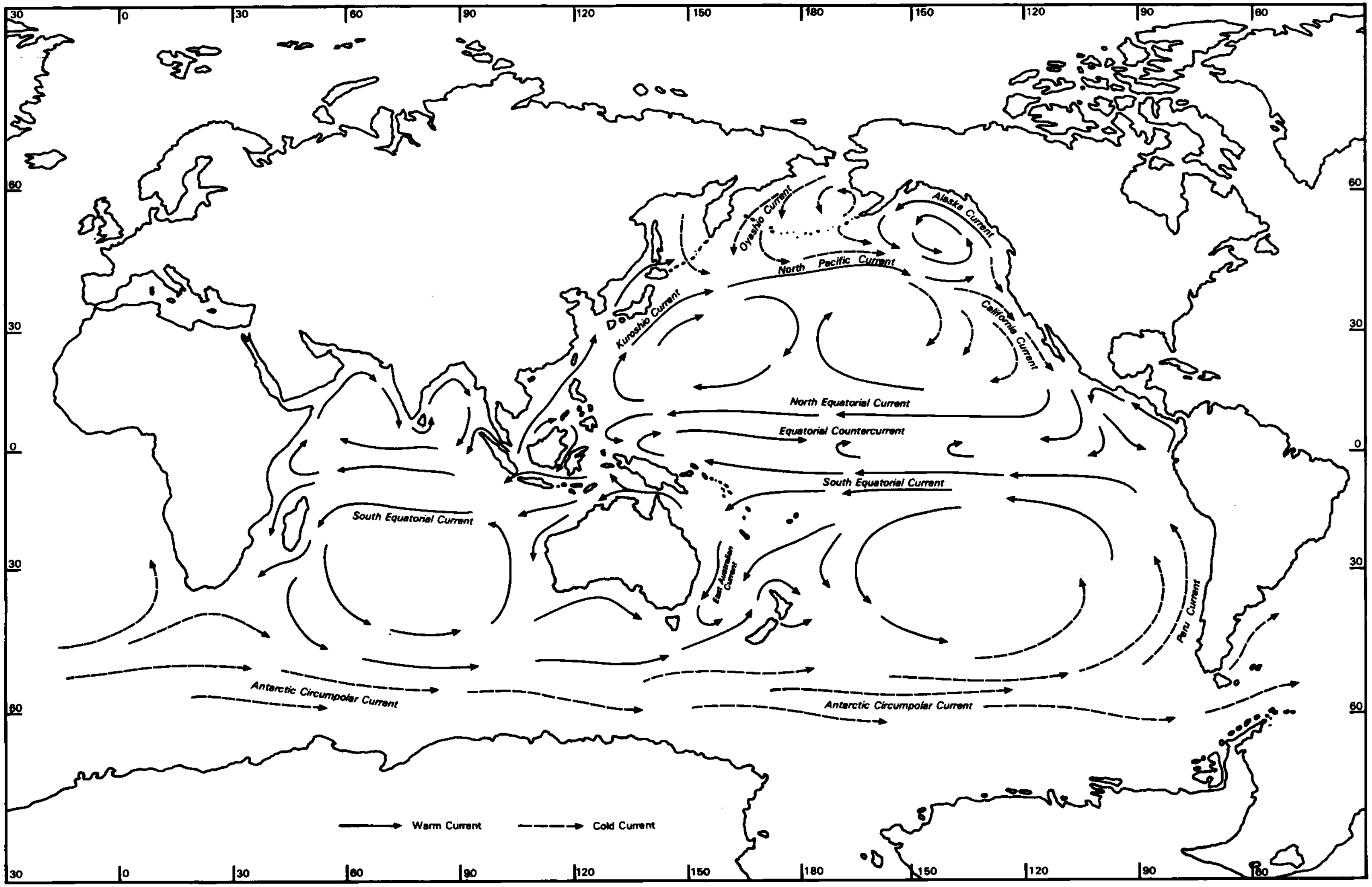
The North Equatorial Current moves north, past the Philippines, Taiwan and Japan, where it is known as the Kuroshio Current. Ishizaki (1977) considers that both the Upper Pliocene — Pleistocene Shinzato Formation (Okinawa) and Upper Pliocene Ananai Formation (Shikoku) were under the influence of a palaeo-Kuroshio Current at the time of their deposition. Holden (1976) also suggests that 3 species present in Miocene and younger sediments from Midway Island were introduced to the atoll from Japan by the Kuroshio Current. An extension of the Kuroshio Current crosses the Northern Pacific (North Pacific Current), mixing with colder water and passes south down the western coast of North America. Thus species from Indonesia and Japan may be carried to Western North America.

The South Equatorial Current passes down the eastern coast of Australia (East Australian Current), possibly accounting for the strong links observed between the faunas of the Southern and Southwestern Pacific (including the Solomon Islands) and those of Eastern Australia.

The west to east currents of the Southern Ocean pass either side of New Zealand. It is possible that the fauna of New Zealand is so endemic because it is surrounded by colder water, although there is some mixing with the warmer East Australian Current off North Island.

The Equatorial Currents of the Pacific divide through the Indonesia archipelago. The South Equatorial Current passes from east to west through the Torres Straits and Timor Sea to the Indian Ocean. The direction of the current through the Malacca Straits is also from east to west. Species from Southern Indonesia may be carried by that current into the Indian Ocean. The South Equatorial Current passes across the Indian Ocean to Madagascar, moving north and south along the eastern coast of Africa. This current may account for the strong faunal links observed between the Southern and Southwestern Pacific, Australia and Southern Indonesia with the Western Indian Ocean.

In the Northwestern Indian Ocean the Equatorial Current, as the Southwestern Monsoon Current, passes from the Arabian region down the Western Indian seaboard. Affinities between the faunas of the Red Sea, Persian Gulf and Western India are strong enough to indicate a single faunal



TEXT–FIG. 22—Map showing the distribution and direction of surface ocean currents in the Indo-Pacific.

province. In the Bay of Bengal, currents pass from Eastern India down the western coast of Sumatra. This current may account for the links between the faunas of the Bay of Bengal and Southern Indonesia, as would the current in the opposite direction through the Malacca Straits.

Surface ocean currents assisting in the active migration of benthonic ostracods may, therefore, account in part for the present day distribution of certain Indo-Pacific species. Apart from currents assisting migration, other factors would also contribute to the distribution of species. It is apparent from Text-fig. 5 that fewer species are able to cross the Pacific Ocean, accounting for the relatively weak links between the provincial faunas across the Pacific. A barrier to movement in any direction would be the long distances of deep open water. A barrier to movement along the continental margins around the Pacific would be changes in temperature in the Arctic or Antarctic regions. These barriers are less prominent across the Indian Ocean where passage of species along the continental margins and migration via the sweepstakes route of Simpson does not involve great changes in temperature. Distances across deep oceans are comparatively much less here than in the Pacific.

It cannot be disputed that benthonic species of ostracods can and do migrate and even achieve cosmopolitan distribution within certain latitudes. Mechanisms of such dispersal must be a combination of active and passive migration. Genera probably migrate by a series of steps with adaptive evolution in new habitats. For example, *Caudites* has reached the Galapagos Islands, the Solomon Islands and Western South America where it has undergone adaptive radiation. The Tethys in the Early Tertiary linked the Caribbean, Mediterranean, Indonesia and Western Pacific Ocean, allowing the migration of genera between these regions. Since the Tethys closed during the Neogene, barriers to migration have resulted in the development of provincial faunas. Some species, however, have been able to migrate since, probably assisted by the world's major ocean surface currents.

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DISCUSSION

Kaesler: Will you please explain how you decided on the boundaries of your biogeographical provinces? Specifically, how similar are samples from within provinces compared to faunas from different provinces?

Titterton: The degree of endemism of the various provincial faunas is discussed fully in the paper and illustrated in Text-figs. 2–4. Because of time restrictions for the presentation of the paper, I decided not to cover this aspect in detail.

Distribution and Dispersal of Littoral Pacific Island Ostracoda

GERD HARTMANN
Zoologisches Institut und Zoologisches Museum, Hamburg, F. R. Germany

ABSTRACT

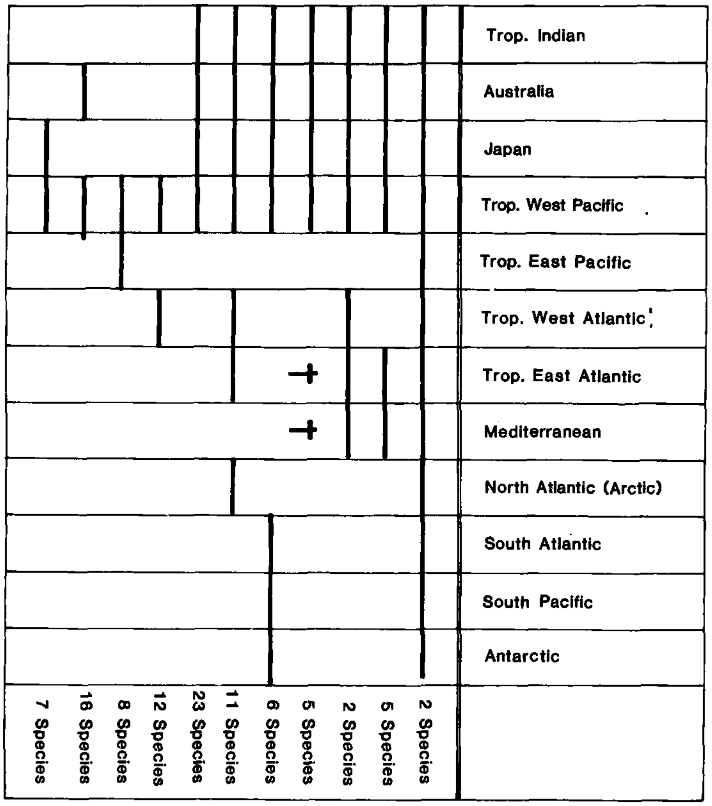
During August and September 1982, ostracods were collected on the islands of Huahinė (Society Islands) and Rangiroa (Taumotu Islands). The results were published in 1984. The present paper deals with results derived from the studies of a checklist of ostracods known from the Pacific islands, established in the mentioned publication. The biology and ecology of the ostracods of the Pacific islands and the surrounding continents (Australia, South America) is studied. The mode of dispersal of the ostracods — both pelagic and non-pelagic is compared with the distribution of these species. It is obvious that many species of ostracods of the tropical Pacific show a wide distribution, in spite of the lack of pelagic larvae in the benthic groups. The checklist reveals, however, that the "East Pacific Barrier" (Ekman, 1935) does exist for the ostracods also. Only a few species of marine animals live on both sides of this barrier (*e.g.* on the Pacific islands and along the tropical American Coast). Many papers on fossil ostracods do not show this form of distribution, but indicate circumtropical distribution. A critical evaluation of the existing data of both recent and fossil ostracods is given.

As an appendix to his paper on ostracods from the Polynesian Islands the author (Hartmann, 1984) published a list of all littoral Pacific benthic Island ostracods known to him to this date. This checklist contained 268 species, while 21 were mentioned in the text of the paper. The author did not at that time draw zoogeographical conclusions from the distribution of the species mentioned. This will be done in the present paper.

If we do not consider the 20 freshwater species of the checklist, we are left to reconsider 269 marine species. Of these, 151 were found only in the islands of the Pacific and are thus not able to show the zoogeographical relationships of the island ostracods. One hundred eighteen species have a wide distribution in that they also occur outside the Pacific islands.

Before we check the distribution of these species it is necessary to point out that the evidence of zoogeographical studies depends on the systematic base of the material in question. Only exactly determined species make zoogeographical studies possible at all. A first examination of the species of the checklist showed the systematic base of the intended study to be poor, and in reality, so confusing, that the author at first did not believe it possible to obtain results. Nevertheless, it seemed in the end interesting to at least give information about the knowledge that exists on Pacific island ostracods.

To achieve a certain order in the distribution pattern of Pacific species, the 118 marine species with wider distributions were placed into distribution pattern groups.



TEXT-FIG. 1—Distribution of the Pacific benthic Ostracoda.

These nine groups will be tested one after the other.

Species with a wide distribution (Text-fig. 1 and Table 1) Thirty-one species belong to a group of ostracods widely distributed or with an unusual distribution.

a) Two species *Krithe bartonensis* and *Pseudocythere caudata* have a worldwide distribution. Several authors have verified this.

b) Five species were found in the Indo-Pacific and in the Mediterranean-Lusitanean province.

c) Two species, distributed similarly to the above, were also reported from the western Atlantic. The localities of these seven species have not been verified. As species of other animal groups have a similar pattern of distribution, however, we are, for the present, allowed to accept the indicated ranges.

d) Five species are recorded as living only in the Indo-west Pacific, but are believed to have been found as fossils outside of this region. Two species were recorded as fossils from Gabon, two from Calabria and one from the Rhône Basin. The author however believes that these findings are questionable, and should be reconsidered.

e) Also at least questionable is the range of six species recorded from the tropical Pacific and from subantarctic or antarctic waters.

f) A 'traditional' pattern of distribution is known for 11 species. These have been found in the tropical Pacific (some also in the tropical Atlantic) and from Iceland, Norway and Great Britain. I call this distribution 'traditional,' because it reflects the distributions used by former ostracod workers (Sars, Baird and Brady, for example) more than the actual range of species. It is probable that even the species with this traditional pattern should each be divided into two or more species.

TABLE 1a—SPECIES WITH UNUSUALLY WIDE DISTRIBUTION

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a) Worldwide distribution
  Krithe bartonensis (Jones, 1956)
  Pseudocythere caudata Sars, 1866

b) Indopacific-Mediterranean-Lusitanian
  Cytherella cuneolus Brady, 1870
  Bairdia formosa (? = *serrata*) Brady, 1868
  Leptocythere crispata (Brady, 1869)
  Xestoleberis variegata Brady, 1880
  Paradoxostoma rubrum G.W. Müller, 1894

c) Indopacific-Mediterranean-Lusitanian-west Atlantic
  Neonesidea crosskeyana Brady, 1866
  Xestoleberis intermedia Brady, 1868

d) Fossils outside the Indo-west Pacific
  Neonesidea attentuata (Brady, 1880)—Gabon
  Radimella convoluta (Brady, 1868)—Gabon
  Bairdia expansa Brady, 1880—Calabrian
  Spinileberis quadriaculeata (Brady, 1880)—Calabrian
  Bythocypris compressa Brady, 1880—Rhône Basin

e) Tropical-Subantarctic-Antarctic
  Bairdoppilata simplex (Brady, 1880)
  Bradleya wyville-thompsoni (Brady, 1880)
  Occultocytheropteron assimile (Brady, 1880)
  Paradoxostoma retusum Brady, 1890)
  Argilloecia affinis Chapman, 1902
  Propontocypris simplex (Brady, 1880)

f) Tropical Pacific—North Atlantic (Iceland, Norway, England, some also found in tropical Atlantic)
  Bairdia acanthigera (Brady, 1880)—also in England
  Bairdia bradyi v. d. Bold, 1957—also in Trinidad, Cape Verde, Norway, Iceland
  Bairdia milne-edwardsi Brady, 1869—also in Cape Verde and Norway
  Bairdia foveolata Brady, 1868—also in Cape Verde, Bermuda, Norway and Iceland
  Bairdoppilata hirsuta (Brady, 1880)—also in Galapagos, Morocco and Iceland
  Neonesidea amygdaloides Brady, 1866—also in Straits of Magellan, Gulf of Mexico, Trinidad, Madeira, Mediterranean, Gabon, Iceland and Norway
  Neonesidea woodwardiana Brady, 1880—also in southern Norway and Iceland
  Cythere cancellata Brady, 1868—also in Iceland Norway (see *Cytheromorpha cancellata*)
  Caudites rectangularis (Brady, 1869)—also in †Italy, Iceland, Norway
  Pontocypris bradyi Chapman, 1941—also in Iceland, Norway
  Propontocypris attentuata (Brady, 1868)—also in Iceland, Norway

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†: indicates fossil occurence.

SPECIES WITH CIRCUMTROPICAL DISTRIBUTION

Four species are known to be circum-tropically distributed:

Triebelina sertata Triebel, 1948
Bythocypris reniformis Brady, 1880
Morkhovenia inconspicua (Brady, 1890)
Keija demissa (Brady, 1868)

Some localities in the range of these four species have been reconsidered by different authors. It is possible that these species do not occur along the tropical Pacific coast of Central America, as to date they have not been found there. A gap in the distribution of circumtropical benthic species on the Pacific coast of Central America has also been recorded in several other animal groups (Decapoda, Echinodermata). The distribution gap may reflect the cold conditions caused by cold water currents directed towards the equator and upwellings of cold water along the coast which led to the extinction of tropical animal species there during the Pleistocene. It should be remembered that there are no reef building corals along the American West Coast. A re-population of the west coast — arising from warm water areas of the Caribbean and the Gulf of Mexico — was not possible after the straits through the Central American isthmus closed during the Tertiary.

WIDE DISTRIBUTION IN THE INDO–WEST PACIFIC (TABLE 2)

A wide distribution throughout the entire Indo–west Pacific has been recorded for 23 species, the range of several of which has been verified by different authors. Indo-west-Pacific distribution is not rare. Nevertheless, the original material of at least the *Xestoleberis* species should be reconsidered, as species of this genus are, without soft parts, extremely difficult to distinguish. Because figures in earlier papers are often incomplete, we need to go back to the type material.

TABLE 2—WIDE DISTRIBUTION IN THE INDO–WEST PACIFIC

Cyprinodea asymmetrica G. W. Müller, 1906—Indian, Malay, Samoa
Cytherella cribrosa Brady, 1880—Indian, Pacific, Tonga
Bairdia globosus Brady, 1880—Indo-Pacific
Bairdia numensis (Brady, 1890)—Indian (Cocos Islands), New Caledonia
Bairdia tuberculata Brady, 1870—Madagascar, Andaman, Mauritius, Australia, New Caledonia, Admiralty Islands
Neonesidea tenera (Brady, 1886)—India, Funafuti, Samoa
Neonesidea schulzi (Hartmann, 1961)—Rota Sea, Madagascar, ?Hawaii
Triebelina bradyi Triebel, 1948—Madagascar to Hawaii
Anchistrocheles fumata Brady, 1880—Madagascar to Hawaii
Cythere obtusalata Brady, 1880—Indian, Australia, Funafuti, Admiralty Islands
Cythere ovalis Brady, 1880—Ceylon, Australia, Fiji
Miocyprideis spinulosa (Brady, 1868)—†Ethiopia, Yemen, Mauritius, India, Malay, New Caledonia, Fiji, Amboina
Trachyleberis goujoni Brady, 1860—Yemen, Southeast Asia, China, New Caledonia
Cletocythereis rastromarginata (Brady, 1880)—Indian, Australia, Hawaii
Hemicythere packardi (Brady, 1880)—Andaman, Australia, Southeast Asia, South-Sea
Loxoconcha gibbera Brady, 1890—Indian, Southeast Asia, Fiji
Loxoconchella anomala (Brady, 1880)—Indian, China, New Caledonia, Fiji, Hawaii
Loxoconchella honoluliensis (Brady, 1880)—Indian, Australia, New Caledonia, Hawaii
Paracytheridea longicaudata (Brady, 1880)—Indian, Southeast Asia, Fiji, ?Chile (A few subspecies or species)
Hemicytherura scutellata Brady, 1890—Andaman Sea, Southeast Asia, Australia, Fiji
Foveoleberis foveolata (Brady, 1880)—Indian, Australia, China, Funafuti
Xestoleberis compressa Brady, 1898—Ceylon, New Zealand, Hawaii
Xestoleberis tumefacta Brady, 1880—Indian, Hawaii

†, indicates fossil occurrence.

WEST ATLANTIC–WEST PACIFIC DISJUNCTION (TABLE 3)

According to existing literature we find 12 ostracod species distributed in this way. Different authors have recorded the same distribution patterns for Crustacea (Decapoda) and Echinodermata species. The Eastern Pacific distribution gap has been mentioned earlier in discussing the circumtropical distribution. Obviously it was caused by the oceanic conditions existing in that region during the Pleistocene and the rise of the Central American land bridge during the Tertiary. Their dispersal to the other side of the land mass might have occured by way of the Mediterranean Tethys or vice versa.

Among the 12 species which show this pattern of distribution, 8 were originally described from the West Atlantic (Carribbean, Gulf Coast). Later they were found by Holden (1976) on Midway Island (Hawaii). Holden himself considered several of his identifications as questionable (aff., cf.). The author believes that none of the Midway species are really identical with the original species described from Atlantic waters. The same might be true for three of the remaining four species. Only *Copytus baculoides* (Brady, 1890), found by Teeter (1975) on the coast of Belize, has been reconsidered by this author as genuine through a comparison with the type material. Teeter, however, believes that the species was imported by ships.

TABLE 3—WEST ATLANTIC—WEST PACIFIC

Sarsiella sculpta Brady, 1890—Australia, Japan, South Seas, Bimini, Atlantic North America
Cytherelloidea umbonata Edwards, 1944—Hawaii, Caribbean, Carolina
Neonesidea cassida (v.d. Bold, 1946)—Hawaii, †Caribbean (Oligocene)
Leptocythere ochracea (Brady, 1890)—New Caledonia, Trinidad
Copytus baculoides (Brady, 1890)—Fiji, Belize
Hermanites barri (v.d. Bold, 1960)—Hawaii, NW Brazil, Venezuela
Hermanites tschoppi (v.d. Bold, 1946)—Hawaii, Central America, Caribbean
Jugosocythere pannosa (Brady, 1869)—Hawaii, Gulf of Mexico, Caribbean, Puerto Rico, Central and North American East Coast
Hemicythere gordoni v.d. Bold, 1965—Hawaii, Caribbean, Puerto Rico, Panama (east)
Loxoconcha antillea v.d. Bold, 1965—Hawaii, Caribbean, Trinidad, Gulf of Mexico, Puerto Rico, Central America
Loxoconcha dorsotuberculata (Brady, 1866)—New Caledonia, Fiji, Belize (Teeter reported it only from Belize)
Paracypris rosefieldiensis Howe and Law, 1936—Hawaii, Caribbean, Gulf of Mexico, North American East Coast

†, indicates fossil occurrence.

EAST PACIFIC–INDO–WEST PACIFIC DISTRIBUTION (TABLE 4)

The number of tropical benthic animal species occurring along the Pacific coast of America and on the Islands of the Indo–west Pacific is small. Ekman (1935) was the first to notice this and believed that the large East Pacific water mass, with its lack of islands suitable for island-hopping dispersal, in connection with barriers of colder waters in the North and South is responsible for

TABLE 4—EAST PACIFIC—WEST PACIFIC (AMPHI-AMERICAN)

Neonesidea gierloffi (Hartmann, 1959)—Hawaii, Admiralty Islands, El Salvador
Triebelina reticulopunctata Benson, 1959—Hawaii, Todos los Santos, (Coast of Mexico), †France (Eocene)
Neonesidea simuvillosa Swain, 1967—Hawaii, Todos los Santos, Clipperton Island, Nicaragua
Cyprideis beaconensis LeRoy, 1943 (= *C. lengae* Hartmann, 1961)—Hawaii, America (bipolar along the west coast)
Xestoleberis nana Brady, 1880—Hawaii, Australia, California
Cythere caudata Brady, 1890—Hawaii, South Seas, Southeast Asia, Florida, Clipperton Island
Aurila lincolnensis (LeRoy, 1943)—Hawaii, Pacific Coast of North America
Xestoleberis gracilis Brady, 1890—Funafuti, Bismarck Archipelago, Samoa, Clipperton Island

†, indicates fossil occurrence.

this pattern of distribution. This theory is supported by the fact that it is mostly those benthic animals which possess a long pelagic larval development, such as Ophiurids (Echinodermata), which are among the species present on both sides of the East Pacific. Ekman (1935) therefore called the East Pacific the "East Pacific Barrier."

It is interesting that, according to the literature, eight species of ostracods are mentioned to have this distribution, interesting especially because the ostracods in question do not possess pelagic larvae. Analyzing the literature, we find that seven of the eight species have been found by Holden on the Hawaiian Islands. Again Holden himself feels that some of his findings are questionable (cf. aff.). Three of the species belong to the family Bairdiidae, two to the Xestoleberididae. The identification of both families is extremely difficult, and, without soft parts, only possible when comparisons with original material are made. Another species, *Cyprideis beaconensis* LeRoy, 1943 (=*C. lengae* Hartmann, 1961) has a bipolar distribution in America. Species of *Cyprideis* are believed to have become distributed by birds. As some Alaskan birds hibernate on Hawaii, the occurence of this species on these islands is possible, and if so, very interesting. The author believes that all these species must be reconsidered.

EAST PACIFIC–WEST PACIFIC (AMPHI–AMERICAN) DISTRIBUTION

In their paper on ostracods from Clipperton Island (tropical East Pacific), Allison and Holden (1971) listed several ostracods formerly described from the West-Atlantic. After critically checking the findings the author believes that only three species:

Cytherelloidea praecipua v.d. Bold, 1963
Zabythocypris helicina Maddocks, 1969
Occultocythereis angulata v.d. Bold, 1963

might really be distributed in this way. *Zabythocypris helicina,* a deep-sea species, probably has a wider distribution.

SPECIES OF THE EAST PACIFIC ISLANDS

Only fourteen species of ostracods are known from the East Pacific islands or their surroundings, with only 10 of these on Clipperton Island. They have been described by Allison and Holden. Among these species is *Xestoleberis eulitoralis* Hartmann, 1959, first discovered on the coast of El Salvador. A comparison of figures shown without doubt that the Clipperton material is not identical with that from El Salvador. It probably belongs to a new species. Three species from the East Pacific island were described from the Galapagos, one from the deep sea of the East Pacific.

PACIFIC ISLANDS AND EAST ASIA (JAPAN), EXCLUDING AUSTRALIA (TABLE 5)

Seven species have this pattern of distribution. Four may be considered as certain, three must be considered as questionable, as the illustrations and descriptions of these species given by workers differ considerably from one to another.

TABLE 5—PACIFIC ISLANDS AND EAST ASIA (JAPAN), EXCLUDING AUSTRALIA

Codonocera polygonia G.W. Müller, 1906—Southeast Asia, Samoa
Cypridina sinuosa G.W. Müller, 1906—Southeast Asia, Samoa
Cylindroleberis cylindrica Brady, 1890—Malay sia (uncertain), Fiji
Neonesidea sp. Egger, 1901—Java, Amboina (uncertain)
Loxoconcha uranouchiensis Ishizaki, 1968—Japan, China, Hawaii (uncertain)
Neomonoceratina entomon (Brady, 1890)—Manila, New Caledonia, Fiji
Tanella pacifica Hanai, 1957—Japan, Fiji, Samoa

PACIFIC ISLANDS AND AUSTRALIA (TABLE 6)

Of the 16 species considered to occur both in Australia and on the Pacific islands, 11 have been checked with the help of the original material. The distribution of five species is questionable.

TABLE 6—SOUTH SEA ISLANDS INCLUDING AUSTRALIA

Gigantocypris australis Poulsen, 1962—New Zealand, Australia, Samoa
Cylindroleberis australis Brady—South Sea Islands (?), New Zealand
Sarsiella simplex Brady, 1890—Australia, New Caledonia
Neonesidea michaelseni Hartmann, 1982—Western Australia, Rangiroa
Callistocythere crenata (Brady, 1890)—Australia, Hong Kong, New Caledonia, ?Fiji, ?Samoa, Hawaii
Cythereis tricristata Brady, 1880—Australia, Admiralty Islands
Quadracythere insulardeaensis Hartmann, 1981—Heron Island, Rangiroa
Quadracythere Heron Island sp. 174 Hartmann, 1981—Heron Island, Rangiroa
Loxoconcha insulaecapricornensis Hartmann, 1981—Heron Island, Rangiroa
Loxoconcha heronislandensis Hartmann, 1981—Heron Island, Rangiroa
Loxoconcha abditocostata Hartmann, 1981—Queensland, Rangiroa (there subsp. *parva* Hartmann, 1984)
Hemicytherura pentagona Hornibrook, 1952—New Zealand, Hawaii
Xestoleberis paraporthedlandensis Hartmann, 1978—Western Australia, Heron Island, Rangiroa, Huahine
Dentibythere dentata Schornikov, 1982—Australia, Solomon Islands
Xiphichilus gracilis Chapman, 1915—Australia, Hawaii
Paradoxostoma romei McKenzie, 1967—South Australia, Hawaii

SUMMARY

The analysis of the distribution patterns of the benthic ostracods of the tropical Pacific islands shows a considerable degree of uncertainty. It is obvious that the study of the ostracod fauna of this region is still very incomplete. The number of species with a well defined and reconsidered range is extremely small.

The larger number of ostracods mentioned from this region belong to a widely distributed Indo-West Pacific fauna.

The fauna of islands of the East Pacific show relationships only with the American mainland. The range of ostracods distributed far beyond the borders of the Indo-west Pacific is certain only in a few cases.

Difficulties with the identification of ostracod species arise especially with species of the Xestoleberididae, Paradoxostomatidae, Loxoconchidae with a reticulated valve surface, and Bairdiidae. Positive identification is only possible by comparison with the original material, or through very good REM photos.

The zoologists among the ostracodologists should ask their colleagues in palaeontology to consider not only the vertical time distribution, but, in the future even more than has been the case up to now, also the horizontal range of species. The dispersal of ostracods has not yet gained the significance it should have. Most benthic ostracods, *e.g.* the Podocopa, do not possess pelagic larvae, so their dispersal is often passive. The basis of all biogeographical studies must be an exact systematic study. We are still far from achieving this and the need for further studies remains.

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APPENDIX

Corrections to the list in Hartmann (1984: 137–142), on the Ostracoda found in Pacific Islands.

The list of Ostracoda of Pacific Islands compiled by the author (1984) contains a series of errors. The errors found are documented here:

p. 137 For *Harbansus bradmeyeri* read *H. slattery*.

p. 138 For *Trebelina* read *Triebelina*.
For *Zabythocypris Heterodoxa* read. *Z. heterodoxa*.
For Capman read Chapman.
Cythere cancellata corresponds to *Cytheromorpha cancellata* (see p. 139, 2nd line).
As to the Bairdiidae, the authors' names often do not meet the nomenclatural rule of putting them in parentheses, as for example in *Neonesidea schulzi* (Hartmann, 1961).

p. 139 ?*Cytheromorpha crispata* (Brady, 1869) *Leptocythere* or *Tanella miurensis* Hanai: 1957 must be struck from the list. The species is only known from Japan.
Hermanites barri (v. d. Bold, 1960) instead of 1980.

p. 140 *Hemicytherura cranecayensis* Puri, 1960 has not been found in Hawaii.
For *Hemicytherura pentagoni* read *H. pentagona*.
For *Occultocytheropteron* read *Oculocytheropteron*.

p. 141 For *Xiphichilus giccilis* read *X. gracilis*.
For *Mungava eleotridis* read *Paracypria eleotridis* (see p. 142).
The *Propontocypris* species described by Brady were not published under this generic name. The author's name should be put in parentheses.

p. 142 *Paracypria eleotridis* should be deleted (see p. 141, below *Mungava*).

DISCUSSION

McKenzie: What do you think of the status of Holden's determination of *Cythere caudata* Brady, 1890, in his fauna from Clipperton Island? The types are available at this symposium for comparison (of the Brady species).

I have identified *Cypridina sinuosa* Müller, 1906, from off the Carpenteria Group, Queensland and even along the coast of New South Wales. Probably, it travels on the current (from Tonga around NE Australia and NSW).

Hartmann: I cannot comment on these questions at the moment.

On the Occurrence of *Javanella* and *Saida* in the Pliocene of Leizhou Peninsula, Guangdong, China

YUN-SIAN GOU AND DE-QIONG CHEN
Nanjing Institute of Geology and Palaeontology,
Academia Sinica, P. R. China

ABSTRACT

The occurrence of *Javanella kendengensis* Kingma, first recorded in the Pliocene of Java, and *Saida* sp. in the Pliocene Wanglougang Formation from the Leizhou Peninsula, Guangdong, gives further evidence of the close relationship between the ostracod faunas from the North Continental Shelf of the South China Sea and those from the Indo-Malayan area, and the possible connection with Australasian ostracod faunas from the Late Cenozoic to Recent. The two samples under study were collected by Gou and He in 1963 from boreholes in Xuwen County in the Southern Part of the Leizhou Peninsula. In the present paper, *Javanella kendengensis* Kingma and *Saida* sp. are described and the distribution of these two genera is discussed.

The marine Pliocene ostracod fauna from the North Continental Shelf of the South China Sea was reported by Gou, Chen, Guan, Zheng, Huang and *et al.* (1981, 1983). There are 51 genera and 107 species described mostly from boreholes in the sea basins, and 65 genera and 166 species described from boreholes in the Leizhou Peninsula and northern Hainan Island, Guangdong. However, the genera *Javanella* and *Saida* have never been found in this area previously. Based on the composition of ostracod genera and species, the aspects of the Pliocene ostracod faunas from the Leizhou Peninsula and northern Hainan Island, and from the sea basins of the North Continental Shelf of the South China Sea are the same.

Javanella is a particular genus established by Kingma (1948) from the Upper Pliocene Klitik Formation of Pentuk, East Java, but Kingma did not indicate the holotype for the type species *Javanella kendengensis* Kingma. Later, Keij (1979) gave a brief review of the type species of the genus from Kingma's collection, and selected a lectotype for *Javanella kendengensis* Kingma, which contains only one left valve and one right valve.

Recently, *Javanella kendengensis* Kingma was obtained from a core sample of the Pliocene Wanglougang Formation in Xuwen County of the southern Leizhou Peninsula. In this sample, *Javanella kendengensis* Kingma is associated with shallow water forms of Ostracoda such as *Keijella hodgii* (Brady), *Neocytheretta faceta* (Guan), *Callistocythere guangdongensis* Gou, *Stigmatocythere dorsinoda* Chen, *S.bona* Chen, *Neomonoceratina delicata* Ishizaki et Kato, *Parakrithella pseudadonta* (Hanai) and *Loxoconcha* sp.

Keij suggests that *Javanella* is a distinct Indo-Malayan genus, however the occurrence of this genus in the Leizhou Peninsula indicates that its distribution is not limited to the Indo-Malayan area, and further proves the close relationship between the faunas from the North Continental

Shelf of the South China Sea and those from the Indo-Malayan area of the same age.

Saida was established by Hornibrook (1952) from New Zealand with the Recent form *Saida truncala* as its type species. This genus is characterised by its tiny carapace. Based on the available data, *Saida* has a wide range in space and time. Since Hornibrook noted the earliest appearance of this genus in the Middle Eocene (Bortonian) of New Zealand, it has been discovered successively in the Upper Cretaceous of Europe and in Australasia where a few specimens have been found. *Saida nettgauensis* was described by Gründel (1966) from the Albian of Germany. *Loxoconcha elliptica,* reported by Bonnema (1941) from the Upper Cretaceous of Holland, was assigned to *Saida* by Szczechura (1965). After reviewing the European *S. elliptica* (Bonnema) from the Upper Cretaceous and the Palaeocene, Herrig (1966, 1967, 1968) proposed four new species: *S. exilis* Herrig (Upper Turonian), *S. media* Herrig (Santonian to Upper Campanian), *S. crassa* Herrig (Lower Maastrichtian to Danian) and *S. nana* Herrig (Maastrichtian). The Australian Upper Cretaceous form *S. rhomboidea* was described by Neale (1975) from the Santonian Chalk of Western Australia.

The European Tertiary forms of *Saida* contain four unnamed species respectively mentioned or described and figured by Deltel (1941) from the Palaeogene (Lutetian) of S. W. France, by Pietrzeniuk (1969) from the Upper Eocene of Poland, by Ascoli (1969) from the Upper Eocene of Italy and by Sissingh (1972) from the Upper Pliocene of Greece. In America, *Cytherelloidea murdercreekensis* Howe and Law (1936), appearing in the Tertiary of Mississippi and Alabama, (Sexton, 1951) is referred to *Saida* (Howe and Howe, 1973) based on its shape and its having a prominent oblique ventrolateral process.

There are two Australasian species of *Saida* found in Holocene to Recent sediments: one of them is *S. torresi,* reported by Brady (1880) from the Torres Straits of Australia, the other is *S. truncala,* recorded by Hornibrook (1952) from New Zealand.

In the South China Sea *Saida herrigi* Keij is recorded from two localities, one of which is situated from 5°21′N: 111°14′E to 6°40′N: 109°34′ 30″ E in the South China Sea and is Holocene in age, and the other is situated off the Xisha-Zhongsha Islands where the specimens were collected from the surface of the bottom sediments (Cai and Tu, 1983).

Recently, *Saida* sp., like *Javanella kendengensis* Kingma mentioned above, was found in the Pliocene Wanglougang Formation in another borehole in the Southern Leizhou Peninsula. Here it is associated with the shallow water forms *Keijella hodgii* (Brady), *Parakrithella pseudadonta* (Hanai), *Cytheropteron uchioi* Hanai, *Stigmatocythere dorsinoda* Chen, *Albileberis asperata* Guan, *Pontocythere subjaponica* (Hanai), *Semicytherura miurensis* (Hanai), *Loxoconcha sinensis* Brady, *Neomonoceratina delicata* Ishizaki et Kato, *Hemicytherura cuneata* Hanai, etc. The similarity of *Saida* sp., described in this present paper, to *Saida herrigi* Keij from the South China Sea and to *S. rhomboidea* Neale from the Australian Cretaceous seems further proof of the possible connection between the ostracod faunas from the North Continental Shelf of the South China Sea and those from the South Pacific and Australasia ranging from Late Cenozoic to Recent, although in these areas Tertiary species of *Saida* have not yet been found.

Judging from the above data, the genus *Saida* is more widely dispersed than hitherto realised;

Plate 1—All specimens described in this paper are kept in Nanjing Institute of Geology and Palaeontology, Academia Sinica. All figures are scanning electron micrographs of gold coated specimens (except Plate 2, figs. 1,2). Figs. 1–6. *Javanella kendengensis* Kingma. Fig. 1. Lateral view of right valve, Plesiotype, Cat. No. 94397, ×100. Fig. 2. Internal view of right valve, Plesiotype, Cat. No. 94397, ×100. Fig. 3. Lateral view of left valve, Plesiotype, Cat. No. 94398, ×100. Fig. 4. Internal view of left valve, Plesiotype, Cat. No. 94398, ×100. Fig. 5. Hinge of right valve, Plesiotype, Cat. No. 94397, ×200. Fig. 6. Hinge and adductor muscle scars of left valve, Plesiotype, Cat. No. 94398, ×200.

Figs. 7–11. *Saida* sp. Fig. 7. Lateral view of right valve, Cat. No. 94402, ×200. Fig. 8. Internal view of right valve, Cat. No. 94402, ×200. Fig. 9. Hinge of right valve, Cat. No. 94402, ×286. Figs. 10, 11. Detail of right hingement, Cat. No. 94402, ×1000.


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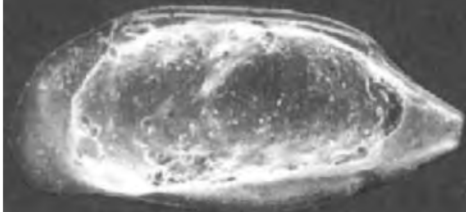
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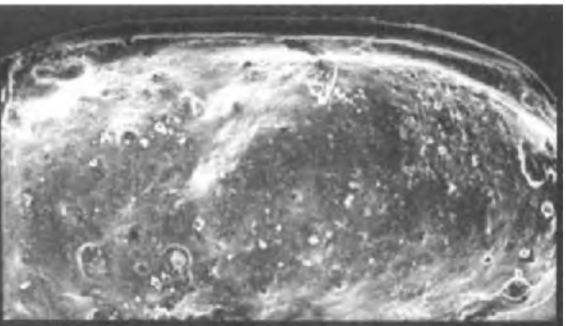
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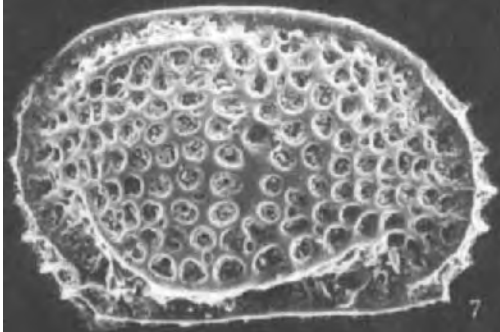
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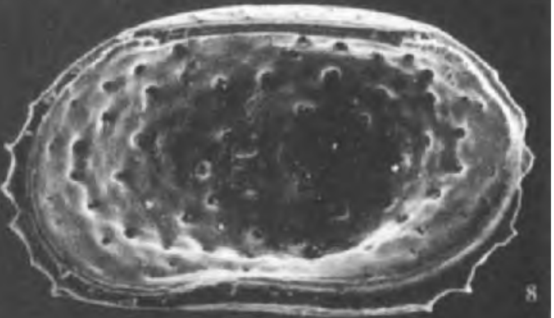
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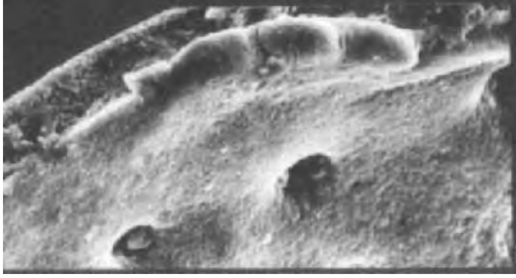
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its species ranged either eastwards from Europe or northwards from Australia into the Indo-west Pacific. This genus is noticeably important for the study of primary dispersal routes and biogeographical distribution.

Genus JAVANELLA Kingma

JAVANELLA KENDENGENSIS Kingma

(Pl. 1, figs. 1–6; Pl. 2, figs. 1–4, 8, 9)

Javanella kendengensis Kingma, 1949, p. 89, Pl. 10, fig. 6; Keij, 1979, p. 60, Pl. 2, figs. 7, 8.

Description.—Carapace moderate in size, thin-shelled, elongate in lateral view, with posterior caudal process, which is situated somewhat below the middle of the posterior part. Posterior end bluntly acuminate in the middle. Anterior margin obliquely rounded. Dorsal margin nearly straight. Ventral margin sinuate, convex in the posterior part and concave in the anteior part. Surface of carapace smooth.

Hinge in the right valve with a narrow, nearly smooth groove along the entire dorsal margin, and with a narrow elongate anti-slip tooth below the anterior end of the groove. Hinge in the left valve with a narrow elongate smooth bar fitting in the groove of the right valve. Marginal zone moderately wide with deep anterior and shallow posteroventral vestibule, marginal pore canals moderate in number, simple and branching. Normal pore canals sieve type. Central muscle scars consisting of slightly oblique row of four adductor muscle scars, a large frontal scar and two connecting large mandibular scars.

Dimensions.—Right valve, Plesiotype, Cat. No. 94397, L - 570 μm, H - 260 μm; Left valve, Plesiotype, Cat. No. 94398, L - 590 μm, H - 240 μm.

Remarks.—Four left valves and two right valves are present in our material. In the Treatise on Invertebrate Paleontology Part Q, *Javanella* was recognized as a synonym of *Pellucistoma,* but a review of the hinge structure shows that the former is quite different from the latter. In *Pellucistoma,* the hinge of the life valve consists of a long, anterior blade-like triangular tooth from which a long serrated bar extends backwards and terminates at the posterior cardinal angle; above this bar and parallel to it is a narrow, incised, line-like groove. The hinge in the right valve has an anterior socket and a crenulate groove. Examination of the hinges of *Javanella* and *Nipponocythere* shows that the right valve hinges in both genera are similar each to other, because in the latter an anti-slip tooth also occurs below the anterior end of the groove of the right valve. However, in *Nipponocythere* the posterior end of the bar of the left valve is roughly crenulated with a tooth in the posterior socket. The types of adductor scars and frontal scar in these two genera are also similar to each other. It seems that, judging from the hinge structure and the muscle scar pattern, *Javanella* is rather closer to *Nipponocythere* than to *Pellucistoma.*

The present specimens differ slightly from the lectotype of *Javanella kendengensis* in their rather larger size and more slender carapace.

Occurrence.—Xuwen County; Wanglougang Formation.

PLATE 2—Figs. 1–4, 8, 9. *Javanella kendengensis* Kingma. Fig. 1. Right valve seen from inside by transmitted light, Plesiotype, Cat. No. 94400, ×100. Fig. 2. Left valve seen from inside by transmitted light, Plesiotype, Cat. No. 94398, ×100. Fig. 3. A sieve-type normal pore canal on the anterior lateral surface of the left valve, Plesiotype, Cat. No. 94401, ×4000. Fig. 4. Muscle scars of left valve, Plesiotype, Cat. No.: 94398, ×800. Fig. 8. Posterior part of left valve hinge, Plesiotype, Cat. No. 94399, ×600. Fig. 9. Anterior part of right valve hinge, Plesiotype, Cat. No. 94397, ×600.

Figs. 5–7—*Saida* sp. Fig. 5. Muscle scar pattern, Cat. No. 94402, ×1000. Fig. 6. Broader mural portion corresponding vertically to the internal muscle scars, Cat. No. 94402, ×600. Fig. 7. Detail of normal pore, ×2000.


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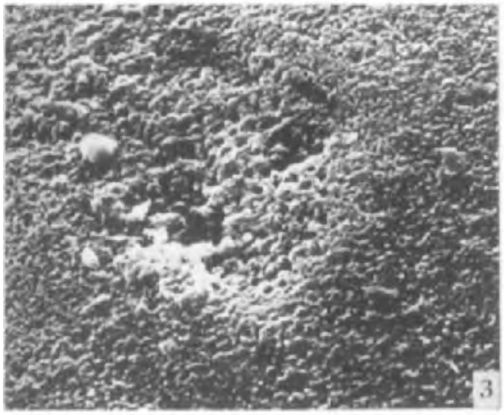
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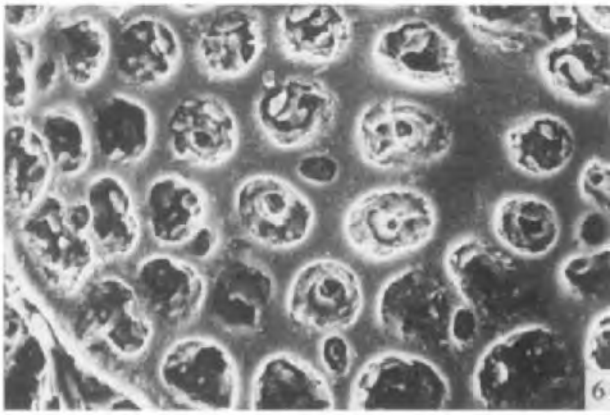
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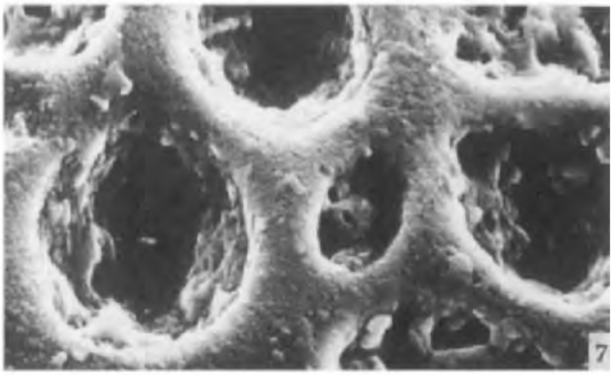
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Genus SAIDA Hornibrook

SAIDA sp.

(Pl. 1, figs. 7–11; Pl. 2, figs. 5–7)

Description.—Small, right valve more or less oval in lateral view. Dorsal margin long and slightly convex. Ventral margin long and straight, the front of the middle concave in inner view. Anterior end drawn out ventrally, with six distinct spines along the outer margin. Posterior one higher than the anterior and symmetrically rounded, with seven sharp spines along the posterior margin. The lateral part of the posteroventral area forms a semicircular protruding ala. The outer edge of the ala itself is defined by a smooth carina, which starting near the anteroventral area at one-quarter the height, runs posteriorly parallel to the venter then curves smoothly upwards to about one-half the height; the inner part of the ala merges gradually with the body of the valve dorso-anteriorly. A smooth, nearly straight carina is present in the posterodorsal area. A thin, smooth marginal rim forms a border all around the valve and is nearly straight along the venter.

Surface covered with a meshwork of deep pits arranged in vague rows parallel to the margins. The rounded fossae on the lateral ala are much larger than the marginal fossae. The sunken sieve plates of the fossae and second-order reticulation are not visible. The smooth muri carry intramural pores (Pl. 2, fig. 7). On the central part, a broader mural portion corresponds vertically to the area of internal muscle scar (Pl. 2, fig. 6). The inside of the anterior rim has six or seven faint, short mural ribs which join with the anterior rim. The same occurs posteriorly.

The lophodont hinge of the right valve (Pl. 1, figs. 9–11) consists of two terminal elongate teeth, subdivided into four or five cusps, and a long straight groove in between.

The marginal zone is broken. Internal openings of normal pores are simple, rather large and widely spaced over entire valve (Pl. 1, fig. 8).

The central muscle scar pattern is a vertical row of four elongate adductor scars set at mid-height. Frontal scar not seen (Pl. 2, fig. 5).

Dimensions.—Right valve, described specimen, Cat. No. 94402, L - 310 μm, H - 220 μm.

Remarks.—Only a single right valve was found. This species of *Saida* differs from *S. truncala* Hornibrook, the type species, and *S. torresi* (Brady) in the presence of a postero dorsal carina, which is lacking in those two species. It is distinguished from *S. herrigi* Keij, from the South China Sea, by its lack of a low, irregular carina running obliquely forwards from the apex of the ala and by a different arrangement of fossae and muri (which are nearly horizontal in *S. herrigi* Keij).

In general outline and alar shape, this unnamed species of *Saida* is closer to *Saida* sp. (Sissingh, 1972) from the Pliocene Pigadia Formation of the South Aegean Island Arc, but is easily distinguished from the latter by the presence of a smooth, nearly straight carina in the posterodorsal area. This *Saida* sp. is also close to *S. rhomboidea* Neale, from the upper Cretaceous of Gingin, Western Australia, but is easily distinguished by its smooth posterodorsal carina.

Occurrence.—Xuwen County; Wanglougang Formation.

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DISCUSSION

Whatley: *Saida* is a strange ostracod with respect to its distribution. It seems to have been widespread since the Cretaceous in Tethyan and Indo/Pacific Seas. However, since at least the Upper Oligocene, it has occurred in deep sea environments although it is never abundant there. Recently, we discovered *Saida* in the Atlantic in Recent sediments. There seems to be no simple explanation of its distribution.

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Distribution of Modern Ostracoda in the Shelf Seas off China

QUANHONG ZHAO AND PINXIAN WANG
Tongji University, Shanghai, P. R. China

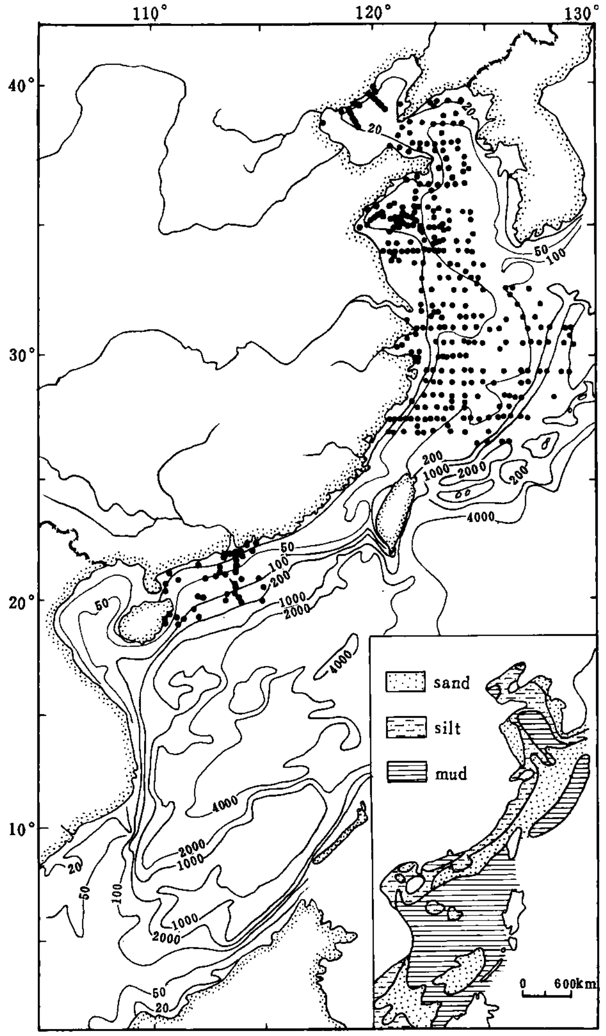
ABSTRACT

Modern Ostracoda in shelf seas off China were qualitatively and quantitatively analyzed in 688 surface sediment samples. As a result, a brackish-water assemblage, an eurythermal and stenohaline assemblage and three temperature-related assemblages were recognized. Variations in faunal composition and species diversity are related largely to water temperature and salinity. The China Sea can be divided into three zoogeographical regions based on Ostracoda. Endemism of the brackish-water coastal fauna and the relationship between the Chinese and Japanese, and Indonesian-Malaysian faunas are discussed.

The shallow part of the China Sea is one of the largest shelves in the world. The shelf of the East China Sea, for example, reaches 530 km in width, and the width of the northern shelf of the South China Sea averages 274 km. Two current systems control the shelf seas off China: the Kuroshio with its branches and the coastal currents. The high-temperature and high-salinity water of the Kuroshio dominates the eastern and southern parts, and the coastal water with low salinity and variable temperature is distributed in the northern and western shallow parts.

During the last ten years, modern Ostracoda in the China Sea have been intensively studied, mainly by Japanese and Chinese scientists (*e.g.*, Nohara, 1976; Nohara and Tomoyose, 1977; Ishizaki, 1977, 1981; Wang, Min and Bian, 1978; Wang, Lu and Cheng, 1980; Wang, Min and Gao, 1980; Cai, 1983; Zhao, 1984, 1985; Wang and Bian, 1985; Wang and Zhao, 1985; Zhao, Wang and Zhang, 1985). The abundant data accumulated, however, still require summarising.

The purpose of the present paper is to sum up our analyses of 688 grab and core-top samples of surface sediments and to delineate the areal distribution of modern ostracods in the shelf seas off China as a whole. Fifty grams of each sample was washed on a 0.063 (or 0.055) mm mesh screen and, when possible, more than 100 ostracod valves were picked from each sample or from a split of it. All the ostracod specimens were identified and counted. The sampling area covers all the seas off China: the Bohai Gulf (30 samples), the Huanghai (Yellow) Sea (364 samples), the East China Sea (224 samples) and the northern shelf of the South China Sea (70 samples) (Text-fig. 1). About 200 of the samples were taken from estuaries, lagoons or littoral zones.

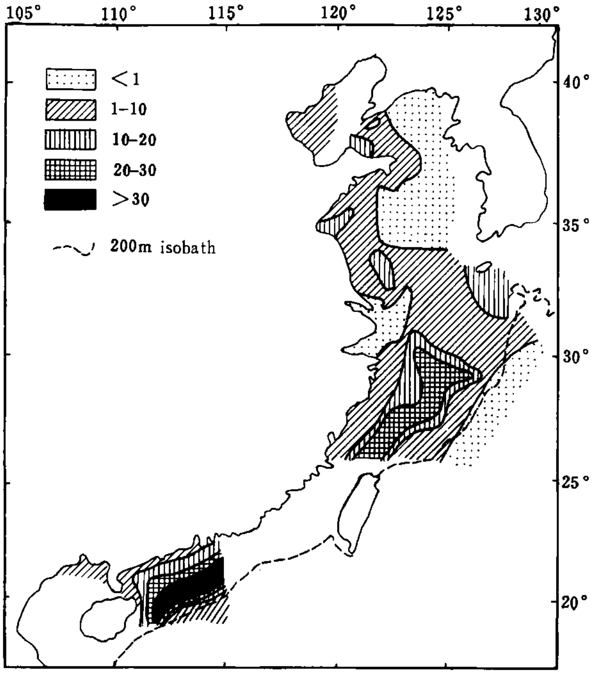


TEXT-FIG. 1—Bathymetry, sampling stations and sediment types in the shelf seas off China (for graphical reasons some of the stations are omitted).

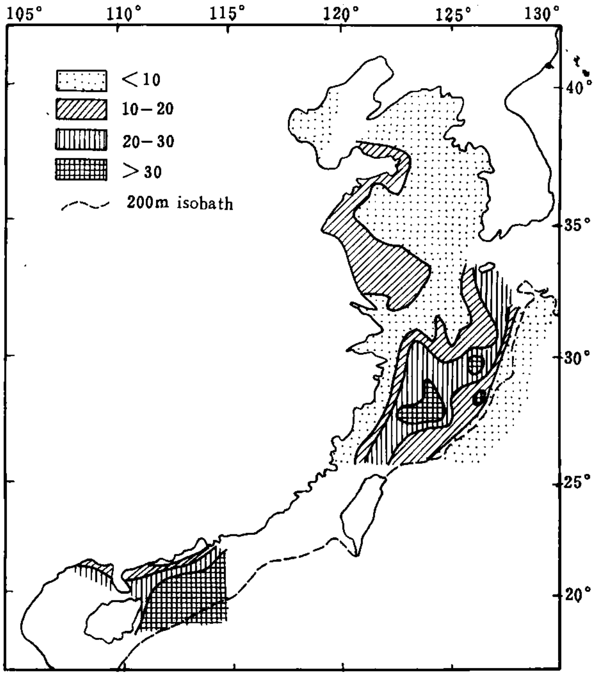
ABUNDANCE AND DIVERSITY

Rich ostracod faunas were found in all the shelf seas under consideration. A total of 116 species belonging to 68 genera were identified in the Bohai Gulf and the Yellow Sea, 126 species representing 83 genera in the East China Sea and 190 species from 90 genera in the northern part of the South China Sea.

The distribution of ostracod abundance (number of valves per gram of sediment) and diversity (number of species per sample) is shown in Text-figs. 2,3 and Table 1. It can be seen that both the abundance and diversity increase generally from the north to the south, from the coast to the shelf edge. The lowest values (<10 species per sample, <1 valve per gram) occur in the estuarine and coastal zones with water depths of less than 20m and in the central part of the Huanghai Sea with



TEXT-FIG. 2—Distribution of ostracod abundance in the surface sediments of the shelf seas off China (number of valves per gram of dry sediment).

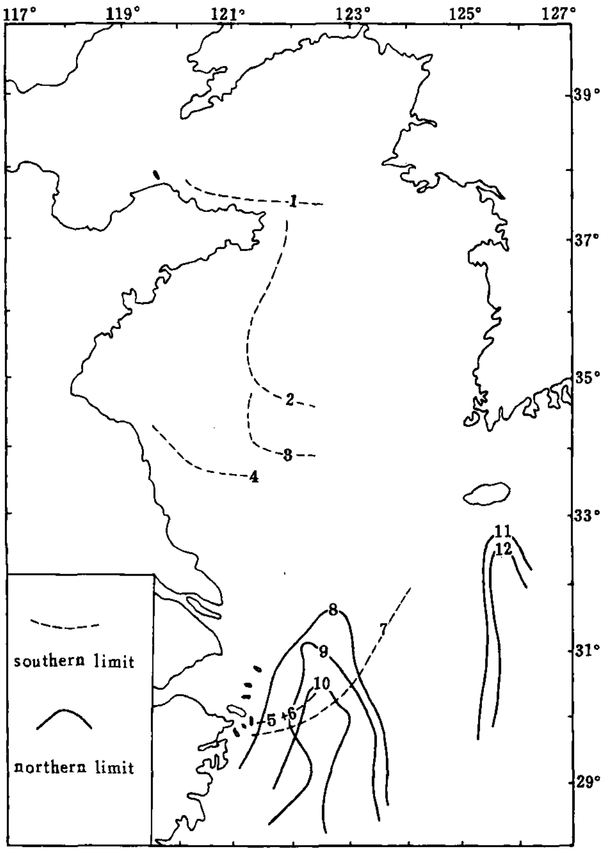


TEXT-FIG. 3—Distribution of number of species of ostracods in the surface sediments of the shelf seas off China.

TABLE 1—AVERAGE OSTRACOD ABUNDANCE AND DIVERSITY IN SURFACES SEDIMENTS OF THE SHELF SEAS OFF CHINA

Water Depth Range	20m	20–50m	50–100m	100–150m	150–200m
Sea Area	average number of valves per gram of sediment				
Huanghai Sea and Bohai Gulf	10.4	9.3	2.8	—	—
East China Sea	2.2	4.6	17.7	17.2	4.6
North Part of South China Sea	18.6	11.5	33.3	27.7	22.0
Sea Area	average number of species per sample				
Huanghai Sea and Bohai Gulf	14.7	11.4	7.6	—	—
East China Sea	7.7	10.6	21.4	18.1	11.8
North Part of South China Sea	15.8	22.1	36.7	31.5	29.2

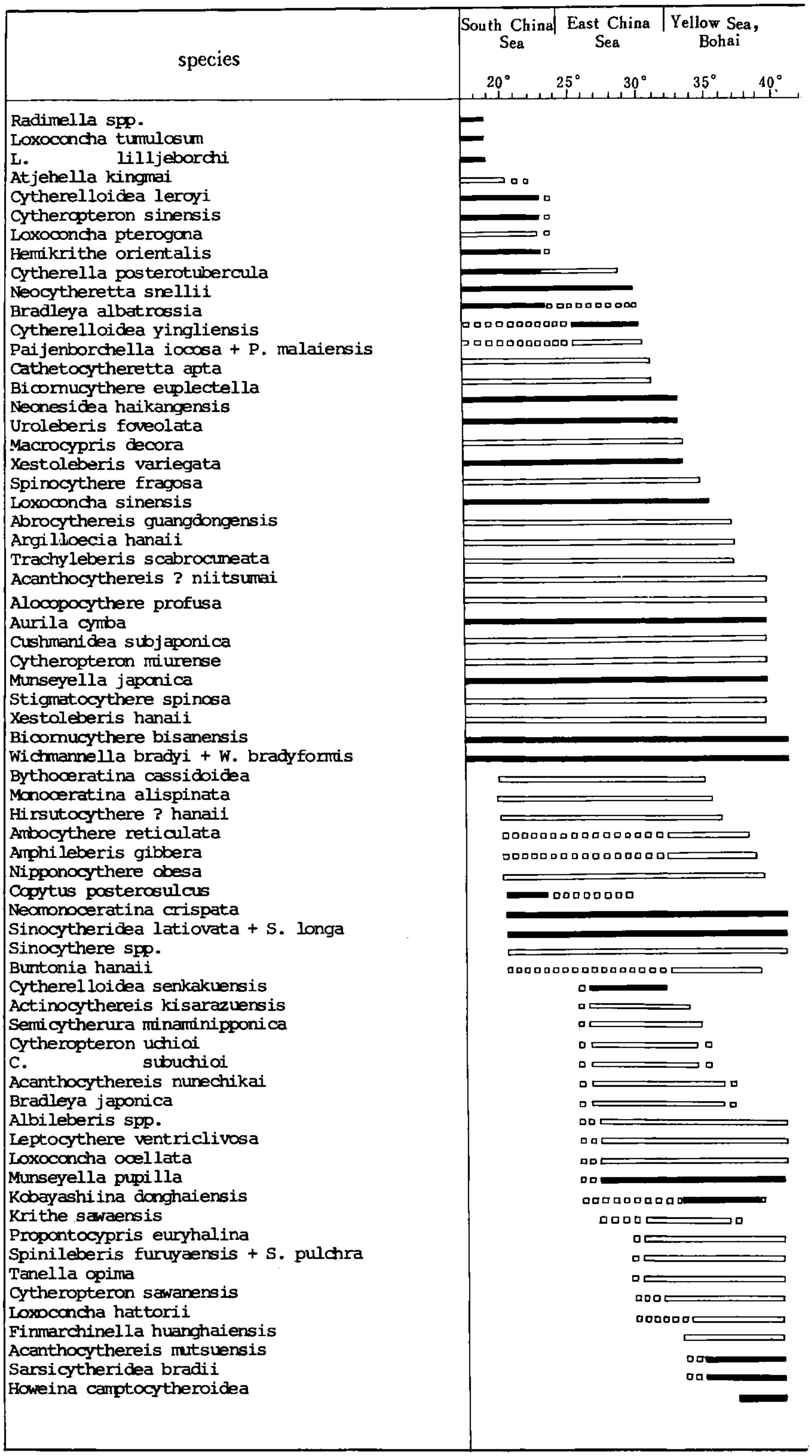
water depths of over 50 m. The low concentration and diversity of ostracods can be attributed to high sedimentation rate and to low water temperature and salinity, since the central part of the Huanghai Sea is occupied by the Huanghai Cold Water Mass and the estuarine and coastal zones are dominated by diluted water of variable temperature. The middle and outer shelves of the East



TEXT-FIG. 4—Occurrence of some cold-water and warm-water species in the shelf seas off China:

Cold-water species: 1, *Howeina camptocytheroidea*; 2, *Acanthocythereis mutsuensis*; 3, *Sarsicytheridea bradii*; 4, *Finmarchinella huanghaiensis*; 5, *Cytheromorpha acupunctata*; 6, *Loxoconcha hattorii*; 7, *Cytheropteron sawanensis*.

Warm-water species: 8, *Cytherelloidea senkakuensis*; 9, *Paijenborchella iocosa* + *P. malaiensis*; 10, *Cytherelloidea yingliensis*; 11, *Uroleberis faveolata*; 12, *Neonesidea haikangensis*.



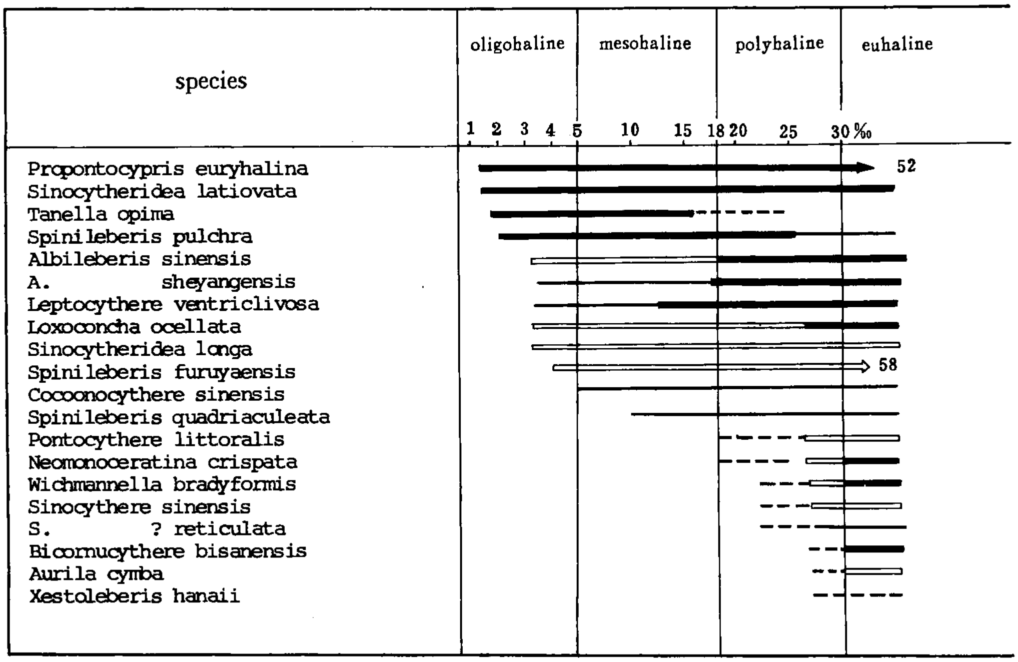
TEXT–FIG. 5—Latitudinal distribution of common species of Ostracoda in the shelf seas off China. (■ abundunt; ☐ few).

China Sea and the northern part of the South China Sea, on the contrary, are controlled by the Kuroshio Current and hence are distinguished by high temperature and salinity, apart from the low sedimentation rate of terrigenous material. As a result, the ostracod concentration and diversity are high in these areas, with more than 10 valves per gram and more than 20 species per sample.

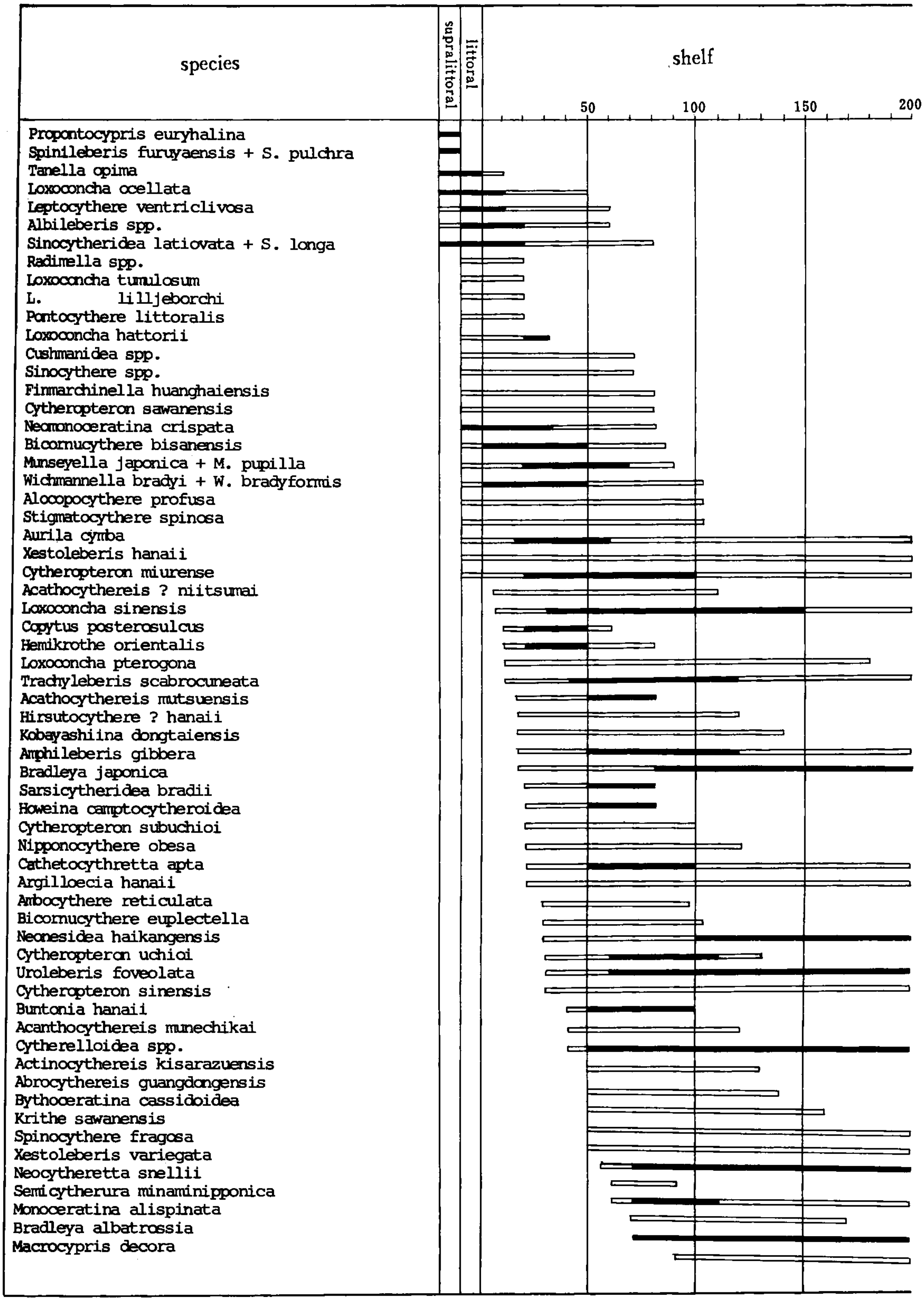
Distribution of Species

As revealed by distribution patterns of individual species in the sea areas studied (see Wang and Zhao, 1985; Wang, Min and Gao, 1980; Wang *et al.*, in press; Zhao, Wang and Zhang, 1985), temperature, salinity and water depth are major environmental factors controlling the areal distribution of Ostracoda.

The China Sea extends across three climatic zones: tropical, subtropical and temperate zone. However, the bottom-water isotherms are not parallel to the latitudes and their pattern is complicated by the influence of the water masses and currents. For example, warm-water species typical of the South China Sea — *Bicornucythere euplectella* (Brady), *Cytherelloidea yingliensis* Guan, *Neonesidea haikangensis* (Guan), *Uroleberis foveolata* (Brady), *Neocytheretta snellii* (Kingma), *Loxoconcha sinensis* Brady, *Xestoleberis variegata* Brady, *Paijenborchella malaensis* Kingma, *P. iocosa* Kingma etc., also occur in the outer shelf area of the East China Sea and are believed to be brought northwards by the warm water of the Kuroshio Current (Text-fig. 4). On the other hand, cold-water species like *Finmarchinella huanghaiensis* Zhao, *Cytheropteron sawanensis* Hanai, *Loxoconcha hattorii* Ishizaki, *Cytheropteron acupunctata* (Brady) and *Howeina camptocytheridea* Hanai are mainly bound to the Huanghai Cold Water Mass, but are distributed by the coastal currents in the northwestern part of the East China Sea as well (Text-fig. 4). The latitudinal occurrence of common species is summarised in Text-fig. 5. In respect to temperature adaptation, three types of species may



Text-fig. 6—Salinity ranges of common species of Ostracoda in the coastal areas of the China Sea. ■ abundant; ☐ common; —— few; - - - rare.



TEXT-FIG. 7—Depth ranges of common ostracod species in the shelf seas off China.
(■ abundant; ☐ few).

be distinguished in the shelf seas off China: 1. warm-water species inhabiting the South China Sea and/or the East China Sea, with a few occurrences in the southern part of the Huanghai Sea; 2. coldwater species distributed mainly in the Huanghai Sea and the Bohai Gulf; 3. eurythermal species found in coastal waters all along the shoreline of the Chinese mainland.

As for the water salinity, there is a general tendency for it to increase southwards and seawards in the sea areas studied. In the open seas, where the salinity variation is negligible, all ostracod species are stenohaline in nature and the water temperature is the main factor controlling their distribution, whereas in coastal and estuarine areas with significant salinity variations in space and time, the ostracod fauna is dominated by euryhaline and hypohaline forms. According to our ecological survey of living ostracods along the Chinese coast (Zhao, 1984, 1985), the salinity ranges of common eury and hypo-haline species are shown in Text-fig. 6. Worth noting are some euryhaline genera such as *Sinocytheridea* and *Albileberis* which are dominant and widespread in the Chinese coastal waters, but have as yet never been reported elsewhere. The world-wide brackish-water form *Cyprideis torosa* (Jones) is conspicuously absent along the Chinese coast and is probably replaced by the endemic species *Sinocytheridea latiovata* Hou et Chen.

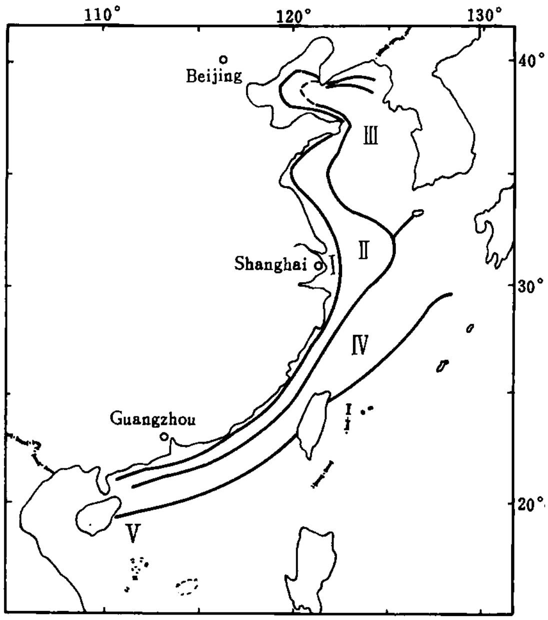
Depth ranges of common ostracod species in the shelf seas off China are given in Text-fig. 7. According to depth occurrence it is possible to distinguish supralittoral, littoral, inner shelf and other forms. However, it has been shown that the water depth in itself is not a purely independent factor in determining the faunal distribution, because many environmental factors such as hydrostatic pressure, density, temperature, salinity, pH, oxygen, diaphaneity, nutrients, etc., change with it. If the same environmental conditions occur at different depths in different areas, the depth range of ostracod species may also be changed. Examples are the warm-water species *Neonesidea haikangensis, Uroleberis foveolata* and *Loxoconcha sinensis* which spread all over the shelf in the South China Sea ranging from the inner to outer part, but are limited to the outer shelf in the East China Sea where the Kuroshio current is running through. The difference in their depth occurrences can obviously be ascribed to the temperature.

DISTRIBUTION OF ASSEMBLAGES

In our previous works, several ostracod assemblages have been dstinguished for each sea off China: three assemblages for the Bohai Gulf (Wang and Bian, 1985), five for the Huanghai Sea (Wang, Min and Gao, 1980), nine for the East China Sea (Wang and Zhao, 1985), and five for the South China Sea (Zhao, Wang and Zhang, 1985). When all these data from individual seas are compared with each other and are summarised, five major ostracod assemblages may be recognised for the entire shelf of the China Sea (Text-fig. 8).

Assemblage I (Pl. 1, Figs. 1–9) is dominated by *Sinocytheridea latiovata, S. longa* Hou et Chen, and *Neomonoceratina crispata* Hu and is widely distributed in coastal and estuarine areas less than 20 m deep all along the Chinese coastline. Some species (*e.g.*, *Albileberis sinensis* Hou, *Leptocythere ventriclivosa* Chen and *Loxoconcha ocellata* Ho) are common in all the areas studied except the South China Sea where they are absent presumably due to its relatively high temperature. Moreover, the species composition also varies with the difference in salinity. Thus, *Tanella opima* Chen, *Propontocypris euryhalina* Zhao, *Spinileberis furuyaensis* Ishizaki and Kato and *S. pulchra* Chen are more frequent in oligo-and mesohaline waters, while in poly and euhaline waters some elements from Assemblage II (*Wichmannella bradyformis, Bicornucythere bisanensis, Sinocythere sinensis* and *S.? reticulata* among others) are common. In fact, this is an eurythermal and euryhaline assemblage.

Assemblage II (Pl. 1, Figs. 10–25) is composed of eurythermal, but stenohaline, shallow-water

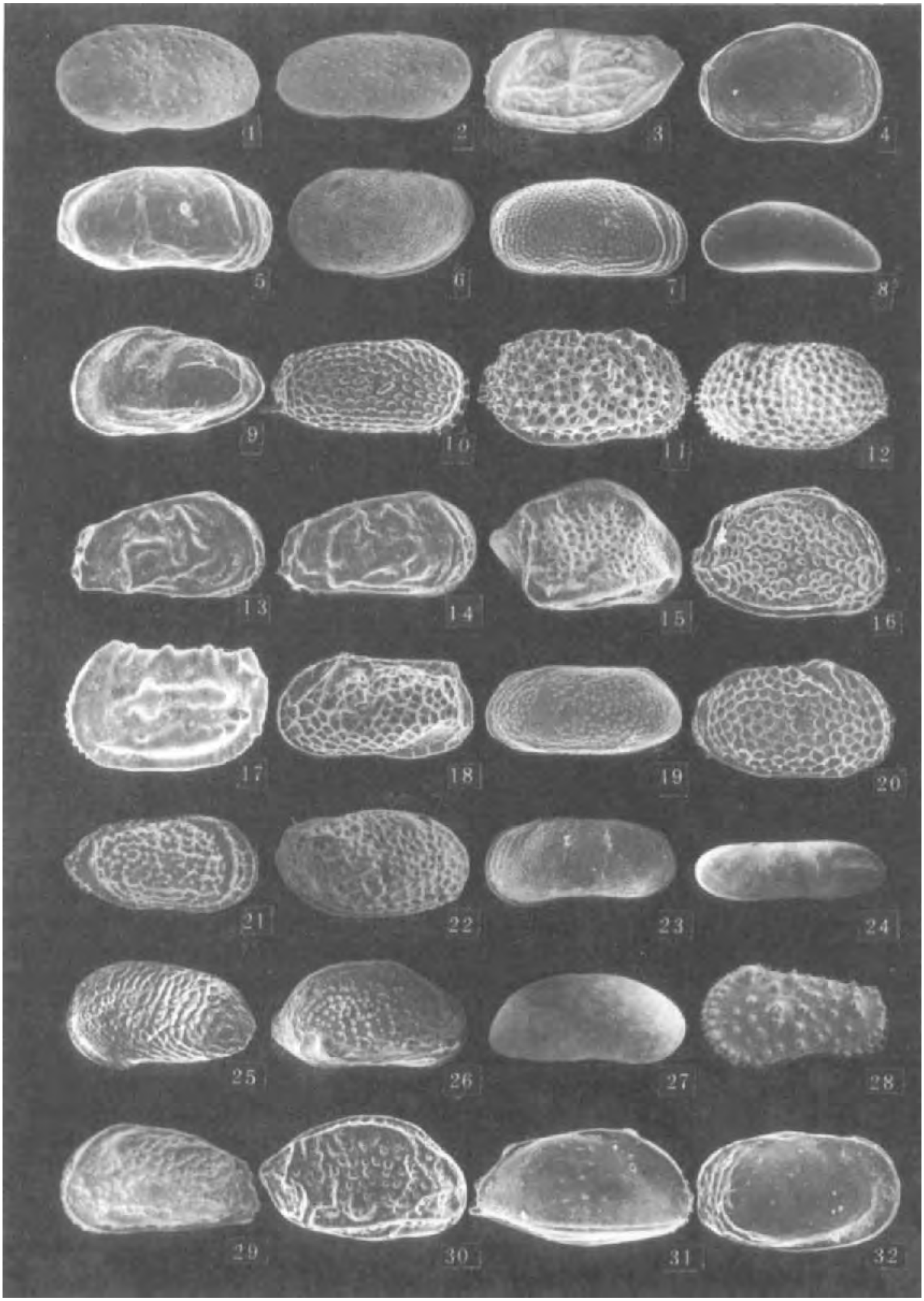


TEXT-FIG. 8—Distribution of five major ostracod assemblages in the shelf seas off China.

species and occurs on the inner shelf at water depths of about 20–50 m throughout all the seas under consideration. *Wichmannella bradyformis* (Ishizaki), *Bicornucythere bisanensis* (Okubo), *Munseyella pupilla* Chen, *M. japonica* (Hanai), *Cytheropteron miurense* Hanai are dominant and *Aurila cymba* (Brady), *Cushmanidea* spp., *Wichmannella bradyi* (Ishizaki), *Stigmatocythere spinosa* (Hu), *Sinocythere sinensis* Hou, *S.* ? *reticulata* Chen, *Nipponocythere bicarinata* (Brady), *Neomonoceratina crispata* and *Sinocytheridea latiovata* are common. Again, there are variations in species composition related to water temperature. For example, there are warm-water forms like *Loxoconcha sinensis*, *Hemikrithe orientalis* Bold and *Copytus posterosulcus* Wang in the South China Sea, and cold-water forms like *Finmarchinella huanghaiensis*, *Cytheropteron sawanensis* and *Loxoconcha hattorii* in the Huanghai Sea. Generally, this is an eurythermal but stenohaline assemblage.

Assembage III (Pl. 1, Figs. 26–32; Pl. 2, Figs. 1–3) is distinguished by the cold-water character of its dominant and common species with a relatively low species diversity. The assemblage occurs in the central and deeper part of the Huanghai Sea (beyond the 50 m isobath) occupied by the Huanghai Cold Water Mass and, hence, can be called the Cold Water Mass Assemblage. Two subassemblages may be distinguished: the Northern Subassemblage is characterised and dominated by the typical cold-water species *Howeina camptocytheroides*, *Sarsicytheridea bradii* (Norman) and and *Acanthocythereis mutsuensis* Ishizaki, with *F. huanghaiensis*, *C. sawanensis* and others as common forms; while in the Southern Subassemblage more eurythermal, cold-water species like *Amphileberis gibbera* Guan, *Buntonia hanaii* Yajima, *Kobayashiina donghaiensis* Zhao and *Krithe sawanensis* Hanai are dominant and *Ambocythere reticulata* Jiang and Wu, *Nipponocythere obesa* (Hu), *Cluthia ishizaki* Zhao and others are common. The boundary between the two subassemblages is at approximately latitude 36° N.

Assemblage IV (Pl. 2, Figs. 4–25) is distributed beyond the 40–50 m isobath in the middle and outer shelves of the East China Sea and the northern part of the South China Sea, being closely related to the open-sea water and the Kuroshio Current with its branches. The assemblage is characterised by a great number of warm-water species and a high diversity and abundance; hence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it may be termed a warm-water assemblage. The dominant and characteristic species include *Argilloecia hanaii* Ishizaki, *Cathetocytheretta apta* Guan, *Cytherelloidea senkakuensis* Nohara, *C. yingliensis, Loxoconcha sinensis, Neocytheretta snellii* (Kingma), *Neonesidea haikangensis, Uroleberis foveolata* and *Xestoleberis variegata* among others. The assemblage may be further subdivided into at least two subassemblages: the East China Sea Subassemblage with more frequent *Bradleya japonica* Benson, *Hirsutocythere*? *hanaii, Cytheropteron uchioi* Hanai, *C. subuchioi* Zhao and *Semicytherura minaminipponica* Ishizaki, and the South China Sea assemblage with *Cytherelloidea leroyi* Keij, *Bradleya albatrossia* Benson, *Cytherella posterotuberculata* Kingma, *Cytheropteron sinensis* Zhao and *Loxoconcha pterogona* Zhao.

Assemblage V (Pl. 2, Figs. 26–32) is found in the coral reef area in the southern part of Hainan Island and the Xisha Islands. All the major elements such as *Radimella virgata* Hu, *R. macroloba* Hu, *R. parviloba* Hu, *Loxoconcha tumulosa* (Hu), *L. lilljeborchi* Brady, *Treibelina rectangulata* Hu, *Paranesidea* sp. and *Keijia novilunaris* Zhao are tropical in nature. Therefore, this is a tropical coral-reef assemblage.

To sum up, the distribution of ostracod assemblages in the area is principally determined by the water temperature and salinity, which in turn are controlled by the distribution pattern of water masses and currents, apart from the latitude. Both Assemblage I and Assemblage II are basically consistent in species composition from north to south, implying the similarity of coastal waters along the entire shoreline of the Chinese mainland. The two assemblages differ from each other in their salinity adaptation. All the other three assemblages are related to temperature conditions: Assemblage III represents the Huanghai Cold Water Mass, Assemblage IV corresponds to the warm-water Kuroshio system, and Assemblage V to the tropical surface water in the southern part of the South China Sea.

ZOOGEOGRAPHY

Despite the numerous contributions to ostracod studies in East Asia, a systematic zoogeographical study is still wanting. In a discussion on ostracod zoogeography of the Pacific, Benson (1964) divided the western coast of the Pacific into two realms: the Japonic Realm and the Indo-West Pacific Realm, with a boundary running through the south of the East China Sea. This is, probably, the only ostracod biogeographical zonation of East Asia now available in the literature. Since then, a considerable amount of information has been accumulated on ostracod taxonomy and areal

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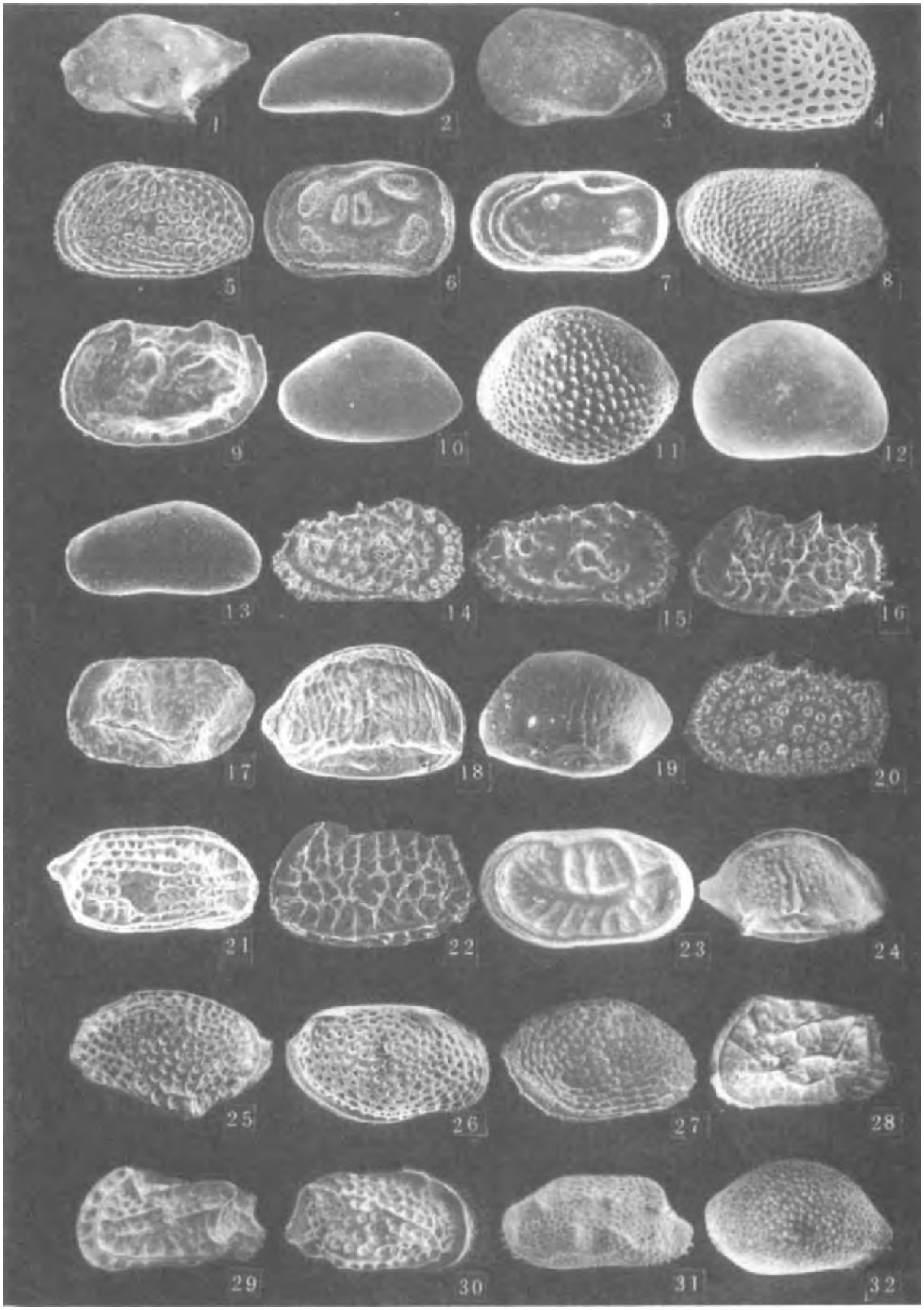
PLATE 1—*Assemblage I*: Fig. 1. *Sinocytheridea latiovata* Hou et Chen. Left valve, ×45. Fig. 2. *Sinocytheridea longa* Hou et Chen. Right valve, ×45. Fig. 3. *Neomonoceratina crispata* Hu. Left valve, ×50. Fig. 4. *Albileberis sinensis* Hou. Right valve, ×55. Fig. 5. *Leptocythere ventriclivosa* Chen. Right valve, ×55. Fig. 6. *Loxoconcha ocellata* Ho. Left valve, ×50. Fig. 7. *Tanella opima* Chen. Right valve, ×55. Fig. 8. *Propontocypris euryhalina* Zhao. Left view of carapace, ×55. Fig. 9. *Spinileberis furuyazsis* Ishizaki et Kato. Left valve, ×50. *Assemblage II*: Fig. 10. *Bicornucythere bisanensis* (Okubo). Right valve, ×40. Fig. 11. *Wichmannella bradyformis* (Ishizaki). Right valve, ×45. Fig. 12. *Wichmannella bradyi* (Ishizaki). Left valve, ×40. Fig. 13. *Munseyella japonica* (Hanai). Right valve, ×80. Fig. 14. *Munseyella pupilla* Chen. Right valve, ×80. Fig. 15. *Cytheropteron miurense* Hanai. Right valve, ×60. Fig. 16. *Aurila cymba* (Brady). Right valve, ×50. Fig. 17. *Stigmatocythere spinosa* (Hu). Left valve, ×60. Fig. 18. *Sinocythere sinensis* Hou. Left valve, ×60. Fig. 19. *Nipponocythere bicarinata* (Brady). Left valve, ×65. Fig. 20. *Alocopocythere profusa* Guan. Right valve, ×40. Fig. 21. *Acanthocythereis niitsumai* (Ishizaki). Right valve, ×45. Fig. 22. *Loxoconcha hattorii* Ishizaki. Right valve, ×55. Fig. 23—*Cytheromorpha acupunctata* (Brady). Left valve, ×60; Fig. 24—*Copytus posterosulcus* P. Wang. Left valve, ×55. Fig. 25. *Hemikrithe orientalis* Bold. Left valve, ×55.
Assemblage III: Fig. 26. *Howeina camptocytheroidea* Hanai. Right valve, ×50. Fig. 27. *Sarsicytheridea bradii* (Norman). Right valve, ×35. Fig. 28. *Acanthocythereis mutsuensis* Ishizaki. Left valve, ×30. Fig. 29. *Finmarchinella huanghaiensis* Zhao. Left valve, ×60. Fig. 30. *Cytheropteron sawanensis* Hanai. Right valve, ×80. Fig. 31. *Amphileberis gibbera* Guan. Right valve, ×50. Fig. 32. *Buntonia hanaii* Yajima. Right valve, ×55.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distribution in the seas off Japan and China, and the time seems ripe to reconsider the ostracod zoogeography of the area.

With regard to modern marine shelf zoogeographical provinces, north-south coastlines in the temperate regions usually have many small provinces because of the steep temperature gradients and, perhaps, the concentration of biogeographers. For example, five provinces have been recognized on both the east and west coasts of North America and six provinces in Europe and North Africa (Dodd and Stanton, 1981). The two realms on the west coast of the Pacific are certainly subject to further subdivision. Because of the lack of agreement between scientists in the usage of biogeographical units of various scales, the terms "zone" or "region" (and "subregion") will be used in our further discussion without specific definition.

Based on the distribution of the five assemblages described above, three ostracod zoogeographical zones may be easily distinguished: the tropical coral-reef assemblage II represents the southern part of the South China Sea, the warm-water assemblage IV belongs to the East China Sea and the northern part of the South China Sea, and the Cold Water Mass assemblage III is related to the Huanghai Sea and Bohai Gulf. As for assemblages I and II, these belong to the Huanghai Sea and Bohai Gulf in the north, and to the East China Sea and the northern part of the South China Sea in the south. As a rule, the euryhaline species are more or less eurythermal and this explains the long north-south range in distribution of the two nearcoast assemblages. The similarity in near-coast assemblages should not present an obstacle to dividing biogeographical zones, because "it is not necessary that all communities in different regions be distinct in order for the regions to be considered provincially distinct". In fact, "it is only necessary that a certain number of the communities differ between provinces" (Valentine, 1973). This is the case for our Assemblages I and II.

Benson (1964) has grouped all the sea areas around Japan into one unit — the Japonic Realm. The modern ostracod faunas, nevertheless, are different in the north and south of Japan. Ishizaki, for example, has pointed out that ostracod genera like *Howeina, Hemicythere, Urocythereis* and *Finmarchinella* only occur on the Japan Sea side, but not on the Pacific side of Japan. Now, *Howeina* and *Finmarchinella* have been found in the Huanghai Sea and the Bohia Gulf. In addition, there are several species restricted in their distribution to the Huanghai Sea, Bohai Gulf and the Japan Sea, namely: *Loxoconcha hattorii, Acanthocythereis mutsuensis* Ishizaki, *Loxocorniculum mutzuense* Ishizaki and *Cytheropteron sawanensis* Hanai amongst others. Consequently, there is a close relationship between the ostracod faunas in the Huanghai Sea and Bohai Gulf on one hand, and in the Japan Sea on the other. Besides this, it is interesting to note the occurrence of *Sarsicytheridea bradii* (*Euchtheridea bradii*) in the Huanghai Sea, as this is a cold water species dwelling in the

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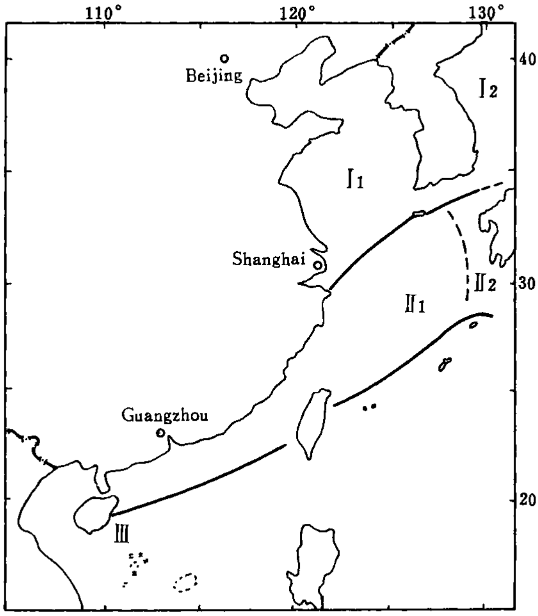
PLATE 2—*Assemblage III* (continuation): Fig. 1. *Kobayashiina donghaiensis* Zhao. Left valve, ×50. Fig. 2. *Krithe sawanensis* Hanai. Right valve, ×40. Fig. 3. *Cluthia ishizakii* Zhao. Left valve, ×95.

Assemblage IV: Fig. 4. *Bicornucythere euplectella* (Brady). Right valve, ×45. Fig. 5. *Cythetocytheretta apta* Guan. Left valve, ×40. Fig. 6. *Cytherelloidea senkakuensis* Nohara. Left valve, ×45. Fig. 7. *Cytherelloidea yingliensis* Guan. Left valve, ×40. Fig. 8. *Loxoconcha sinensis* Brady. Right valve, ×80. Fig. 9. *Neocytheretta snellii* (Kingma). Left valve, ×50. Fig. 10. *Neonesidea haikangensis* (Guan). Left valve, ×20. Fig. 11. *Uroleberis foveolata* (Brady). Left valve, ×50. Fig. 12. *Xestoleberis variegata* Brady. Right valve, ×40. Fig. 13. *Argilloecia hanaii* Ishizaki. Left valve, ×50. Fig. 14. *Acanthocythereis munechikai* Ishizaki. Right valve, ×35. Fig. 15. *Actinocythereis kisarazuensis* Yajima. Right valve, ×35. Fig. 16. *Bradleya japonica* Benson. Left valve, ×30. Fig. 17. *Bythoceratina cassidoidea* Zhao. Left valve, ×50. Fig. 18. *Cytheropteron subuchioi* Zhao. Right valve, ×60. Fig. 19. *Cytheropteron uchioi* Hanai. Left valve, ×45. Fig. 20. *Hirsutocythere? hanaii* Ishizaki. Left valve, ×30. Fig. 21. *Semicytherura minaminipponica* Ishizaki. Right valve, ×100. Fig. 22. *Bradleya albatrossia* Benson. Left valve, ×40. Fig. 23. *Cytherelloidea leroyi* Keij. Left valve, ×70. Fig. 24. *Cythereopteron sinensis* Zhao. Right valve, ×60. Fig. 25. *Loxoconcha pterogona* Zhao. Left valve, ×60.

Assemblage V: Fig. 26. *Loxoconcha lilljeborchi* Brady. Right valve, ×55. Fig. 27. *Loxoconcha tumulosa* (Hu). Right valve, ×70. Fig. 28. *Radimella virgata* Hu. Left valve, ×45. Fig. 29. *Radimella macroloba* Hu. Left valve, ×40. Fig. 30. *Radimella parviloba* Hu. Right valve, ×50. Fig. 31. *Triebelina rectangulata* Hu. Left valve, ×50. Fig. 32. *Paranesidea* sp. Left valve, ×55.



TEXT-FIG. 9—Ostracod zoogeographical zonation of the shelf seas off China.
I. North Pacific Region: I_1=East Asia Subregion, I_2=Far East Subregion; II. Sino-Japanese Region: II_1=Sinian Subregion, II_2=Japanese Subregion; III. Indo-West Pacific Region: Indonesian-Malasya Subregion.

northern part of North Atlantic and in the Arctic waters. It can be clearly seen, therefore, that the ostracod fauna in the Huanghai and Bohai areas is closer to the northern faunas than to those of the East China Sea and South China Sea. Thus, the Huanghai and Bohai areas can be classified together with the Japan Sea into a North Pacific Region with two subregions: a Far East Subregion for the Japan Sea, and an East Asia Subregion for the Huanghai Sea and Bohai Gulf (Text-fig. 9).

The ostracod faunas in the East East China Sea and in the northern part of the South China Sea are subtropical in nature, consisting mainly of warm-water and eurythermal species with a few cold water forms in the north. Some of the warm-water species, such as *Cytherella posterotuberculata, Cytherelloidea leroyi, Neocytheretta snellii, Hemikrithe orientalis, Loxoconcha sinensis, Uroleberis faveolata, Xestoleberis variegata, Paijenborchella iocosa, P. malaiensis* and *Bradleya albatrossia* have not been reported either from the adjacent seas of Japan or from the Huanghai Sea and Bohai Gulf, with the sole exception of *L. sinensis* which occurs on the southern coast of Japan. These species are believed to originate in the Indonesian-Malay area and suggest a close relationship with the tropical fauna. Meanwhile, quite a number of endemic species exist in the East China Sea and the northern part of the South China Sea, *e.g. Cathetocytheretta apta, Bicornuncythere euplectella, Copytus posterosulcus, Cytherelloidea yingliensis, C. senkakuensis, Neonesidea haikangensis, Cytheropteron sinensis, C. subuchioi* and *Loxoconcha pterogona*. Several genera (*Sinocytheridea, Albileberis, Abrocythere, Cocconocythere, Sinocythere* and others) and some of the common species (*Propontocypris euryhalina, Leptocythere ventriclivosa, Loxoconcha ocellata, Alocopocythere profusa, Argilloecia hanaii, Ambocythere reticulata, Munseyella pupilla, Hirsutocythere*? *hanaii, Stigmatocythere spinosa* among others) are restricted to this area only and to the Huanghai sea and Bohai Gulf. Consequently, the East China Sea and the northern part of the South China Sea is a separate biogeographical zone distinguished from the Indonesian-Malay one. On the other hand, the ostracod fauna off the Pacific coast of Japan (Honshu, Shikoku, and Kyushu) is, to a certain extent, similar to that from the above-mentioned part of the China Sea. The Pacific shelf area of Japan and the East China Sea with the northern part of the South China Sea may thus be considered biogeographically as two subregions of a subtropical Sino-Japanese Region: the Japanese Subregion and the Sinian Subregion.

The species composition of Assemblage V resembles that from the Philippines and Malaysia, so the southern part of the South China Sea belongs to the Indonesian-Malay Subregion.

The above described triple zonation of the shelf seas off China for Ostracoda agrees well with the zoogeographical zonation for other groups of invertebrates such as molluscs, arthropods and polychaetes. "From south of Hainan to the Ryukyu Is. there is a typical tropical fauna; a subtropical fauna occurs in an area extending from the east of Guangzhou through the East China Sea to the South of Japan; the fauna in the Huanghai Sea is a warm-temperate one with both cold and warm elements" (Chinese Society of Zoology, 1963).

CONCLUSIONS

1. The abundance and the diversity of Ostracoda in surface sediments of the shelf seas off China generally increases from north to south and from the coast to the shelf edge depending on the rate of clastic sedimentation and the water temperature and salinity.
2. The euryhaline assemblage characterised by *Sinocytheridea latiovata* is eurythermal as well and is distributed along the whole coast of the Chinese Mainland. Most elements of this assemblage are endemic to the Chinese coast.
3. The inner shelf assemblage, with *Wichmannella bradyformis* and *Bicornucythere bisanensis* as characteristic forms, is eurythermal and stenohaline in nature. In contrast to the previous assemblage, the main components also occur in other sea areas of East Asia.
4. The variations of species composition in open-sea ostracod assemblages are largely related to water temperature. There is a cold-water assemblage in the Huanghai Sea, a warm-water assemblage in the East China Sea and the northern part of the South China Sea, and a tropical coral-reef assemblage in the southern part of the South China Sea.
5. The China Sea can be divided into three ostracod zoogeographical zones: the East Asia Subregion of the North Pacific Region, the Sinian Subregion of the Sino-Japanese Region, and the Indonesian-Malaysian Subregion of the Indo-West Pacific Region.

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DISCUSSION

Hazel: Do you consider that your temperate fauna is a biofacies that falls in the category of "warm-temperate"?

Wang: Perhaps, but I think we need more detailed information.

Ishizaki: It seems to me that assemblage 2 is typical of an embayed area, and that you have it off Guangzhou. How did you define the boundary there between assemblages 1 and 2?

Wang: We have found this assemblage, for example, outside the Pearl River estuary, etc., but we have no data from the Taiwan Strait. A further survey is required.

Questioner uncertain: Do you have any figures concerning the accumulation rate along the Chinese coast?

Wang: The sedimentation rate along the Chinese coast varies significantly with the highest rate in estuarine areas. For example, it can be as high as about 3 m per thousand years for the Yangtze delta area.

Paleobiogeography of Tethyan Cretaceous Marine Ostracods

JEAN-FRANCOIS BABINOT AND JEAN-PAUL COLIN
University of Provence (U.A. 1208 of C.N.R.S), Marseille and
Esso Production Research, European Laboratories, Bègles, France.

ABSTRACT

During the Cretaceous, the geographic distribution of marine Tethyan ostracods always displays a dual trend: endemism and ubiquity. At the species level, major palaeogeographical entities can be defined. These are essentially the two main Southern and Northern provinces. With few exceptions, relations between both margins of the Tethyan Ocean are limited. Sub-provinces can also be recognized. At the genus level, the distinction between provinces is less apparent. Recent studies have reported identical generic associations on both sides of the Tethys during the Early Cretaceous. Some genera are synchronous, *e.g.*, *Protocythere* s. l., in the western Tethys and *Arculicythere* and *Majungaella* in the eastern Tethys and the Proto-Indian Ocean. Other genera seem to be diachronous. Some "pioneer" genera, often without known ancestors, are reported later on the opposite continental margin. This may be the result of migrations controlled by factors such as climate, bathymetry and oceanic circulation. Faunal exchanges could have therefore happened during the Cretaceous. A north-south direction has often been suggested. This is the case for the genera *Tethysia, Curfsina* and *Limburgina.* Possible affinities between some genera in different provinces can also be advanced: *Majungaella, Neocythere, Novocythere* and *Tickalaracythere.*

Endemism can be observed at different taxonomic levels and in geographic areas of various extension. It is essentially controlled by the relative position of the continental blocks and the paleobathymetry.

To conclude, knowledge of the dynamics of marine ostracod associations contributes to a better understanding of the structural and dynamic evolution of the Tethyan continental margins during the Cretaceous.

INTRODUCTION

Our knowledge of the distribution of ostracod associations in space and time has made tremendous progress in the past few years. Very comprehensive documentation is now available and can be used for paleogeographic reconstructions in a more global framework. This paper will take into consideration the published literature (references are too numerous to mention all and as yet unpublished information, concerning the marine Cretaceous from the Caribbean domaine and North America to the East-African, Indian and Australian margins).

In other words, a palaeobiogeographic synthesis of the ostracods of the Tethys margins during the Cretaceous has been undertaken. The primary aim of this research is to try to define the main affinity trends existing between the different geographical areas and to characterize bioprovinces. These problems are essentially treated at the genus level although a few examples at the species level will be evoked. The main paleobiogeographic implications will be used to better understand the dynamics of the associations during time, and in general, to contribute to improving our knowledge of the structural evolution and relationships of the Tethyan margins.

First of all, it is important to define precisely the word "Tethys." According to Suess (1893), the Tethys concept corresponds to a wide latitudinal Mesozoic ocean situated between Africa and Eurasia. This concept was modified later by Wegener, Tethys becoming the ocean separating the two main blocks of his structural reconstructions: Laurasia and Gondwana land. The geographical and physical characteristics of this ocean have subsequently been intensively discussed. Was this ocean wide or narrow? Was it thermo-or psychrospheric? How deep was it? In fact, a more precise definition of the Tethys can be given through different methodologies. This has been judiciously noted by McKenzie (1982, p. 313), ". . . modern biogeographers studying Tethys are encouraged to evaluate two differing options of its nature — one, the by now conventional Wegenerian model updated to conform with paleomagnetism and sea-floor spreading, the other based more on faunal distribution and general geology." However, concerning the Cretaceous, there is general agreement on the existence of a rather narrow seaway between the African and Eurasian blocks, connecting two much wider marine areas: one in the West, equivalent to the Proto-Atlantic Ocean (Gulf of Mexico, Caribbean and Northern part of South America), the other in the East, paleogeographically located between East Africa-India-Australia and Eastern Asia (Barron *et al.,* 1981).

In 1900, Douvillé created the word "Mesogea" for a latitudinal sea corresponding to the palaeogeographical extension of rudists during the Cretaceous. This sea more or less coincides with the Tethyan realm. In both cases, the definition of the oceanic area is related to the distribution of mollusk faunas. Paleoclimates played a fundamental role. A more recent definition for the Mesogea has been proposed (Philip, 1982), characterized by the development of rudist limestone formations. This definition, although in perfect agreement with Douvillé's thinking, is restricted to a peculiar sedimentologic domaine of carbonate platforms. Ostracod biotopes being much more diversified, the Tethyan concept is more appropriate because it involves not only paleoclimatic and sedimentologic criteria, but other parameters.

Our bibliographical knowledge on Cretaceous ostracods of this extensive area is not negligible. It is, however, worth noting the disparity of the available information, *e.g.* scarcity of data concerning the Valanginian-Aptian interval versus sound knowledge of the Senonian, and especially of the Cenomanian.

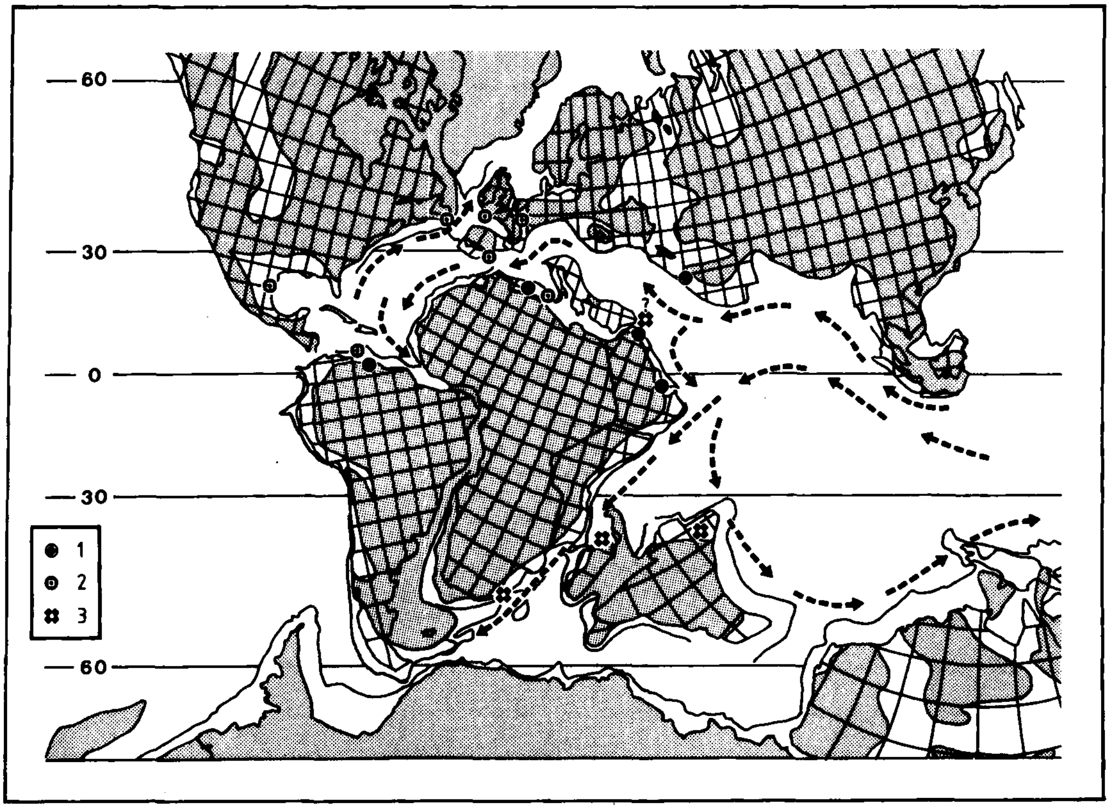
In recent years, few palaeogeographical attempts extending from strictly regional frameworks have been made. This is the case for the relations between North American and European margins (Neale, 1977; Tambareau, 1982), African and European (Donze, 1975, 1977; Babinot, 1985), South-African and Australian (Dingle, 1982). In 1982, McKenzie proposed a paleobiogeographic synthesis concerning the whole Tethys since the Paleozoic. Several judicious remarks and many problems are expressed. Our contribution essentially consists of reviewing these palaeogeographical problems during the Berriasian-Maastrichtian interval and extending these investigations to the outer limits of the eastern Tethys as far as Australia.

MAINS TYPES OF OSTRACOD ASSOCIATIONS: THEIR EVOLUTION DURING THE CRETACEOUS

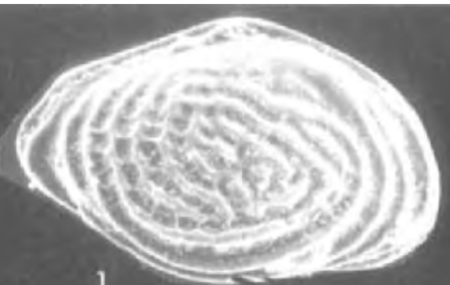
Berriasian-Aptian (Text–fig. 1)

During this stratigraphic interval, it appears that the Berriasian has been studied more intensively. The available literature is relatively abundant, particularly for southeast France and North Africa. For the other stages, data are much more limited.

Berriasian.— It is mainly the works of Donze (1975, 1977) which have illustrated the very strong affinities existing since the uppermost Jurassic between the North African and South European margins (southeast France, Iberian Peninsula), during the Berriasian hinge-stage between the Jurassic and the Cretaceous. It is however, worth noticing the absence of a few "European" genera in North Africa: *Cythereis* s. s., *Pseudobythocythere, Kentrodictyocythere, Annosocythere*. Genera in common correspond for most of them to different species although very similar (Donze, 1977), for example: *Protocythere* aff. *mazenoti* Donze, *P.* aff. *revilli* Donze, *Oligocythereis* aff. *bogis* Donze. Possible migration phenomena have been proposed (Donze, 1975) through the Morocco-Gibraltar-Iberian Peninsula. This opinon was later revised (Donze, 1977) with the intervention of



TEXT–FIG. 1—Paleobiogeography of marine ostracods in the Tethyan Early Cretaceous (map after Barron *et al.*, 1981, modified; oceanic circulation after Haq, 1985). 1, *Antepaijenborchella*; 2, *Hechticythere derooi or alexanderi*; 3, *Majungaella*.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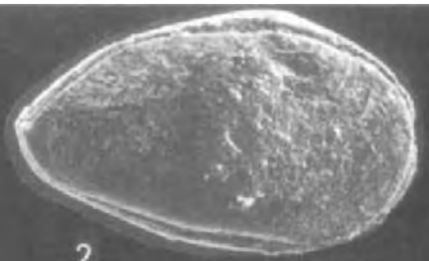
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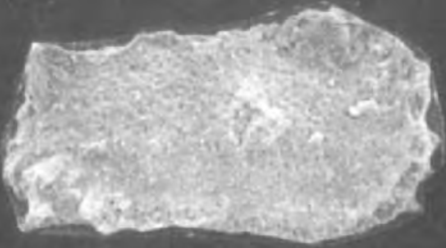
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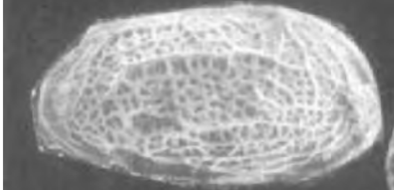
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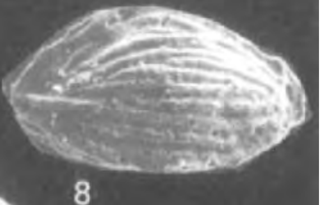
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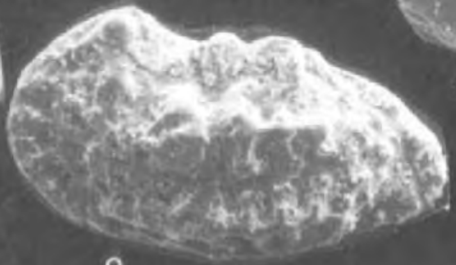
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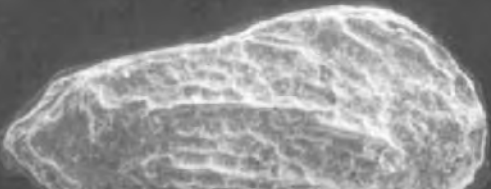
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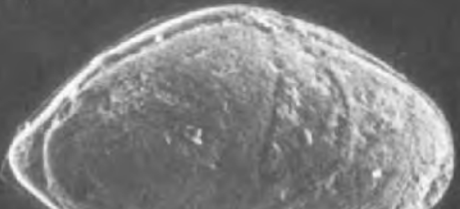
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a possible micro-plate with shallow water paleoenvironments located at the position of the present Alboran Sea. Data are practically nonexistent for the other sectors of the Tethyan realm.

Valanginian.—Most studies are again limited to southeast France and are very scattered and limited in the Iberian Peninsula. Data are available concerning India (Guha, 1976), Madagascar (Grekoff, 1963) and Israel (Rosenfeld and Raab, 1984).

In Western Europe, associations are essentially characterized by Neocytherinae, and the genera *Protocythere* s. l. and *Schuleridea.* In India and mostly in Madagascar, associations are very different, peculiar with dominance of the genera *Majungaella, Pirileberis* (known since the Callovian) and *Arculicythere.* These genera are essentially confined to the Southern hemisphere although a few doubtful representatives of some of these genera (*Majungaella* and *Arculicythere*) have been reported in the Berriasian-Valanginian of Israel (Rosenfeld and Raab, 1984).

Hauterivian-Barremian.—Ostracods of this stratigraphic interval are still very poorly known. Data are often very scattered, imprecise and difficult to utilize. In Israel (Rosenfeld and Raab, 1984), ostracod associations, although containing so-called "austral" forms, are dominated by genera such as *Protocythere* s. l. and *Schuleridea.* Also to be noted is the presence of the genus *Antepaijenborchella.* On the East Coast of the U.S.A. (Swain, 1981), faunas are also dominated in marine environments by the genera *Schuleridea, Asciocythere* and *Protocythere* s. l. Genera *Hutsonia* and *Fabanella* in the marginal marine facies are also known in Europe (offshore Ireland, Colin *et al.*, 1981).

The Barremian has been relatively well studied in the southern regions of the U.S.S.R. (Kuznetsova, 1961; Andreev and Mandelstam, 1971). The characteristic associations of the so-called "Mediterranean province" are pratically generically identical to the southeastern European ones with the genera *Protocythere* s. l., *Eocytheropteron, Neocythere-Centrocythere, Clithrocytheridea, Quasihermanites, Macrodentina, Annosocythere* and *Kentrodictyocythere.* It is interesting to note the presence of the genus *Antepaijenborchella* in the U.S.S.R., which is never mentioned in Europe, but reported from the Barremian of the Persian Gulf with numerous *Schuleridea* and *Metacytheropteron* (Grosdidier, 1973).

Aptian.—Ostracod associations from the Aptian of southeast France are directly derived from the Barremian with the same generic taxa (Oertli, 1958). Of particular note is the appearance of the *Hechticythere alexanderi-Hechticythere derooi* group which has a very remarkable palaeogeographical distribution. This group, which persists into the Albian, is known in southeastern France, the Paris basin, Great Britain, U.S.A. (Gulf of Mexico), Venezuela and Ecuador (J. P. Colin, unpublished) and in North Africa (Bismuth *et al.*, 1981).

As noted previously, the communications between the southern margins of the U.S.S.R. and Western Europe are obvious. Microfauna are practically identical, particularly the genera *Veenia* s. l. and *Parataxodonta.* The species *Parataxoxodonta uralensis* Mandelstam is common to the U.S.S.R. and to the Aptian stratotype in southeast France. A continuity at the generic level also

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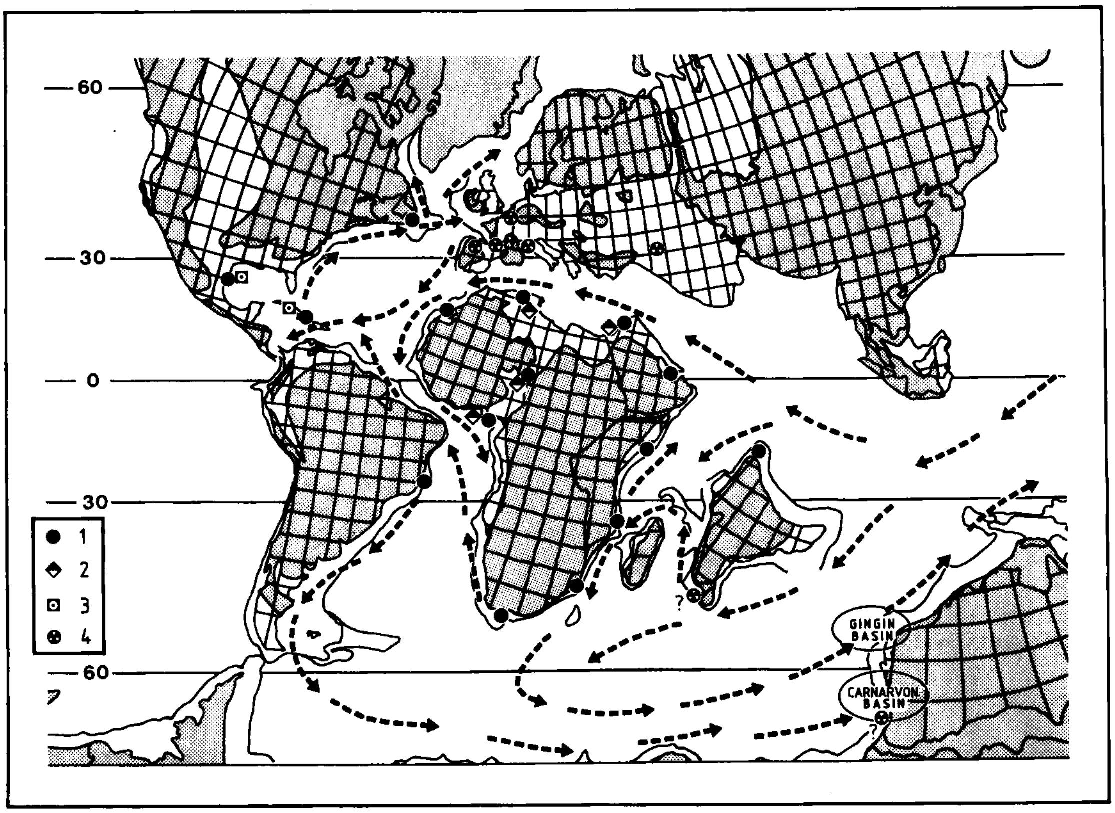
PLATE 1—Fig. 1. *Neocythere mertensi* Oertli, 1958. Carapace, right lateral view, Aptian, Celtic Sea (Ireland). ×80. Fig. 2. *Schuleridea* sp. Carapace, right lateral view, Aptian, Venezuela. ×81. Fig. 3. *Chapmanicythereis* aff. *triebeli* (Mertens, 1956). Right valve, Late Cenomanian, Dordogne (S.W. France). ×70. Fig. 4. *Hechticythere* cf. *alexanderi* (Howe and Laurencich, 1958). Carapace, right lateral view, Aptian, Venezuela. ×68. Fig. 5. *Annosocythere nuda* Colin, 1974. Carapace, right lateral view, Late Cenomanian, Dordogne (S.W. France). ×150. Fig. 6. *Majungaella perforata* Grekoff, 1963. Carapace, right lateral view, Berriasian, Majunga (Madagascar). ×80. Fig. 7. *Nigeroloxoconcha* sp. Carapace, right lateral view, Senonian, Ivory Coast. ×81. Fig. 8. *Metacytheropteron berbericus* (Bassoullet & Damotte, 1969). Carapace, left lateral view, Cenomanian, Tunisia. ×81. Fig. 9. *Veeniacythereis jezzineensis* (Bischoff, 1963). Carapace, left lateral view, Cenomanian, Tunisia. ×68. Fig. 10. *Haughtonileberis acies* (Esker, 1968). Carapace, right lateral view, Maastrichtian, El Kef (Tunisia). ×81. Fig. 11. *Cophinia* cf. *apiformis* (Reyment, 1960). Carapace, right lateral view, Senonian, Algeria. ×81.

exists in the area of Isreal and Persian Gulf. Unpublished data from Venezuela show that the Aptian contains, in addition to *Hechticythere derooi,* the genera *Schuleridea, Centrocythere* and *Antepaijenborchella.* Species of *Protocythere* related to *Protocythere bedoulensis* Moullade, originally described from the Aptian of southeast. France, have been found in Ecuador (J. P. Colin, unpublished). In the northwestern Atlantic (Scotian Shelf), the Aptian has yielded faunas very similar to the European ones (Ascoli, 1976). Affinities at the specific level are known during the entire Jurassic and Early Cretaceous.

Albian–Cenomanian (Text–fig. 2)

Albian.—This period is particularly important for the general evolution of ostracod faunas; termination of numerous Early Cretaceous genera and intense renewal prefiguring the Late Cretaceous and even the Cenozoic occurred. This stage is essentially characterized by a progressive impoverishment during the Early Cretaceous of a very flourishing family, the Protocytherinae, progressively replaced by new Trachyleberididae genera. A similar phenomenon can be observed for the Schulerideinae; genus *Schuleridea* s. s. becomes less frequent, and, in Europe, new genera such as *Dordoniella* and *Risaltina* appear.

In Europe (including the southern U.S.S.R.), two important facts are worth mentioning: diversification of the *Pterygocythere* group and the appar at the end of the Albian of the first representatives of several genera which will strongly flourish and diversify: *Mauritsina, Dumontina,*



TEXT–FIG. 2—Paleobiogeography of marine ostracods in the Tethyan Middle Cretaceous (map after Barron *et al.,* 1981, modified; oceanic circulation after Haq, 1985). 1, *Metacytheropteron berbericus–Veeniacythereis jezzineensis*; 2, *Metacytheropteron minutum*; 3, *Arculicythere*; 4, *Mauritsina–Limburgina.*

Limburgina, Oertliella, Planileberis. Other genera, recently appeared, remain restricted to Europe; this is the case, for example, with the *Platycythereis-Chapmanicythereis* group.

Since the Late Albian, North Africa and the Middle East have constituted a paleobiogeographical entity characterized by the individualisation of very typified association with *Metacytheropteron, Veeniacythereis* (*e.g. V. jezzineensis*) and *Kamajcythereis* (including *Cythereis ghabounensis*, in Lebanon, Bishoff, 1963). In the Gulf of Mexico (Alexander, 1929; Moysey and Maddocks, 1982), generic associations present real affinities with those from Western Europe with genera such as *Asciocythere, Schuleridea,* and *Neocythere-Centrocythere.* These facts are confirmed by the DSDP holes (Leg 14) offshore Guyana (Swain, 1976), where the African and Middle Eastern element, *Metacytheropteron minuta* Swain (*M. dvoracheki* Rosenfeld and Raab, 1984), is also reported. In the northwest Atlantic region, faunas are identical, even at the specific level, with those from northern Europe (Ascoli, 1975; J. P. Colin pers. observ.).

In Madagascar (Collignon *et al.*, 1979), associations display a mixed character, with both genera typically European (*Dolocytheridea, Batavocythere* and representatives of the Late Jurassic to Early Cretaceous austral group: *Arculicythere* and *Majungaella.*

In southern India (Jain, 1976) and offshore Northwest Australia (Oertli, 1974) the persistence of the genus *Arculicythere* is noticeable. This genus is also known in the Albian of South Africa (Dingle, 1984). Other specific identities exist between these three regions. This, for example, is the case for *Cytherura*? *oertlii* Dingle (Oertli, 1974; Jain, 1978). The genus *Arculicythere* progressively restricts itself to a very precise area, the southeastern margin of the Tethys and the Proto-Indian Ocean. The separation with Australia is more and more obvious with individualisation (Artesian Basin, in Krommelbein, 1975b) of a very endemic association in which dominant genera are *Allaruella, Tickalaracythere, Artesiocythere,* new "*Majungaella*" (systematic position to be checked) and forms related to the genus *Rostrocytheridea* which are known since the early Cretaceous in South Africa and South America (Dingle, 1982).

Cenomanian.—The Cenomanian is a stage of intensive renewal already prefigured since the Late Albian with total extinction of the Protocytheridae and explosion of the Hemicytheridae and Trachyleberididae: *Limburgina, Oertliella, Curfsina, Mosaeleberis, Mauritsina, Spinoleberis, Trachyleberidea, Haughtonileberis, Parapokornyella, Brachycythere.* This fauna persists into the Turonian and the Senonian prefiguring Cenozoic faunas. It is very important to point out that since this period, relations between the northern and southern margins of the western Tethys practically cease. Two very well differentiated bioprovinces become individualised (Babinot, 1985): a west European province with the previously mentioned genera (without *Brachythere*), (associations described in the southwestern part of the U.S.S.R. are very close) and a bioprovince in North Africa and the Middle East with predominancy of the genera *Brachycythere, Protobuntonia, Reticulocosta, Peloriops,* the *Veeniacythereis-Glenocythere* group, *Nigeroloxoconcha,* and in the marginal marine facies, *Perissocytheridea.* Strong, affinities exist with the West African coastal basins (Grosdidier, 1979), indicating the possibility of trans-Saharn epicontinental marine seaway (Reyment, 1980). Recent studies have shown an extension of the so-called "maghrebian" and Middle-Eastern faunas to East Africa, Ethiopia, Somalia (J. P. Colin, pers. observ.) and Oman (Babinot, pers. observ.). In Tanzania (Bate and Bayliss, 1969), some elements known in the Persian Gulf are present, such as *Cythereis lindiensis. Amphicytherura distincta,* originally described from Israel, has even been found in Mozambique (J. P. Colin, pers. observ.). In the western Atlantic coastal plain and in the Gulf of Mexico (Alexander, 1929; Swain and Brown, 1972; Neale, 1977), associations still have a North European generic outlook with the genera *Cythereis* s. l., *Schuleridea* and *Hazelina.*

Data concerning the southeastern Tethys and its austral limits are too scattered to be used accurately.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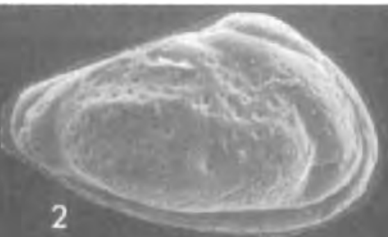
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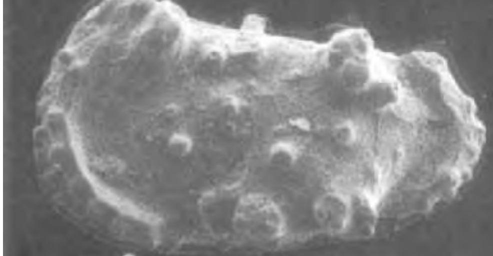
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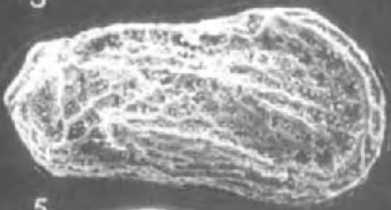
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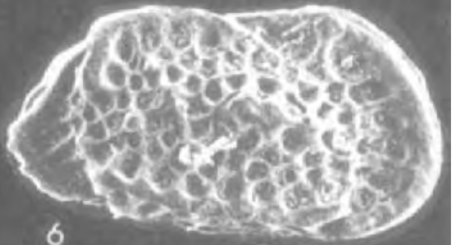
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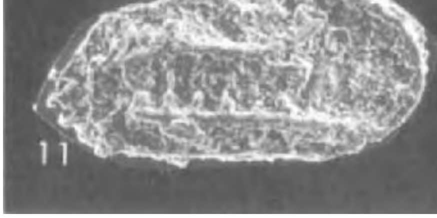
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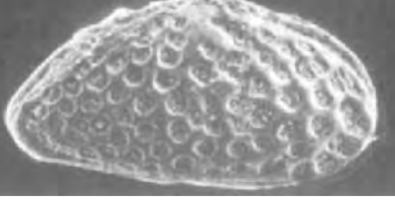
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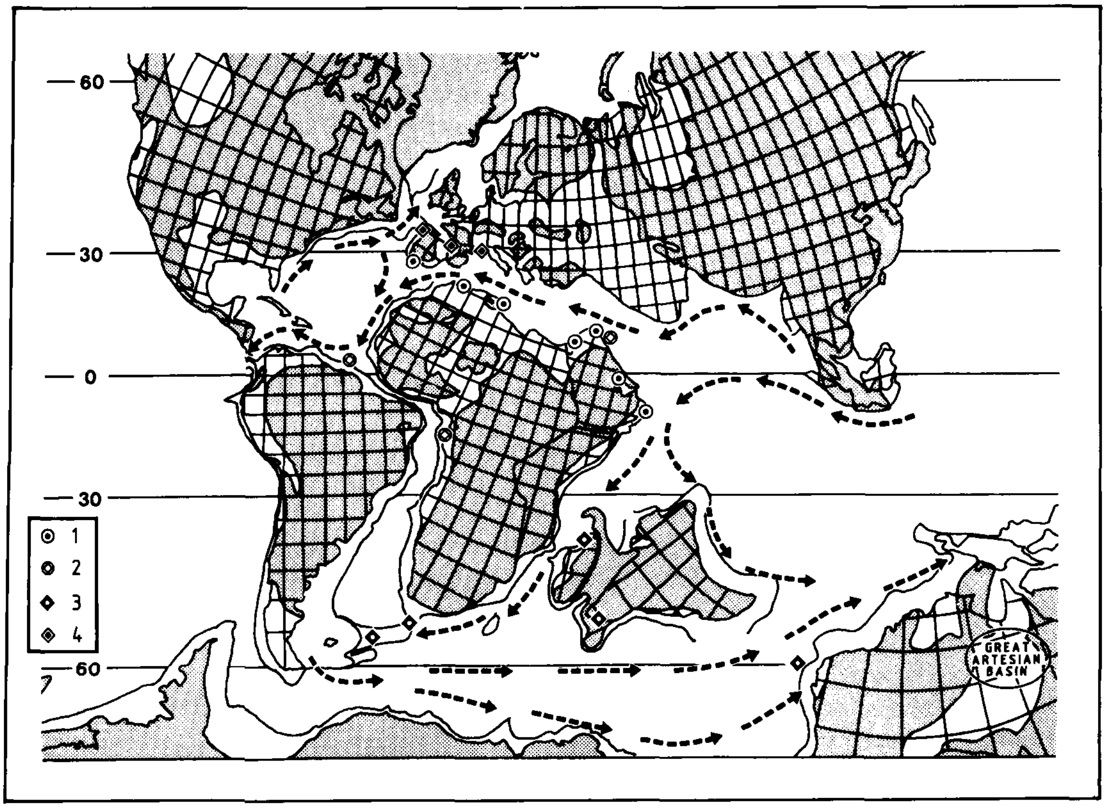
Turonian–Senonian (Text–fig. 4)

Turonian.—This stage is essentially characterized by the persistence of the generic associations established during the Late Albian and the Cenomanian. The Early Turonian is, however, marked by a drastic impoverishment of the faunas most likely related to the strong and rapid global eustatic sea-level rise (Hancock and Kaufmann, 1979) which modified the paleogeographic framework with the disappearance of many carbonate platform environments. At the same time, anoxic facies develop (Jenkyns, 1980; Haq, 1984), and facies with rudists and larger foraminifers disappear. In North Africa and the Middle East, the differentiation with the Cenomanian is well marked:



Text–fig. 3—Paleobiogeography of marine ostracods in the Tethyan Late Cretaceous (Senonian) (map after Barron *et al.*, 1981, modified; oceanic circulation after Haq, 1985). 1, *Brachycythere*; 2, *Buntonia–Ovocytheridea–Cophinia*; 3, *Fissocarinocythere-Ascetoleberis*; 4, *Mauritsina-Limburgina*.

Plate 2—Fig. 1. *Brachycythere* sp. Carapace, right lateral view, Senonian, Algeria. ×81. Fig. 2. *Buntonia opulenta* Apostolescu, 1963. Carapace, right lateral view, Senonian, Senegal. ×81. Fig. 3. *Aphrikanecythere phumatoides* Damotte and Oertli, 1982. Left valve, Maastrichtian, Le Kef (Tunisia). ×81. Fig. 4. *Protobuntonia* sp. Carapace, right lateral view, Senonian, Algeria. ×60. Fig. 5. *Paracaudites* (*Dumontina*) *puncturata* (Bosquet, 1854). Carapace, right lateral view, Upper Campanian, Dordogne (S.W. France). ×81. Fig. 6. *Limburgina* sp. Carapace, right lateral view, Senonian, Algeria. ×81. Fig. 7. *Dordoniella strangulata* Apostolescu, 1955. Carapace, right lateral view, Upper Cenomanian, Dordogne (S.W. France). ×81. Fig. 8. *Mauritsina* cf. *hieroglyphica* (Bosquet, 1847). Right valve, Late Campanian, Dordogne (S.W. France). ×80. Fig. 9. *Haplocytheridea renfroensis* Crane, 1965. Left valve, Winona Formation, Alabama, U.S.A. ×81. Fig. 10. *Nigeria arachoides* (Berry, 1925). Right valve, Navarro Formation, Texas, U.S.A. ×81. Fig. 11. *Fissocarinocythere pidgeoni* (Berry, 1925). Right valve, Winona Formation, Alabama, U.S.A. ×81. Fig. 12. *Antibythocypris gooberi* Jennings, 1936. Right valve, Prairie Bluff, U.S.A. ×81.

total disappearance of the *Veeniacythereis jezzineensis-Glenocythere Metacytheropteron* group, and development of the genera *Brachycythere* and *Ovocytheridea,* which continue during the remaining part of the Late Cretaceous in Africa. The genus *Brachycythere* will later have a very wide paleobiogeographical repartition to Tanzania, Mozambique, India and North and South America (Brazil, Surinam, Ecuador).

Senonian (Text-fig. 3).—In southern Europe (including southern U.S.S.R.), associations remain practically unchanged at the generic level. Faunal differences remain important between the northern and southern margins of the western Tethys. The few genera in common are generally in the deep environments — *Phacorhabdotus* and *Trachyleberidea.* In North Africa, several types of associations characterise different environments. On the platform, faunas remain typically "African" with the genera *Cophinia, Ovocytheridea, Buntonia, Protobuntonia* and *Veenia.*

In outer-neritic environments and basins, there appear new genera such as *Doriclythereis, Megommatocythere, Kefiella, Aphrikanecythere, Palaeocosta* (Donze *et al.,* 1982). Most of these genera persist into the Paleocene and Early Eocene in North Africa, Saharan West Africa, Saudi Arabia and Pakistan (Siddiqui, 1971; Al Furaih, 1980).

In the African framework, it is interesting to note an accentuation of the north-south relations, especially on the eastern margins. This is, for example, the case for the genus *Haughtonileberis,* also present in the Senonian of Algeria (Vivière, 1985). Some elements are common with South Africa (relations with Tanzania, in Dingle, 1982, p. 384).

Morphological convergences between isochronous, but geographically separated, genera are also noticeable; *Kefiella* in North Africa, *Dutoitella* in South Africa and *Atlanticythere* in the deep South Atlantic.

Concerning India, Jain (1975) reports Neocytherinae and the genus *Brachycythere* in the northwest (Jain, 1977), north-Tethyian affinities are rather obvious with the presence in the Maastrichtian of a fauna very similar to that of Maastricht (Deroo, 1966), with genera such as *Curfsina, Limburgina, Murrayina, Dumontina, Echinocythereis* and probably *Mauritsina.*

In Australia, the works of Neale (1975, 1976) and of Bate (1972) provide a tremendous amount of information, including five main points which must be emphasized:

A cosmopolitan stock with *Cytherella, Cytherelloidea, Eucytherura, Hemiparacytheridea, Hermanites, Curfsina* and *Oertliella.*

An endemic stock with *Anebocythereis, Apateloschizocythere, Eorotundracythere, Hystrichocythere, Paramunseyella, Premunseyella, Scepticocythereis, Toolongella,* *Ginginella, Hemingwayella, Rayneria* and *Verseya.* Older genera, relics of the South Africa-Madagascar entity, *Majungaella* and *Rostrocytheridea* persist.

Apparition of the genera *Munseyella* and *Cytheralison* which will later spread out of this geographic area. The first in the Cenozoic of Japan, South America and Gulf of Mexico, the second restricted to Australasia.

Total absence of the North and West African genera *Brachycythere, Buntonia, Ovocytheridea, Cophinia,* and *Nigeria.*

Here also, cases of homeomorphy have been reported (Bate, 1972) between *Apateloschizocythere* and *Schizocythere, Hystrichocythere* and *Echinocythereis, Majungaella* and *Neocythere-Centrocythere* (Krommelbein, 1979).

Dingle (1982) demonstrated that some generic affinities existed during the Santonian-Campanian between South Africa and Australia (*Rayneria, Apateloschizocythere*).

In North America, in the Gulf of Mexico (Hazel and Brouwers, 1982), a certain endemism is present. One can see the apparition of new genera such as *Fissocarinocythere, Ascetoleberis, Escharacytheridea,* and *Antibytocypris.* There are very few genera in common with the European area of the Tethys, except perhaps a few forms attributed to the genera *Trachyleberidea, Limburgina,* *Pterygocythere* and *Neocythere*. Few affinities are also detected with North and West Africa with the genera *Veenia* and *Brachycythere*. Cytherideinae are also represented by numerous species of *Haplocytheridea* which will remain very common in shallow water environments during the Cenozoic. The genus *Buntonia* will appear only during the Paleogene.

In the Campanian-Maastrichtian of Cuba (Ljubimova and Sanchez-Arango, 1974), ostracod associations are similar to the ones of the Gulf of Mexico, particularly the genera *Brachycythere, Ascetoleberis* and *Neocythere*. Similar associations are also found in the northwestern Atlantic province (Scotian Shelf: Ascoli, 1975).

PALEOBIOGEOGRAPHIC IMPLICATIONS / BIOPROVINCES

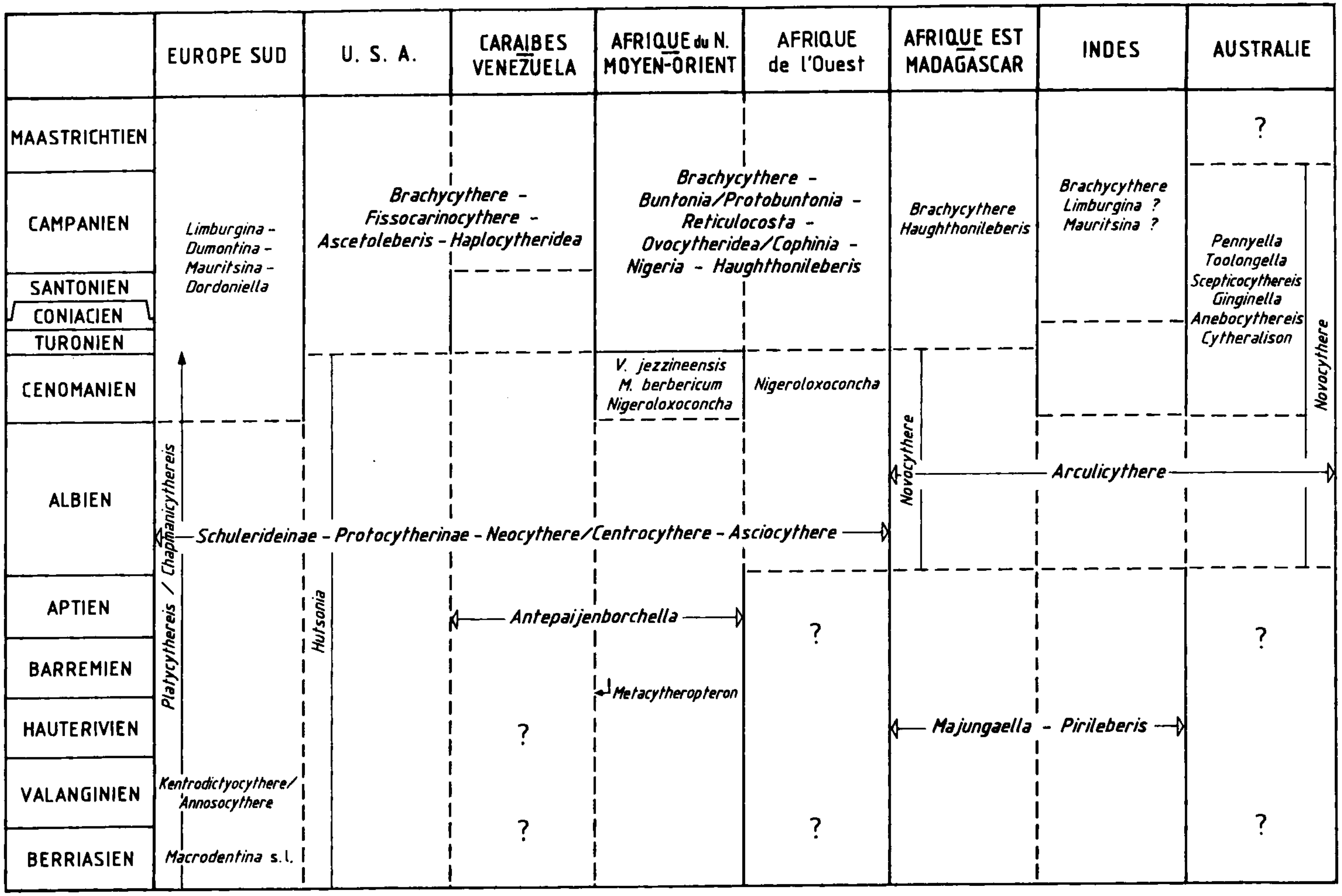
From the observations made in the previous chapter, it is possible to deduct certain conclusions of paleobiogeographical order and in particular, to recognize several ostraçod bioprovinces whose dynamics can be followed during the Cretaceous (Text-fig. 4).

In the Early Cretaceous, and especially during the Berriasian, it is too early to speak of well individualised bioprovinces, although a separation between the African and European margins may already exist. The rare closely related species would testify for the existence of epicontinental communications (Donze, 1975, 1977) despite a certain time lag affecting the apparition of some species, generally more precocious in North Africa, since the Early Jurassic. From the Valanginian to the Aptian, a bioprovince with numerous genera in common corresponding approximately to the Caribbean and Mediterranean provinces becomes individualised. It is essentially characterized by the genera *Protocythere* s. l., *Schuleridea, Neocythere-Centrocythere, Rehacythereis*. In the southern part of this entity, from the Middle-East (Israel) to North Africa and even to Venezuela, a latitudinal province characterized by the genus *Antepaijenborchella* is superimposed. The southern part of the U.S.S.R. (Mediterranean realm sensu lato) (Andreev and Mandelstam, 1971) belongs to this last paleobiogeographic entity. In the Southern hemisphere, another province becomes differentiated with the dominant genera *Majungaella, Pirileberis* and *Arculicythere* (Madagascar, India, South Africa, Argentina). This bioprovince is situated on the extreme border of the Tethyan realm.

During the Albian and mainly the Cenomanian, the separation between the northern (European) and southern (African) margins becomes total. A very homogenous (even at the specific level) province is formed, which comprises the whole of North Africa, the northern part of East Africa (Somalia, Ethiopia) and the Middle East to the Persian Gulf (Babinot, 1985), which can be called "bioprovinces of *Veeniàcythereis jezzineensis* and *Metacytheropteron berbericus*." As pointed out by Bismuth *et al.* (1981), this fits well into the recent models of global tectonics. These models show that the Tethys, a deep-sea realm that may constitute a significant enough obstacle to prevent exchanges of benthic faunas, includes northern littoral domains (Euroasiatic plates) and southern litoral domains (African plate and its Arabic and Italian promontories).

It is still too early to define the north-European Tethyan province, our knowledge being limited to southern France and the Iberian Peninsula (Spain and Portugal). This southwestern European bioprovince (Babinot, 1985) is, however, well characterised and differentiated from the North-African and the more boreal north-European provinces. Characteristic genera are mainly *Mauritsina* and *Limburgina*. The generic content of this province will evolve very slowly during the Late Cretaceous.

During the Albian, North America is still very poorly differentiated from northern Europe at the generic level, but the separation is effective at the specific level in the Gulf of Mexico, whereas faunas of the Canadian continental shelf are very closely related to the north-European faunas. During the



TEXT–FIG. 4—Evolution of ostracod faunas in the Tethyan paleobiogeographic provinces during the Cretaceous.

Cenomanian, this separation increases, probably in relation to an accentuation of sea-floor spreading between the Iberian Peninsula and North America (Tambareau, 1982).

In the austral realm, Early Cretaceous trends are confirmed with the presence of *Arculicythere* faunas in southern India, Madagascar, South Africa and offshore southwestern Australia. In central Australia, another province with endemic fauna situated slightly out of the Tethyan realm in the strict sense become differentiated.

From the Turonian to the Maastrichtian, the genus *Brachycythere,* which might have originated in the Aptian of Venezuela (J. P. Colin, person. observ.), appears as a key-genus. It is present in the U.S.A. from the Gulf of Mexico to the Canadian shelf, in the Caribbean (Cuba), in the west African basins, Tarfaya Basin (Morocco), North Africa and Middle East, East and South Africa, northwestern India, Brazil and Ecuador. This extremely widespread distribution is a rather unique case among ostracods. The genus is absent from Australia. It is necessary to point out that this genus has been created by Alexander (1929) from Texan material (Austin-Taylor formations: Coniacian-Santonian), the type-species being *Cythere sphenoides* Reuss, originally described in Europe in the Austrian Alps. In fact, this form may belong to another genus, most likely *Pterygocythere.* It is therefore highly probable that this genus does not exist in Europe.

The south-European province keeps its identity with the remarkable development of the Trachyleberididae and Hemicytheridae. We must mention, however, the occurrence of representatives of the genus *Mauritsina* in North Africa (Bellion *et al.,* 1973; Vivierel, 1985).

North Africa, the Middle East and the coastal basins of West Africa seem to belong to the same bioprovince, essentially characterised by the development of the genera *Ovocytheridea-Cophinia, Buntonia-Protobuntonia, Nigeria* and *Reticulocosta.*

An American bioprovince from the Caribbean to Canada is clearly individualised during the Senonian, in particular the development of the genera *Fissocarinocythere, Ascetoleberis, Escharacytheridea* and *Antibythocypris* and the extreme scarcity of European Trachyleberididae.

Also to be noted are the very strong affinities between the North-Tethyan realm and southern India (Jain, 1977) and the progressive isolation of Australia (western coastal basins of Gingin and Carnarvon) despite a stock of cosmopolitan and ubiquitous genera and more affinities with South Africa and Argentina.

CONCLUSIONS AND GEODYNAMIC PERSPECTIVES

It has been demonstrated that ostracod faunas were very important for paleogeographical reconstructions and the characterisation of bioprovinces evolving over time. If most genera are widely distributed geographically, this is not the case at the specific level, associations often being more or less endemic. This palaeobiogeographical restriction can be explained by the low dispersal capacity of ostracods, which are essentially benthic animals, the very restricted migratorial capacity of the larval stages, which are also benthic, and the biological and metabolic factors of each organism. Therefore, the depth obstacle generally cannot be overcome by continental shelf species. This is, for example, the case for the Africa-Europe relations, during the Late Cretaceous, where the few genera in common between the two margins are deep thermospheric genera (*Trachyleberidea, Phacorhabdotus, Monoceratina* s. l.).

In basins which are far from each other, the presence of common shelf species is a reliable indication of marine communication through epicontinental margins. It is, however, important to be prudent and to avoid falling into two major traps:

Too quick specific assimilations between areas which are very far apart. This is the case for numerous North-American species abusively attributed to European species. Mosf of the works on North American Cretaceous ostracods being generally relatively old, illustrations often do not allow reliable conclusions.

Morphological convergence phenomena at the generic level. The knowledge of paleohydrological phenomena (direction of currents, superficial water circulation systems and water mass stratification) is necessary for a better integration of ostracodological data to paleogeographical knowledge. On the contrary, the study of ostracod faunas helps to confirm or deny paleoceanographical interpretations. These results may also lead to arguments over certain structural interpretations of the positions of major plates and the existence of great oceanic depths.

Tambareau (1982) has shown that during the Cretaceous, the qualitative and quantitative changes in the affinities of the ostracod populations of the North Atlantic floor support the mobile hypotheses on the formation of the North Atlantic. She clearly shows, and our data confirm, that during the Early Cretaceous, the latitudinal faunal affinities evolve in a manner that is inversely proportional to the enlargement of the basin. During the Late Cretaceous, faunal affinities and differences are interpreted as resulting from the interaction of several events such as enlargement of the basin, opening to the South Atlantic towards the Arctic Ocean, and the establishment of a system of currents in response to all these changes.

The paleoceanographical models proposed by Haq (1984) show, during the Albian, a globally southeast-northwest direction for the currents along the African margins, inferring a Middle-Eastern origin for the *Metacytheropteron berbericus* and *Veeniacythereis jezzineensis* associations in the Persian Gulf, since the uppermost Albian. Such a scheme can also explain the geographic distribution of *Metacytheropteron minuta,* from Israel to the Guyanas and the West African Coastal Basins (dispersion in "loop"). In the North Atlantic, Tambareau (1982) suggested an East-West migration system along the North continental margin of the basins. Recent oceanic circulation models allow a better understanding of the relations between the Australian faunas and those from South Africa and Argentina.

During the Albian-Cenomanian, North African faunas contain elements known from Equatorial Africa. This implies either a migration along West African coasts (this cannot be confirmed at present), or more likely a trans-Saharan connection, a pathway which requires further clarification.

Ostracod faunas with both Tethyan and Atlantic aspects have recently been found (J. P. Colin. person. observ.) in the Cenomanian-Turonian of the eastern Niger.

A problem exists concerning the ostraocod faunas of southern India during the Late Cretaceous. It has been demonstrated that this region is characterised by ostracod associations very close to those of the European Tethyan realm. A problem therefore is posed concerning the paleogeographical position of this block. This has already been evoked by McKenzie (1982) who wrote: "Possibly India was much closer to the northern shore of Tethys than current plate tectonics accepts or else Tethys was shallower. Both may well have been true in part." Similar observations have recently been made by Anglada and Randrianasolo (1985) on planktonic foraminiferas of the Late Cretaceous of Madagascar and of the Indian subcontinent. Recent paleogeographical maps (Barron *et al.,* 1981) locate them between -100 and -07 MY at the level of 45° S latitude. Planktonic foraminifera associations and palynology would indicate for these authors a latitude of about 15° N. They deduct that at equal palaeolatitudes, the water masses of the Southern hemisphere are, during the Cretaceous, warmer than those of the Northern hemisphere, and that the paleocurrents played a fundamental role in the evolution of the populations of the southern province.

Present data concerning the ostracods from the Late Cretaceous of India are still too scattered and imprecise to provide a valid answer to this problem. A detailed analysis of these faunas would certainly add useful information to this puzzle. To explain the diachronous nature of the apparition of several genera in distant areas the Tethys, Neale (1976, 1984) is convinced that currents have a determining effect on the distribution and dispersion of ostracod species. He indicates that to traverse the distance between Great-Britain and Australia, a species needs to travel a distance of only 10 m per year during a period of 2 MY.

As shown by Tambareau (1982), there is an important relation between global eustatic sea-level rises and renewal of ostracod faunas through epicontinental connection of previously isolated areas. The presence of Tethyan faunas in the Late Cenomanian-Early Turonian in western Africa is most likely the result of the main transgression during this period of time (Hancock and Kaufmann, 1979).

In conclusion, it appears that the Tethys played an essential and determining role for the composition and biogeographical repartition of Cretaceous and resulting Cenozoic ostracod faunas. Individualisation of faunal provinces and the relations (similarities and differences) between them are the results of several events and phenomena: plate tectonics, presence or absence of oceanic depths, importance and direction of currents, global eustasy and sensibility level of the different species to environmental changes.

This study is only a global overview of the spatial-temporal evolution of Cretaceous ostracod faunas of the Tethys. A detailed study would certainly need a far greater number of pages. In addition, a fundamental gap exists in our knowledge: the total absence of data concerning the ostracods from southeastern Europe, Italy, Yugoslavia, Greece, Turkey (Apulian platform) and the Far East.

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DISCUSSION

Cronin: Has this extensive paleobiogeographical data base for Mesozoic ostracods been applied to identifying the existence and provenance of accreted terrains or exotic tectonic blocks?

Colin: Yes, studies are in progress concerning the Apulian Plate in the Mediterranean (Italy, Dinarids, Turkey).

Hazel: Years ago I found some rare specimens of what I thought to be *Ovocytheridea* in the Santonian and Campanian of Texas. This needs verification. There is no question, however, that *Ovocytheridea* occurs in the latest Campanian and Maastrichtian of Jamica, along with several species of *Buntonia* and *Schizoptocythere.*

Keen: You have shown that there were great differences between the Cretaceous ostracod faunas of the northern and southern margins of Tethys throughout most of the Cretaceous. This distribution persisted into the Tertiary until the Oligocene or Miocene. Can you offer any explanation for why the benthonic ostracods were unable to cross this fairly narrow "seaway", while other benthonic organisms, such as the benthonic foraminifera, had no difficulty at all? It is even more puzzling when it is known that many species of ostracods in the Cretaceous and Tertiary had a great latitudinal distribution along the Tethyan shores, *i. e.* North Africa to Iran.

Colin: I don't really know, maybe benthonic foraminifera juvenile stages were pelagic and therefore could have been more easily transported by surface currents.

Neale: In congratulating the speaker on a most interesting paper I would welcome details of the publication which gives the palaeocurrent reconstruction shown on the screen since the reconstruction shown would appear to give a water mass problem in the proto-North Pacific. I would also be interested in hearing the evidence used to postulate a southwesterly flowing current along the east coast of India.

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Marine Ostracod Distributions during the Early Breakup of Southern Gondwanaland

RICHARD DINGLE
University of Cape Town, South Africa

ABSTRACT

Plate tectonic and palaeo-oceanographical development of southern Gondwanaland, in particular the South Atlantic and Indian oceans, is documented in its marine Jurassic and Cretaceous ostracod faunas. During breakup, which commenced in mid-Jurassic times, seaways developed across the supercontinent via the Falkland Plateau and southern Africa, to Madagascar, India, and Australia. These were connected (probably via the SE Pacific) to the Neuquen Basin of west Argentina, but were isolated from the Equatorial South Atlantic by the Walvis-Rio barrier. The southern Gondwanaland oceans fostered a distinctive ostracod fauna that can be recognized in Bajocian to Cenomanian strata: South Gondwana Fauna (SGF). It contains numerous endemic forms, with the most characteristic species belonging to the Progonocytheridae. A major faunal change occurred between late Cenomanian and early Turonian times, when new taxa migrated from the Equatorial South Atlantic, via the Temperate South Atlantic, and ousted the extant SGF. Vigorous colonisation and rapid speciation was probably encouraged by radical oceanographical changes resulting from modifications in palaeogeography, especially the flooding of the Walvis-Rio barrier between the Equatorial and Temperate South Atlantic oceans. By Coniacian time at the latest, a cosmopolitan Pan Gondwana Fauna (PGF) was established, characterized by species belonging to the Trachyleberididae and Brachycytheridae. Subtle alterations in composition of the SGF and PGF may also be related to palaeogeographical changes.

INTRODUCTION

The use of ostracods for demonstratng the original continuity, and then timing the breakup of Gondwanaland, was pioneered by Krommelbein in his publications dealing with the faunas of Gabon and NE Brazil (*e.g.* 1966a, 1966b, and 1976, and Krommelbein and Wenger, 1966). This theme has been exploited to investigate broad trends in the palaeogeography of the super-continent, as well as to study specific aspects of the evolving southern hemisphere oceans (*e.g.* Neale, 1976, 1984; Reyment, 1980a; Tambareau, 1982; Dingle 1982). In this paper I will summarize some of the earlier work, and add new observations, some generated from a database that contains 1,325 ostracod taxa and their stratigraphical ranges. Implications from recent studies on tectono-eustatic sea-level changes (*e.g.* Reyment, 1980b, 1983), and Deep Sea Drilling Project data from the South Atlantic (Bolli *et al.*, 1978; Barker, 1983 and Hay *et al.*, 1984) are assessed.

Correlation of numerical and biostratigraphical ages follows Odin (1982).

DISCUSSION

Marine Ostracod Provinces in Southern Gondwanaland

During the Mid-Jurassic to Upper Cretaceous phase of continental separation, marine conditions were established across Gondwanland in early ocean basins and epicontinental seas. Areas affected included Argentina and the Falkland Plateau, southern Africa, eastern Africa and Madagascar, India, and Australia. These Mesozoic oceans were characterised by distinctive ostracod assemblages (*e.g.* Krommelbein, 1976; Bertels, 1977; Tambareau, 1982; Dingle, 1982 and Neale, 1984).

Two major faunal associations occur in southern Gondwanland: the South Gondwana Fauna (SGF), and the Pan Gondwana Fauna (PGF). These can be recognized by the presence of various taxa (mainly cytheraceans), and are separated temporally by a major mid-Cretaceous faunal dichotomy. Text-Figure 1A also suggests that there was a significant difference in the diversity of the two populations, with the PGF rapidly establishing greater diversity after its inception in Turonian times. The data indicate this for the total ostracod population, although only cytheraceans are plotted.

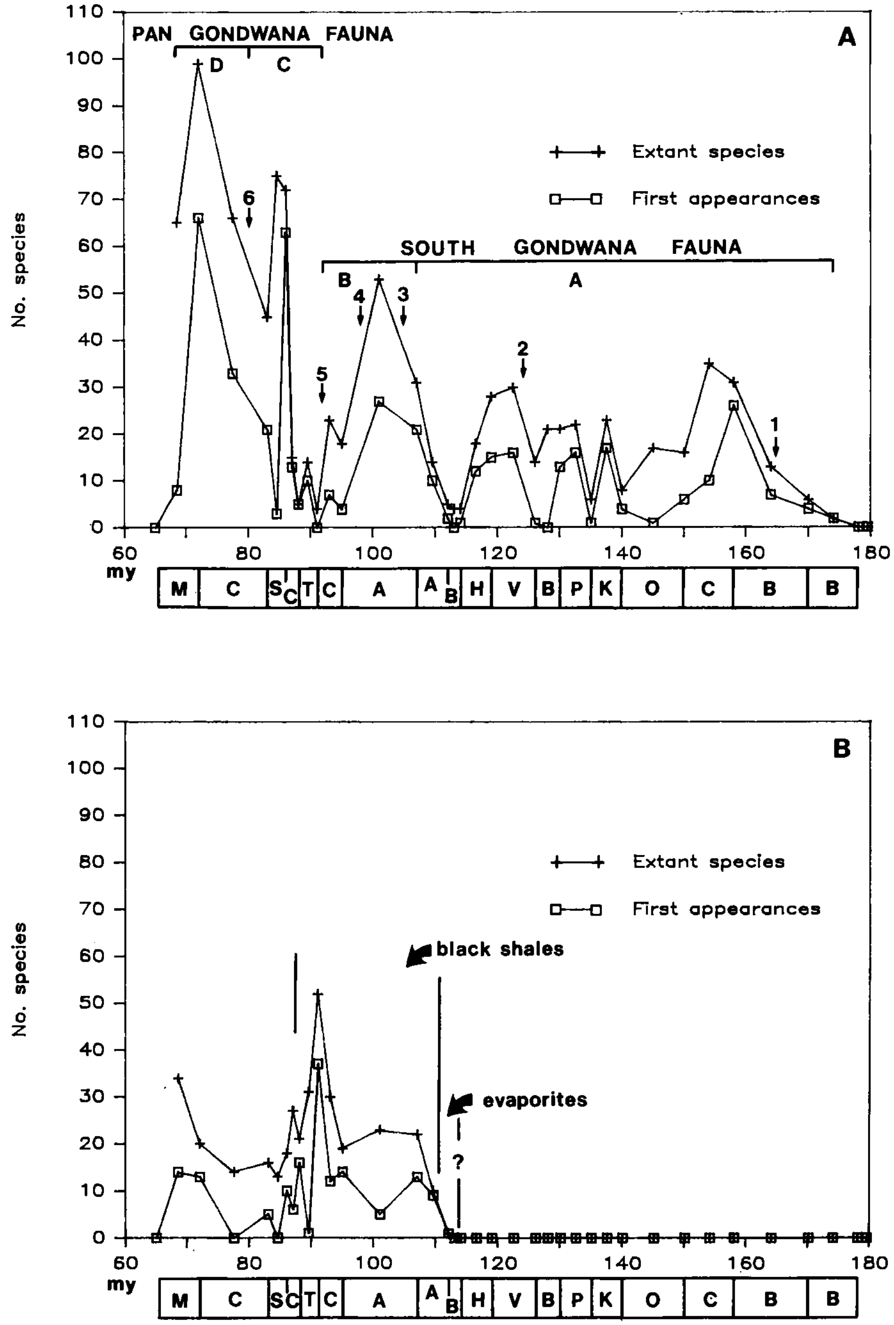
South Gondwana Fauna (Bajocian to Cenomanian)

The Earliest Jurassic or Lower Cretaceous sediments from all the regions of southern Gondwanaland contain an ostracod fauna whose cytheracean component is characterised by several

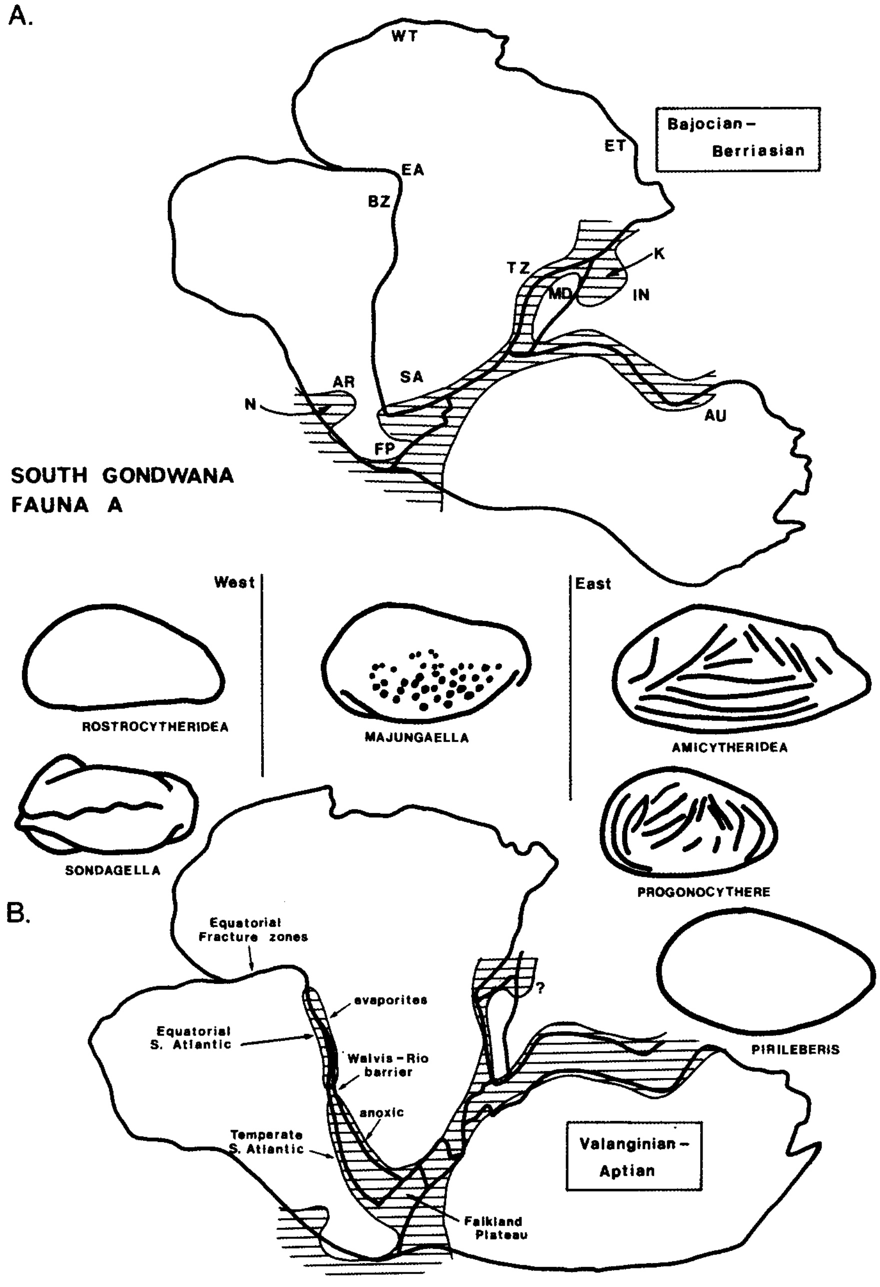
TABLE 1—CHARACTERISTIC ELEMENTS OF THE SOUTH GONDWANA FAUNA.

		AR	FP	SA	MD	TZ	IN	AU
Fauna A (Bajocian to Aptian)								
Majungaella nematis		*		*	*		*	
M. 2 sp.		*		*	*	*		
Sondagella theloides		*		*				
Rostrocytheridea ornata		*	W	*				
R. sp.		*		*				
Amicytheridea brentonensis				*		*		
A. triangulata						*	*	
A. inhopyensis					*	*		
Progonocythere befotkaensis					*	E	*	
P. accessa					*		*	
Pirileberis progonata					*	*	*	
Arculicythere sp.					*			
Fauna B (Albian to Cenomanian)								
Majungaella nematis	(o)	?		*				
M. sp.			*	*		*		*
Sondagella theloides	(o)			*				
Arculicythere tumida			*	*				*
A. sp.					*			
Pirileberis sp.				*				
Isocythereis sealensis			*	*				
other trachyleberids				*		*	*	*
Rostrocythereidea sp.								*

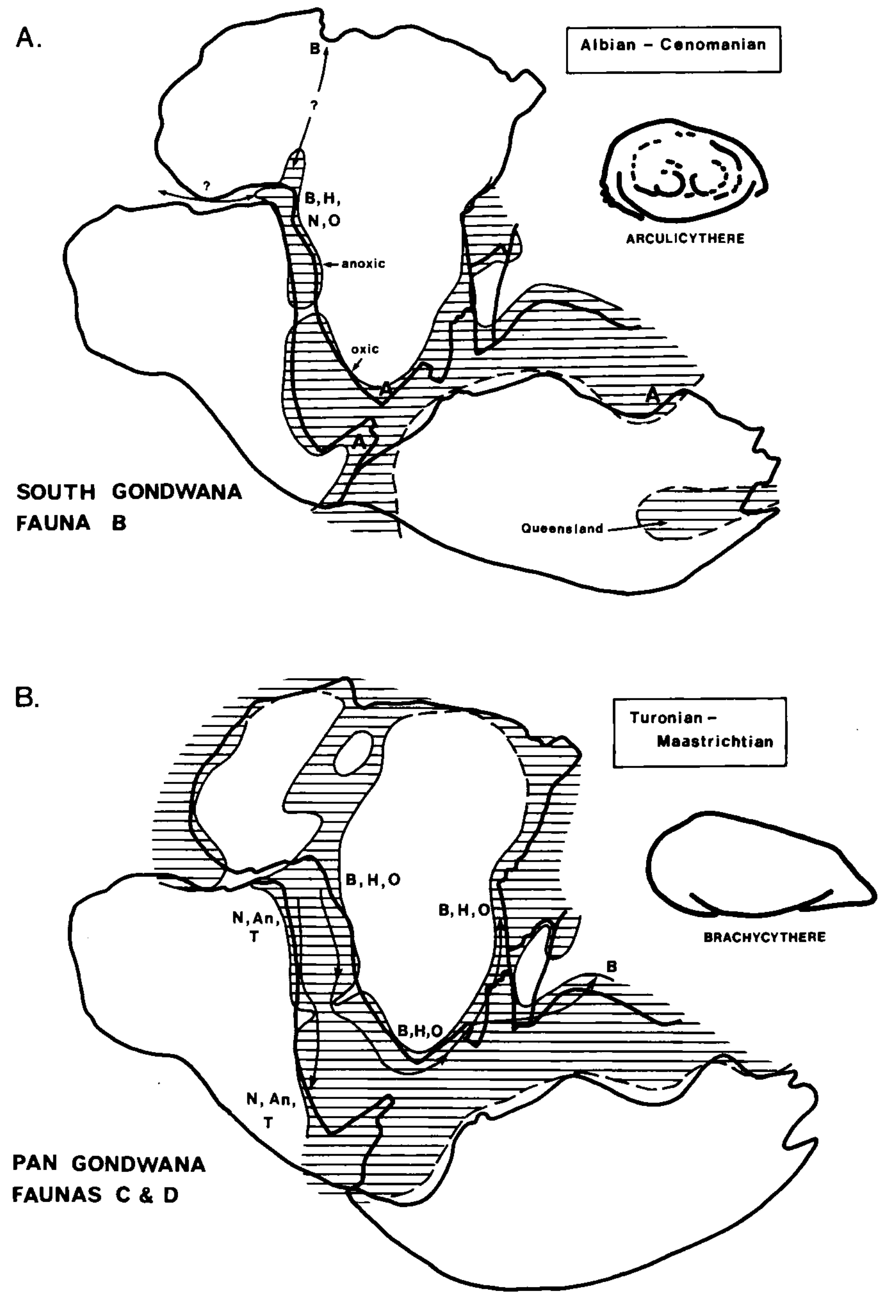
AR = Argentina, FP = Falkland Plateau, SA = southern Africa, MD = Madagascar, TZ = Tanzania, IN = India, AU = Australia. sp. refers to other species, (o) = "old" elements, W = western population, E = eastern population.



TEXT-FIG. 1—Cytheracean ostracod species extant and making first appearances. A: Southern Gondwanaland, summed from records in Argentina, Falkland Plateau, southern Africa, Madagascar, Tanzania, India, and Australia (636 citations). B: Equatorial South Atlantic, summed from records in Brazil and west and equatorial Africa (190 citations). Database generated on a decimal scale, but plotted at half-stage intervals. Converted to numerical time-scale using Odin (1982). Ostracod range and locality data from sources indicated in reference list by "*". Stages run Bajocian (B) through Maastrichtian (M). Events arrowed 1–6 refer to Table 3. Number of species refers to records occurring between start of interval and next half stage. Dating of black shale events after Bolli *et al.* (1978) and Stow and Dean (1984).



TEXT-FIGS. 2 and 3—Paleogeographical sketches of Gondwanaland, showing continental outlines and marine environments Continental edges are marked by thick lines, marine areas by horizontal ruling. Flooded continental extensions formed shallow shelf seas, with intervening regions comprising deep-water oceanic basins. 2A: Bajocian-Berriasian (Bajocian continents, Upper Jurassic seas) – South Gondwana Fauna A. 2B: Valanginian-Aptian (Valanginian continents, Aptian seas) – South Gondwana Fauna A. 3A: Albian-Cenomanian (Albian continents and seas) – South Gondwana Fauna B. 3B. Turonian-Maastrichtian (Turonian continents and seas) – Pan Gondwana Faunas C and D. In reconstruction 3B, the paleogeography along the Equatorial Fracture zones has been simplified to emphasize the continent-to-continent connection until Campanian times,



when deep-water routes were established on oceanic crust between the Central and Equatorial South Atlantic oceans. Marine sediments do occur in the marginal basins of this region, and complex inter-basin connections across structural highs obtained from Mid-Cretaceous times onward. Based on Norton and Sclater (1979), Reyment (1980b), Dingle *et al.* (1983) and Dingle (1985). Abbreviations: AR = Argentina, FP = Falkland Plateau, SA = southern Africa, MD = Madagascar, TZ = Tanzania, IN = India, AU = Australia, BZ = Brazil, EA = Equatorial Africa, WT = West Tethys, ET = East Tethys, A = *Arculicythere*, AN = *Anticythereis*, B = *Brachycythere*, H = *Haughtonileberis*, N = *Nigeria*, O = *Oertliella*, T = *Togoina*.

progonocytherid species and a number of other types. This is a common thread that runs through the assemblages until Cenomanian times, and it gives the South Gondwana Fauna (SGF) a distinctive composition. On the basis of waning in the progonocytherids, and the appearance of new species (including the local earliest trachyleberids), Dingle (1984) recognized a subdivision of the SGF into Fauna A, which comprised the "old", or original elements, and Fauna B which was a mixture of remnants of the "old" fauna, plus new types (Table 1). The change probably occurred in the early Albian, where there is a short break in the succession in southern Africa. In Text-fig. 1A, the establishment of Fauna B is marked by an increase in the number of new appearances from a Barremian-Aptian low, and an extended high in the "extant species" curve during Albian time. The former may be partly influenced by paucity of data, particularly on Barremian assemblages. It should be emphasized that the difference between faunas A and B is not of the same magnitude as that between the South and Pan Gondwana faunas, and that so far it has only been recognized in southern Africa (the relevant succession at other localities is poorly known).

Earliest records of Fauna A are from the Middle Jurassic of Madagascar (Grekoff, 1963), where five species of *Progonocythere* occur in Bajocian-Bathonian sediments. Callovian, Upper Jurassic, and Lower Cretaceous assemblages are known from most of the other localities across southern Gondwanaland, and all show the characteristic features summarised in Table 1. Various species of *Majungaella* have a wide distribution, and *M. nematis* ranges from the Neuquen basin in the west, to the Kutch area of India. Within the SGFA, there were two geographically distinct populations: one in the west (Argentina to southern Africa) which has common species in *Sondagella, Rostrocytheridea* and *Cytherelloidea*; and one in the east (Madagascar, Tanzania, and India) which has common species in *Amicytheridea, Progonocythere* and *Pirileberis* (Table. 1, Text-fig. 2). There is insufficient information to place Australian ostracod assemblages unequivocally within the SGFA, but the presence of *Aitkenicythere* sp. (Oxfordian) and *Procytherura aerodynamica* (Kimmeridgian) at DSDP sites 261 and 263 (Oertli, 1974) suggests links with the eastern population.

Figure 1A shows a relatively low, but constant diversity in the cytheracean component of Fauna A from Middle Jurassic to Lower Cretaceous time, with important Callovian and Valanginian/Hauterivian episodes of speciation (the total fauna shows a similar trend).

The taxonomic complexion of the SGF changed in early Albian time, giving rise to Fauna B (Table. 1). In Figure 1A this coincides with an increase in faunal diversity, and the appearance of a relatively large number of new taxa. Various species of *Majungaella* (including *nematis,* which has a total range Portlandian to Cenomanian) continued to have a wide distribution throughout the Albian and Cenomanian, but are generally numerically less abundant and are not accompanied by other progonocytherids (the exception being the Queensland Albian-Cenomanian epi-continental sea (Krommelbein, 1975), where a related genus first appears: *Tickalaracythere*). Other noteworthy features are the appearance of trachyleberids at most localities, and the wide distribution of the species *Arculicythere tumida* (Falkland Plateau to western Australia) (Table 1, Text-fig. 3A). In addition, the distinction between eastern and western populations appears to have broken down, and a more cosmopolitan aspect assumed. This fauna was relatively short-lived (14 my) and underwent a total eclipse in late Cenomanian or early Turonian times. As far as I can see, none of its species survived to become members of the new order.

Pan Gondwana Fauna (Turonian to Maastrichtian)

Dingle (1985) has reviewed the problem of trying to pinpoint the first appearance of the inheritors of the southern Gondwanaland oceans. Using the Kilwa succession described by Bate and Bayliss (1969), and the Zululand sequence zoned by Kennedy and Klinger (1975), he concluded that the colonisers arrived in southern and east Africa between Cenomanian III (probably *Rotalipora cushmani* zone) in South Africa, and Turonian with *Globotruncana helvetica* and *G. linneiana* in Tan-

TABLE 2—CHARACTERISTIC ELEMENTS OF THE PAN GONDWANA FAUNA.

A. Geographical distribution	Fauna C (Tur.–San.)					Fauna D (Cam.–Maa.)				
	AR	SA	TZ	IN	AU	AR	SA	TZ	IN	AU
Brachycythere sp.		*	*	?			*		*	
Haughtonileberis sp.		*	*				*			
Cythereis sp.		*	*	?	*		*		?	
Gibberleberis/Akrogmocythere		*	*				*			
Oertliella sp.		*								*
Rayneria sp.		*			*		*			
Apateloschizocythere sp.		*			*		*			*
Unicapellinae		*					*	*		
Curfsina sp.			*				*			
Anebocythereis sp.						*				*
Nigeria sp.						*				
Anticythereis sp.						*				
Togoina sp.						*				

B. Dominant species of the Turonian/Coniacian colonization of southern Africa (upper range in parenthesis)

Species	Upper range
*Brachycythere longicaudata**	(Maastrichtian)
*Haughtonileberis haughtoni**	(Campanian)
Cythereis klingeri	(Maastrichtian)
Cytherelloidea umzambaensis	(Campanian)
Gibberleberis africana	(Santonian)
Oertliella pennata	(Campanian)
Bythocypris richardsbayensis	(Maastrichtian)
Rayneria nealei	(Campanian)

* occurs in Turonian of Tanzania

zania, *i.e.* between late Cenomanian and mid-Turonian.

The Pan Gondwana Fauna (PGF) is marked, on a regional basis, by a relatively high diversity, which peaks in the lower part of the Maastrichtian (Text-fig. 1A). There are two maxima of first appearances, which allow a subdivision into Fauna C (Turonian-Santonian), and Fauna D (Campanian-Maastrichtian) (Table 2A). To a large extent, this subidivision is based on the addition of new species, rather than a major turnover of the fauna.

PGFC is first seen in the Tanzanian Turonian (Bate and Bayliss, 1969), and shortly afterwards in the Coniacian of southern Africa. One interesting feature of these earliest assemblages is the rapidity with which taxa that remained numerically dominant for the rest of the Cretaceous moved into their new niches (Table 2B). They must have been aggressive colonisers — *Brachycythere longicaudata, Haughtonileberis haughtoni,* and close relatives of *Gibberleberis africana* (*Akromocythere wamiensis*), and *Cythereis klingeri* (*Cythereis luzangaziensis*) occur in the Turonian of Tanzania.

Fauna D in southern Africa is marked by an early Campanian influx of new species. This resulted in considerable specific diversity by early Maastrichtian time in genera that were already well-established in the area, as well as numerous new genera: Santonian (17 genera, 30 species); Campanian (24, 50); Maastrichtian (29, 48).

Recognition of the PGF in south and east Africa, and India can be simplified to the arrival of *Brachycythere* and an upsurge in trachyleberid taxa. In Argentina and Australia, *Brachycythere* has not been recorded, but in both areas the Upper Cretaceous faunas have several trachyleberid species and it is clear that in these regions the old SGF was routed with equal efficiency. At present, this event cannot be timed because the relevant faunas have not been described. In Argentina, no equivalent to Fauna C is known, and the local PGFD (early to middle Maastrichtian) has close affinities in cytheracean genera with Equatorial South Atlantic faunas (Table 2A).

With only Santonian and Campanian faunas from the west coast well-known, it is premature to draw firm conclusions from the Australian data. Taken at face value, there seems to have been a drop in diversity across the Santonian/Campanian boundary, but whether this reflects a change equivalent to the faunas C and D, is not clear. Neale (1975, 1976, 1984) has discussed some of the paradoxes of these faunas, which have some intriguing links with both southern Africa and South America (Table 2B).

Ostracod Migrations and Gondwanaland Breakup

Many of the main plate-tectonic events in the fragmentation of Gondwanaland have been relatively well-dated by geophysical means, so that we can view the evolution of the South Gondwana ostracod faunas within a reasonably secure framework. Dates particulary relevant to our study are shown in Table 3, and all except event 5 (communication between Equatorial and Temperate South Atlantic oceans across the Walvis-Rio barrier) are well-established in the literature. Plotted on Figure 1A they show a strong correlation with changes in the complexion of the SGF (Table 3), that allows us to trace its development in terms of the plate-tectonic evolution of Gondwanaland (Text-figs. 2 and 3).

East and West Gondwanaland began to drift apart in the Middle Jurassic, with the separation of Madagascar (and probably Antarctica) from eastern Africa (prior to M25, Rabinowitz *et al.*, 1983). The appearance of the SGFA in the Bajocian-Bathonian of the Majunga Basin of NW Madagascar and the Kutch region of India, followed by Callovian (Tanzania), Oxfordian/Kimmeridgian (western Australia), and Portlandian (southern Africa) records, as well as unfossiliferous Oxfordian marine strata on the Falkland Plateau, show that epi-continental or small oceanic seas rapidly spread across central Gondwanaland in late Jurassic time (Text-fig. 2A). At the same time (Callovian), the SGFA established itself in the Neuquen Basin of Argentina, probably via Cape Horn

TABLE 3—PLATE TECTONIC/PALEOGEOGRAPHICAL EVENTS AND GONDWANA OSTRACOD FAUNAS.

event	age	fauna	
1. Initial separation between East and West Gondwana	Bathonian 165 my		
2. Commencement of South Atlantic separation	Valanginian 124 my	A	SOUTH GONDWANA FAUNA
3. Opening pole change, deep-water circulation between Temperate South Atlantic and SW Indian oceans	Albian 105 my		
4. Separation of Falkland Plateau and southern Africa, shallow water circulation between Temperate South Atlantic and SW Indian oceans	Albian 98 my	B	
5. Communication between Equational and Temperate South Atlantic oceans across Walvis-Rio Barrier	Late Cenomanian 92 my	C	PAN GONDWANA FAUNA
6. Final separation across Equatorial fracture zones, ?deep water circulation between Equatorial South and Central Atlantic oceans	Campanian 80 my	D	

dates for events after: 1. Rabinowitz *et al.* (1983); 2. Austin and Uchupi (1982); 3 and 4. Martin (1984b); 5. this paper; 6. Reyment and Bengtson (1985).

From its geometry, it is understandable that there were certain differences between the populations of the eastern and western ends of this long narrow sea.

A Valanginian-Hauterivian influx of new species, and a small increase in population diversity (Text-fig. 1A) appears to have been a direct consequence of the commencement of continental separation between Africa and South America (124 my), which created the South Atlantic and a small ocean basin off south-east Africa (Natal Valley). Presumably, alterations in ocean currents were responsible for the environmental changes that stimulated speciation, although it should be stressed that the changes were not large and the integrity of the SGFA was not affected. The long narrow basin created by this phase of drifting was bounded in the north by the subaerial Equatorial Fracture Zones, and in the south by the Falkland Plateau-southern Africa connection. It was subdivided by a narrow continental/ocean basement complex (Walvis-Rio barrier) (Text-fig. 2B). Recent work (*e.g.* Martin, 1984a) suggests that the rift propagated from south to north, so that the northern (Equatorial) is younger than the southern (Temperate) South Atlantic perhaps by as much as 3 my (M10 to M4). No pre-Albian marine ostracods have yet been reported from the South Atlantic, probably because of unsuitable lithofacies — evaporites and anoxic sediments (Equatorial) and anoxic sediments (Temperate, including the epi-continental Falkland sea) (Text-figs. 1B and 2B).

The situation shown in Figure 2B was relatively shortlived (*ca.* 14 my): the opening pole shifted at 105 my BP (early Albian) (Martin 1984b); the Falkland Plateau cleared the southern tip of Africa at 98 my (late Albian) (Martin 1984b) and mid-late Albian major eustatic sea-level highs affected the Equatorial South Atlantic (*e.g.* Reyment and Bengtson, 1985, p. 26). These events allowed deep and shallow water connections between the Temperate South Atlantic and the southern oceans, and gave rise to extensive marine transgressions in west Africa (Text-fig. 3A). I suggest that these palaeooceanographical and paleogeographical alterations were significant in influencing the evolutionary development of the SGF and were at least partly responsible for the speciation changes that distinguish faunas A and B (Text-fig. 1A and Tables 1 and 3). In this respect, event 3 (Table 3) seems the most significant: the pole change probably led to deep-water passages forming along the line of the Falkland–southern Africa fracture zones, allowing the anoxic Temperate South Atlantic to be flushed by oxygenated waters. Certainly it seems more than coincidental that *Arculicythere tumida* turns up in Albian sediments in southern Africa, the Falkland Plateau and off western Australia, and at the same time elements of Fauna A finally make their way to Australia (*Majungaella* and *Rostrocytheridea*). The dispersal of trachylebrids in the southern Gondwanaland seas may have been encouraged by the Albian oceanographical regimes, but their appearance in the region is likely to reflect the rapid, world-wide speciation of the family in Aptian-Cenomanian times (Whatley and Stephens, 1976). Finally, it should be noted that *Anticythereis* (Aptian), *Haughtonileberis* (Albian), *Brachycythere* (Cenomanian) *Oertliella* (Cenomanian) and *Nigeria* (Cenomanian) first appear in the Equatorial South Atlantic, but that none are known at this time from southern Gondwanaland. They evolved during a speciation spurt that peaked in Cenomanian–Turonian times, following the establishment of ?Barremian marine conditions (Text-fig. 1B). Interestingly, this peak coincides with a "first appearance" low in Gondwanaland (Text-fig. 1A).

*Several events affected various parts of Gondwanaland during the remainder of Upper Creta*ceous time: major Turonian/Coniacian and Maastrichtian transgressions; final continental separation across the Equatorial Fracture Zones (80 my, Campanian); the northward motion of India; and the breakdown of the Walvis-Rio barrier to ostracod migration. As previously discussed, the appearance of new faunal elements in southern Gondwanaland (PGF) has been narrowed to a late Cenomaian-early Turonian interval, and several characteristic taxa (in particular *Brachycythere* and *Haughtonileberis*) had already appeared in the Cenomanian Equatorial South Atlantic. Possible routes taken by the colonisers into the Indian Ocean have been assessed by Dingle (1985) who concluded that the most important was across the Walvis-Rio barrier, rather than via Arabia from the southern shores of Tethys. Reasons for this include: no Tethyan record prior to the Danian of *Haughtonileberis,* or to the Santonian of *Oertliella;* middle Cretaceous surface ocean currents around the northern and western sides of Africa were probably anti-clockwise; *Pondoina,* which is locally important in the Santonian of southern Africa occurs in the Equatorial South Atlantic, but not in the Tethys or east Africa.

Two lines of evidence favour a late Cenomanian passage across, or around the Walvis-Rio barrier for ostracods moving from the Equatorial to the Temperate South Atlantic.

1. Late Cenomanin-early Turonian high sea levels are well-documented from west Africa, where trans-Saharan and trans-Equatorial Fracture Zone faunal communications have been recorded (*e.g.* Reyment, 1980b, 1983). Eustatically-controlled flooding across the Walvis-Rio barrier is thus an obvious possibilty that has previously been considered (*e.g.* Reyment, 1980a).
2. Sediment samples from DSDP sites 363 (Bolli *et al.,* 1978) and 531 (Hay *et al.,* 1984) on the eastern Walvis Ridge indicate that between at least Hauterivian (118 my) and Albian (97 my) times its top stood at, or very close, to sea-level. Crustal sinking curves for site 531 (Hay *et al.,* 1984) and geophysical data (Sibuet *et al.,* 1984) suggest that the continental eastern end and the accreting (oceanic) western ends of the barrier did not subside below sea-level until Cenomanian time. DSDP data from the Rio Grande Rise suggest that this sector formed a subaerial barrier until 84 my (Santonian) (Barker, 1983). Consequently, earlier faunal crossings of the Walvis-Rio barrier are likely to have resulted solely from high sealevel stands (*e.g.* the austral-like Aptian and Albian benthic foraminifers described from the northern side of the barrier by Schiebnerova, 1978 and McNulty, 1984, respectively).

Once they had penetrated into the Temperate South Atlantic and Indian oceans, the immigrants rapidly speciated and ousted the incumbent SGFB I conclude this from evidence in the earliest faunas available (Turonian in Tanzania, and Coniacian in southern Africa), where the PGFC is established to the total exclusion of older elements. Finally, the severance of deep-water barriers in the Equatorial Fracture Zones at 80 my (Campanian) may correlate with the increase in speciation that has been used to differentiate the PGFD This linkage is tenuous and it also/or may be related to late Cretaceous sea level changes (*e.g.* Reyment 1980b). The latter were responsible for the early-middle Maastrichtian transgressions in Argentina, where Bertels (*e.g.* 1974, 1975) has recorded a fauna with distinctly Equatorial South Atlantic overtones (Table 2A, Text-fig. 3B).

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DISCUSSION

Colin: I have found the earliest *Brachycythere* in the Aptian of Venezuela with *Choffatella decipiens*. Grekoff has reported *Arculicythere* in Northern Madagascar (Diego Suarez Basin) and Jain has found it in SE India.

Dingle: These are valuable comments. The first implies that *Brachycythere* originated outside the Equatorial South Atlantic, and migrated into the latter region across the Equatorial Fracture Zones route I have tentatively indicated in Fig. 3A. I was not aware of the additional records of *Arculicythere* and thank you for bringing them to my attention.

Hazel: Are *Brachycythere* of Albian-Maastrichtian age of *ekpo* type?

Dingle: Generally speaking, yes. Those in the Indian Ocean area have drawn out and frequently spinose posterior outlines. As I have discussed earlier (Dingle, 1985) there is considerable uncertainty in differentiating the two key species in the Equatorial South Atlantic and Indian oceans, *B. sapucariensis* and *B. longicaudata*, respectively, in middle and upper Createaceous time.

Reyment: It would perhaps have been interesting to have heard you speculate about the Late Cretaceous and early Palaeogene ostracod affinities between Argentina and West Africa in relation to your interpretation of the Walvis Ridge as a migrational route for benthonic organisms. Also, Boltenhagen (1980: Thèse, Museum Histoire Naturelle, Universite Paris) has documented interesting late Cretaceous palaeogeographic connections on the basis of pollen.

Dingle: I refrained from mentioning this in my paper and presentation because of the lack of a mid-Cretaceous or early Maastrichitian record in Argentina, which precludes dating the establishment of the PGF in the latter region. The absence, for example, of *Brachycythere* from Argentina, and *Nigeria* and of *Anticythereis* and *Togoina* from the Indian Ocean, may reflect the environmental preferences and tolerances of these genera and their consequent abilities to take advantage of the migration routes that were available via newly-created ocean circulation patterns when the Walvis-Rio barrier was no longer effective.

Dias-Brito: The palaeoecological data obtained by PETROBRAS along the Brazilian continental margin, including hundreds of wells, point to the idea that there was not any effective barrier during the Albian time, just from the north to the south of the Brazilian coastal basins. The benthonic and planktonic foraminifera and the calcareous nannoplankton contents, at this time, were very homogeneous, being the same species present along the several basins at the Brazilian Atlantic margin. During the transition from Cenomanian to Turonian the subsidence increased and bathial conditions became common in the South Atlantic. This can be, probably, the cause of the migration of the ostracods to the developed ocean at the southernmost South Atlantic. On the other hand, along the Turonian-Maastrichtian at the Brazilian equatorial coastal basins, the sedimentation occured under bathial conditions, as evident by the benthonic foraminiferal content. At this time the connection between the South and North Atlantic which was started in Albian time, was absolutely effective.

Ostracoda of the Early Jurassic Tethyan Ocean

ALAN R. LORD
University College London, England

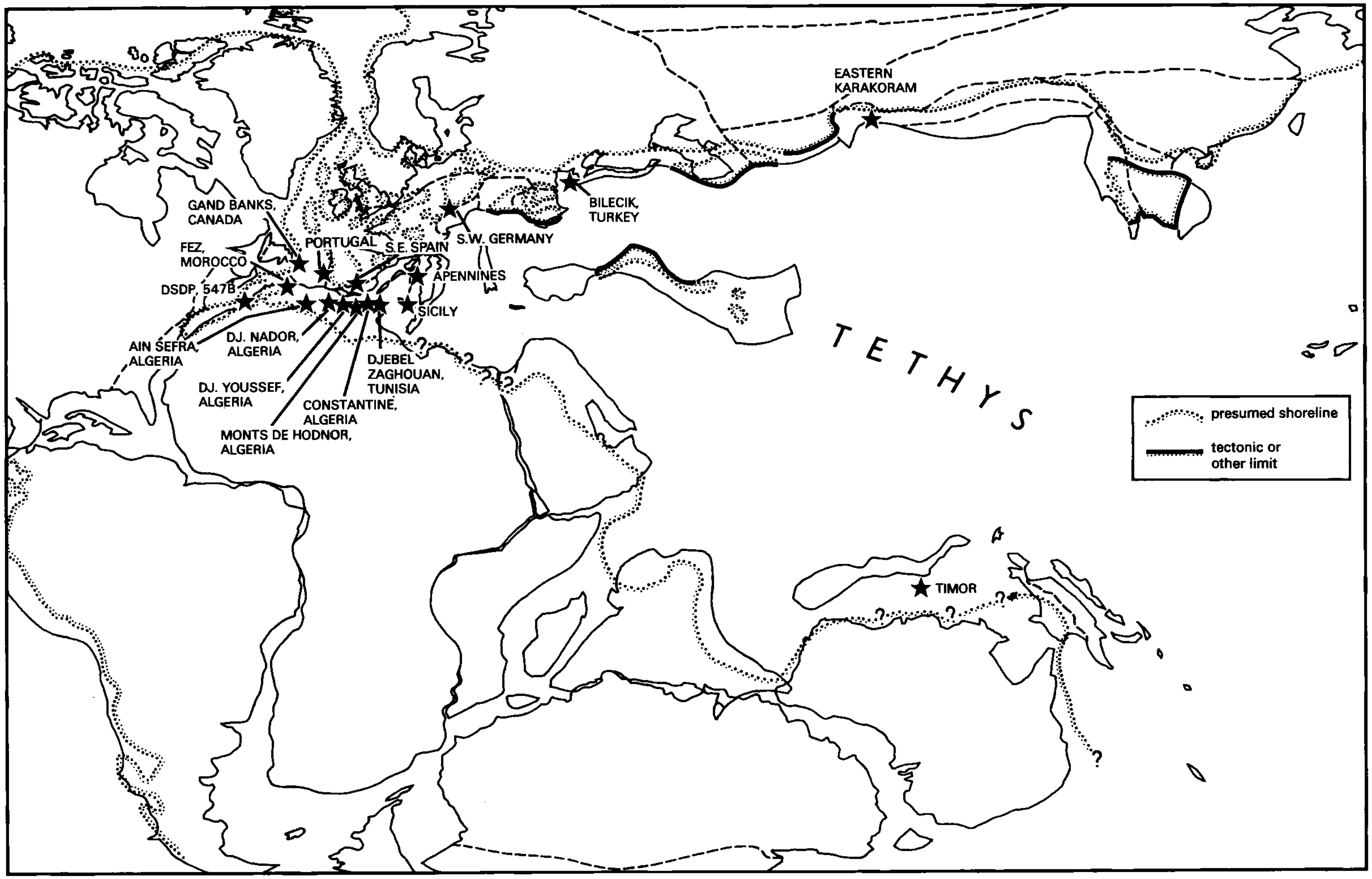
ABSTRACT

The occurrence of ostracods in the Tethyan Ocean during early Jurassic times is reviewed with special reference to assemblage compositions in relation to contemporary geographical and oceanographical conditions. The Tethyan material is compared with the well-known and diverse early Jurassic assemblages from Northern and Western Europe and also with Triassic Tethyan ostracods. Particular attention is paid to the temporal and spatial distribution of (a) ornate bairdiids, (b) vallate healdiids, and (c) cytheracean species.

INTRODUCTION

Our understanding of early Jurassic ostracods, and therefore our ability to interpret their evolutionary significance and to understand the constraints upon their distribution patterns, is effectively limited to material from Europe and in particular from north-western Europe. This restriction is not entirely due to the 'Eurocentric' character of much of the early work in the field but does reflect natural distributional and facies limitations upon our ability to obtain Lower Jurassic ostracods from the continental masses and the ocean floors. There is very little Lower Jurassic sediment remaining in the ocean basins and much of the continental material has been involved in tectonism (Himalayas, etc.). In areas such as Italy and Greece, carbonate sedimentation during early Jurassic time has left us with lithologies unsympathetic for the extraction of ostracods. These natural limitations upon study of the Lower Jurassic outside north-western Europe mean that only fragmentary data are available from elsewhere and it is appropriate to review that slowly growing body of information in the context of this conference to see what can be learned of relevance to the evolution of Mesozoic Ostracoda. The time is also suitable because considerable effort is being made at present to understand Mesozoic oceanographical (*e.g.* Kennett, 1983) and climatic conditions (*e.g.* Barron, Sloan and Harrison, 1980; Hallam, 1985; Hay *et al.*, 1982) and how these control or influence patterns of sedimentation (Hay *et al.*, 1981) and biotic distribution.

Available information about north-western European Lower Jurassic ostracods is comparable in level with that for other parts of the Jurassic (see Michelsen, 1975; reviews by Donze, 1985; Lord, 1978). A transgressive phase in the late Triassic brought healdiid ostracod genera from Tethyan areas to the south into the available biotopes of a newly forming north-west European epicontinental sea. The healdiids were particularly successful during Hettangian, Sinemurian and Pliensbachian times until their spectacular disappearance in the earliest Toarcian. Cytheracean forms, which had



TEXT-FIG. 1—Location of sites referred to in paper. Hettangian palaeogeography based on unpublished work by R. V. Tyson; palaeocontinental reconstruction by A. G. Smith, modified after Audley-Charles (*in press*).

also colonised the new shelf sea bottom, developed rapidly in diversity and density and appear to have been well able in the early Toarcian to occupy the habitats left by the extinction of the healdiids. This biostratigraphical pattern was set against a background of fluctuating sea level (Vail, Hardenbol and Todd, 1984; Van Harten and Van Hinte, 1984: fig. 3) and bottom water anoxia, especially during the early Toarcian when benthonic organisms were rare or absent over much of the area. This general pattern of events is well known, but should be borne in mind when considering areas away from the north-west European shelf. It is also important to note that thanks to the work of, amongst others, Bolz, Gramm, Kollmann, Kristan-Tollmann, Kozur, Sohn and Urlichs, the hitherto poorly known ostracod faunas of the Triassic are now more familiar than those of the extra-European Lower Jurassic.

THE NATURE OF TETHYS

During the Jurassic the area to the south of the north-west European shelf sea was occupied by a major east-west marine feature: Tethys. The name was first used by Eduard Suess in 1893 for a pre-Mediterranean seaway which connected the Alpine and Mediterranean areas with the Himalayas. The concept was originally that of Melchior Neumayr who had mapped a Jurassic 'Zentrales Mittelmeer' extending latitudinally from Central America through the Mediterranean to Iran and the Himalayas (Jenkyns, 1980: 109–110). During the last century ideas about what Tethys may have been and its geographical extent have varied with the geological age and author (see Adams and Ager (Editors), 1967), so much so that the very imprecision was the main linking theme of a vague palaeogeographical idea (see Şengor, 1985: 3–5). Even with palaeomagnetic-based continental reconstructions, plate-tectonic theory and modern understanding of tectonic terrains it is still possible for there to be major differences in interpretation of temporal and spatial relationships. Şengor (1985, and Şengor, Yilmaz and Sungurlu, 1984) recognises a Permian 'Palaeo-Tethys' which preceded the real Tethys of Neumayr and Suess (or 'Neo-Tethys'). Şengor (1985: fig. 6B) shows Palaeotethys closing during the Rhaetian as Neotethys opens. A good discussion of Palaetotethys, Neotethys and Pangaea in the context of the evolution of the eastern Mediterranean is given by Robertson and Dixon (1984). In the present work, Tethys (=Neotethys) is a biogeographical as much as an oceanographical feature. In early Jurassic times the Atlantic was no more than appendix, an embayment between north-west Africa and eastern North America (Text-figs. 1, 2). Rifting preceding the opening phase was in progress during the late Triassic and early Jurassic, but there is no palaeontological evidence for full marine connections between the Atlantic and the Gulf of Mexico prior to the Callovian (Scott, 1984: 51). For our time period then, Tethys was linked northwards to Siberia via the north-west European shelf but had no westerly outlet to the area of the modern Pacific. Eastwards it widened rapidly, presumably to the point where genuine oceanic conditions obtained. The sedimentary sequences of Jurassic Tethys are interpreted (Jenkyns, 1980: 115) as having been deposited in intra-continental basins and continental margins around Gondwanaland. Pelagic sediments which accumulated in deep oceanic conditions are not at present recognised.

There is considerable uncertainty about the palaeocontinental position of certain areas of south-east Asia during the Jurassic. Smith, in various reconstructions, places Sumatra and other islands on the northern margin of Tethys with New Guinea adjacent to Australia on the southern margin. A recent reconstruction places Sumatra, parts of Borneo, Sulawesi, etc. together with much of Malaysia, Thailand and Burma close to Australia on the southern margin of Tethys (Audley-Charles, *in press:* fig. 4). This latter pattern is followed here for the material from Timor and the island is placed, palaeogeographically, just off the north-west margin of Australia. The dramatic differences in the palaeocontinental reconstructions reflect the relative scarcity of palaeomagnetic data.

TETHYAN LOWER JURASSIC OSTRACOD ASSEMBLAGES

Available data from the author's collection and the literature are reviewed, from the area of the 'Proto-Atlantic' in the west to Indonesia in the east.

Deep Sea Drilling Project Site 547B, Leg 79.

The site is important as it provides a marine Lower Jurassic sequence (dated by the ostracods plus calcareous nannofossils) from within the incipient Atlantic Ocean. The ostracods listed and figured by Bate, Lord and Riegraf (1984) are revised and summarised in Table 1, but are the subject of continuing study by the author. Many elements are common to north-west Europe; healdiid genera (*Ogmoconcha, Ogmoconchella, Ledahia*) occur with cytheraceans, especially small cythe-

TABLE 1—DISTRIBUTION OF OSTRACODA AT D.S.D.P. SITE 547 (REVISED AFTER BATE *et al.*, 1984).

24CC	23–1	22–1	21CC	20–2 (59–61)	20–2	20–1	20–1 (126–129)	18–2 (5–7)	18–1 (22–24)	18–1	17CC	15–2 (58–65)	15–1 (0–4)	11CC	11–4 (99–103)	11–4 (68–74)	DSDP Site 547B samples-
●	Indeterminate steinkerns	Indeterminate steinkerns	●														'*Limnocythere*' (= *Lutkevichinella* of Bate *et al.*)
●			●														*Darwinula*
●																	Gen. et sp. D Bate *et al.*
				●													*Ektyphocythere* cf. *E. luxuriosa*
				●													*Ogmoconchella* juv.
				●	●						●				●		*Bairdja* spp.
				●										●			*Isobythocypris* spp.
				●			●	●	●					●			small cytherurids
						●						●	●	●			*Ogmoconcha* cf. *O. contractula*
							●										*Ogmoconcha* juv.
							●										*Monoceratina scrobiculata*
							●	●					●				?*Gramannicythere* sp.
								●									*Polycope* cf. *P. pelta*
								●						?			*Ektyphocythere* sp. juv.
								●	●				●	●	●		*Paracypris*
								●	●								*Acrocythere michelseni*
									●	●							?*Ogmoconchella* sp.
									?		●			●			*Paracypris redcarensis*
											●			●	●		*Polycope*
													●	●			'*Cytheropteron*' spp.
														●			*Bairdia guttulae*
														●			*B. molesta*
														●			*B.* cf. *B. carinata*
														●			*Ptychobairdia hahni*
														●			*Pt. aselfingenensis*
														●			*Cytherelloidea* sp.
														●			*Ledahia* cf. *L. septenaria*
														●			*Bairdiacypris*
?Rhaetian				I	S							P					Stages (tentative assignments based on ostracods)

rurid forms, while the larger cytheracean genera common in the north are restricted to single species of *Ektyphocythere* and *Monoceratina*. Other elements, *e.g. Ptychobairdia hahni* Lord and Moorley are apparently Tethyan (see below) but vallate healdiids (*Hermiella*) were not observed.

Portugal

Range data for the Pliensbachian—Toarcian sections at Zambujal (Exton, 1979) and Peniche (Lord, 1982: 270–71) have recently been supplemented by Exton and Gradstein (1984) in a valuable comparative discussion of the Lower Jurassic sequences of Portugal and the Grand Banks off eastern Canada. The two areas were adjacent during the Lower Jurassic (Text-fig. 2) and a comparison of the ostracod assemblages is therefore of interest, although the material is not abundant. In both Portugal and the Grand Banks no microfossils older than late Sinemurian (Raricostatum Zone) are recognised. In the Portuguese Lower Pliensbachian *Gammacythere ubiquita* Malz and Lord occurs, a form widespread at this time in north-west Europe (Malz and Lord, 1976: fig. 1). In the Upper Pliensbachian (Spinatum Zone) *Ogmoconcha* species (including *O.* cf. *O. amalthei* (Quenstedt)) occur with the vallate healdiid *Hermiella* cf. *H. ambo* (Lord and Moorley) and are succeeded in the Lower Toarcian by assemblages dominated by '*Bairdiacypris*' with the cytheraceans *Ektyphocythere debilis* Bate and Coleman and *Kinkelinella sermoisensis* Apostolescu. The *Ektyphocythere* and *Kinkelinella* forms were described from Britain and France respectively; *K. sermoisensis* is particularly widespread, while a number of species closely resembling *E. debilis* occur throughout Europe and also in North Africa (Table 3). Middle to Upper Toarcian assemblges contain *Kinkelinella costata* Knitter and *Cytherella toarcensis* Bizon from the Paris Basin, *Rutlandella transversiplicata* Bate and Coleman from Britain, *Polycope pelta* Fischer and *Cytheropteron alafastigatum* Fischer from south Germany, *Monoceratina scrobiculata* Triebel and Bartenstein and *Praeschuleridea* spp.

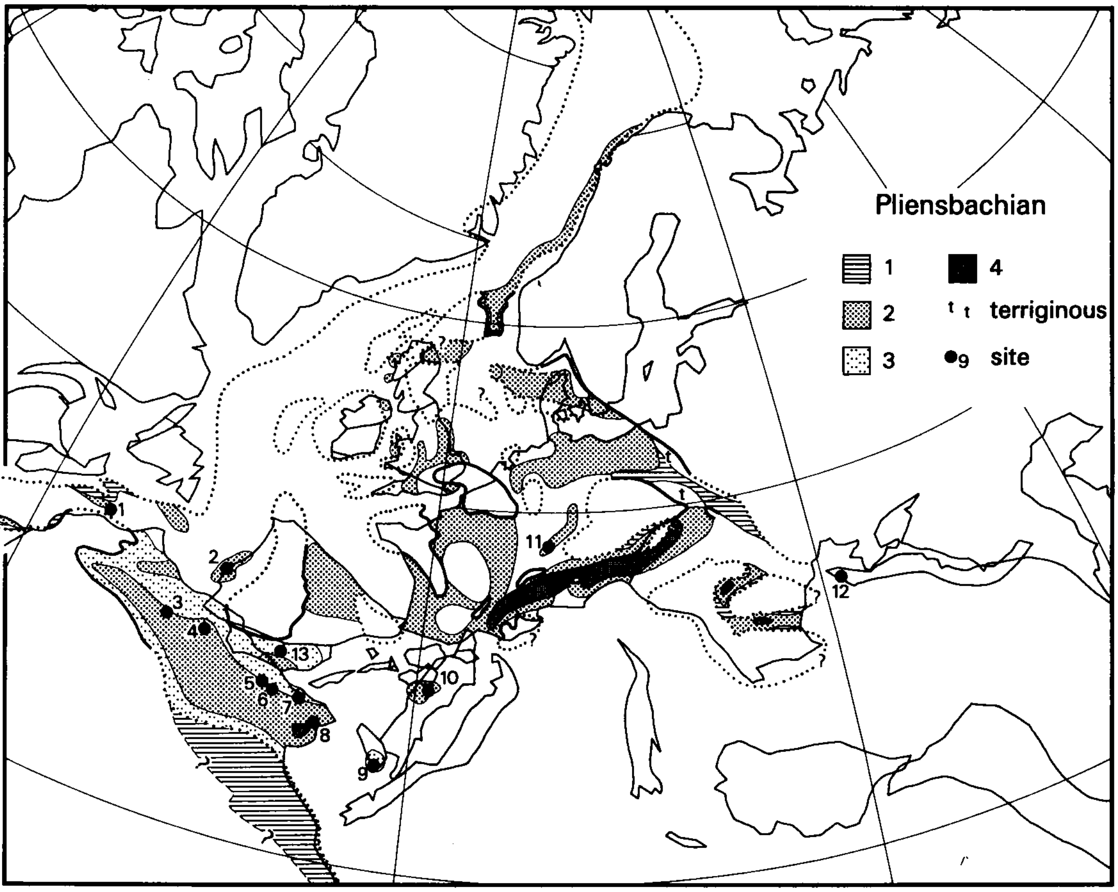
The Grand Banks assemblages are at present sparse, consisting of *Ogmoconcha* spp., *Polycope* spp. (including *P. cincinnata* Apostolescu and *P. decorata* Apostolescu) in the Pliensbachian, '*Bairdiacypris*' in the (?)Lower Toarcian and *Kinkelinella sermoisensis, K. costata, Polycope pelta, C. toarcensis, Praeschuleridea* sp. and *Monoceratina ungulina* Triebel and Bartenstein in the Toarcian-Aalenian. The assemblages, as known so far, consist of large cytheraceans, healdiids and *Polycope,* many known from north-west Europe, but with the presumed Tethyan element *Hermiella* in Portugal especially. Lithostratigraphically, the Lower Jurassic in the Portuguese Lusitanian Basin is essentially the same as in the Grand Banks Basin, both of which are similar to the Cantabrian and Aquitaine Basins. These occupy an intermediate position in palaeogeographical and facies terms between the north-west European basins and the early Jurassic Tethyan carbonate platform to the south. This pattern is reflected by the ostracod assemblages.

Spain

Upper Pliensbachian assemblages collected by British Petroleum from Rincon del Obispo in the Sub-Betic zone have been examined.

The samples contain *Polycope* sp., *Ogmoconcha, Ogmoconchella, Hermiella, Paracypris, Isobythocypris, Bairdiacypris, Cardobairdia, Bairdia* (including *B. rostrata* Issler) and *Ptychobairdia* forms. The *Ptychobairdia* are particularly strking; *P.* sp. A is large, distinctive and resembles *P. kuepperi* Kollmann, while '*P*'. sp. B is comparable with *Anisobairdia salisburgensis* Kollmann from the Triassic of Austria.

The assemblage composition pattern is a significant one, with dominant healdiid and bairdiid forms and a lack of Cytheracea. The distinctive *Ptychobairdia* sp. A also occurs in North Africa.



TEXT-FIG. 2—Palaeogeography and generalised lithofacies distribution pattern for the Pliensbachian of western Tethys (after Tyson unpublished). 1 = marginal marine, 2 = argillaceous shelf, 3 = carbonate platform, 4 = 'pelagic' facies.

Morocco

Boutakiout, Donze and Oumalch (1982) have described 5 cytheracean species from rocks west of Fez dated as Pliensbachian and Toarcian. The *Ektyphocythere* and *Kinkelinella* species could be of Lower Jurassic age but may be younger, as indicated by the presence of *Marslatourella*, (not known below the Middle Jurassic). The assemblages may in fact be Bajocian or even Bathonian. No associated ostracods are mentioned and the assemblage is anomalous when compared with the assemblage composition pattern found in Lower Jurassic samples from Algeria and Tunisia; a younger age for this material is likely.

Algeria

The record for Algeria is fragmentary because much of the Lower Jurassic consists of dolomites overlain by oolitic limestones, but it is important as, together with Morocco and Tunisia, the area provides information about the southern margin of Tethys, *i.e.* the coast and shelf of northern Gondwanaland.

Maupin and Vila (1976) figured poorly preserved material of supposedly Toarcian age from Djebel Youssef, south of Setif: *Cytherella* cf. *C. toarcensis, ?Liasina lanceolata, ?Isobythocypris, 'Bythocypris'* (?=*Bairdiacypris* from the Toarcian of Portugal—Exton and Gradstein, 1984: Pl. 2, fig. 5), *?Kinkelinella, ?Monoceratina.* The specimens are steinkerns, but the lack of healdiids and the tentatively identified cytheracens, plus '*Bairdiacypris*' is not inconsistent with a Toarcian age. Maupin (1977) has also figured material of Upper Pliensbachian and Toarcian age from 2 sections north of Constantine, containing *Ogmoconcha, Hermiella* and *Ektyphocythere* (Upper Pliensbachian) and *Cytherella toarcensis, K. sermoisensis* and *Ektyphocythere* cf. *E. bucki* (Bizon) (Toarcian). The material is not well-preserved. The *Hermiella* is only weakly vallate and therefore a suspect identification. Age assignments are based in part on the ostracods themselves and the Upper Pliensbachian assemblage might in fact be early Toarcian.

The most complete survey of Algerian Jurassic Ostracoda is that of Lasnier (1965. MS), who described and figured Lower Jurassic material from 3 regions (Monts de Hodnor, Djebel Nador and the Ain Séfra-Méchéria area) of north-east, north and western Algeria. Upper Pliensbachian assemblages contain a number of *Ogmoconcha* species, one *Ogmoconchella* form, *Hermilla* cf. *H. ambo, Liasina, Bairdia, Isobythocypris* and a small cytherurid (called *Orthonotacythere* by Lasnier). At Djebel Nador the large and distinctive *Ptychobairdia* sp. A occurs, a form also found in Spain and Tunisia. Toarcian assemblages contain *Kinkelinella, Ektyphocythere,* and '*Bythocypris*' (?= '*Bairdiacypris*'?) The occurrence of *Ptychobairdia* sp. A with *Hermiella* in the Upper Pliensbachian, succeeded by cytheraceans and ?'*Bairdiacypris*' in the Toarcian is a pattern observed elsewhere.

Tunisia

Much of the Lower Jurassic is in a massive carbonate facies and the only record of ostracods is of two assemblages of Upper Pliensbachian age from Djebel Zaghouan, north-east Tunisia (Lord 1982: 271). The ostracods present are: *Ogmoconcha* spp., *Ogmoconchella* spp., *Hermiella, 'Isobythocypris', Liasina* and *Ptychobairdia* sp. A .The assemblage composition is one recorded elsewhere in this work; note the absence of cytheraceans.

Italy

a) Sicily

Barbieri (1964) has described Upper Sinemurian to Toarcian ostracods from a borehole at Ragusa. The Pliensbachian material includes *Ogmoconcha* spp. (with '*Hungarella*' *hyblea* Barbieri which may be a vallate *Hermiella*), *Bairdia* spp., *Isobythocypris, Liasina* and *Polycope cincinnata,* but no cytheraceans. In the Toarcian, sparse assemblages contain single species of *Ektyphocythere* and *Kinkelinella* with *Cytherella* and *Bythocypris* (?=*Bairdiacypris*). These assemblages closely resemble material from the Apennines and are typical of the general assemblage pattern found elsewhere. Certain species are forms described from northern Europe (the ornamented *K. costata, P. cincinnata*), but with the unornamented forms, *e.g.* one resembling *Bairdia rostrata,* it is less easy to be certain.

b) Apennines

Much of the Lower Jurassic is represented by massive carbonates and the Toarcian by 'Ammonitico Rosso' in which ostracods were not found. At Strettura in Umbria, however, a sequence of argillaceous beds in carbonates has yielded ostracods of Upper Pliensbachian age. Lord (in Farinacci *et al.,* 1979) provides a brief account of the material, which contains *Ogmoconcha* spp., *Ogmo-*

conchella sp., *Hermiella* spp., *Liasina, Bairdiacypris* spp., *Bairdia, Paracypris, Ptychobairdia aselfingenensis* Lord and Moorley and *Polycope cincinnata.*

Turkey

A Lower Pliensbachian assemblage from Bilecik, in the north-western corner of Asiatic Turkey, has been described by Lord (1982: 276–77). The ostracods include *Ogmoconcha* spp. (including *O. amalthei* (Quenstedt)), *Bairdia, Paracypris, Isobythocypris* and *Polycope.* The assemblage is too old to contain *Hermiella* (late Pliensbachian to earliest Toarcian), but characteristically lacks cytheracean species; in certain respects it is comparable with contemporaneous north-west European material.

Himalayas, Eastern Karakoram

Pant and Gergan (1983) recorded 6 ostracod species from the Burtsa Formation, a unit considered to be about 1,000 m. thick and apparently ranging in age from Jurassic (?Triassic) to Cretaceous. The ostracods appear to be Lower Jurassic in age and have been compared with European species, viz. the healdiids *Ledahia septenaria* Gründel, *Ogmoconcha intercedens* Dreyer, *O. klingleri* Malz, *O.* sp., *Ogmoconchella* cf. *Olla propinqua* Malz and the cytheracean ?*Procytheropteron* sp. Although small and isolated, this assemblage is nonetheless an impressive record. Current interpretation of the structural setting of the Eastern Karakoram places this material on the northern edge of Tethys.

Timor

Samples from the Aitutu (Triassic to (?)Lower Jurassic) and Wai Luli (Lower and Middle Jurassic) Formations of Timor studied by Mr. D. J. Carter have been made available. The assemblages are summarised on Table 2 and are of particular interest in that they compare in general composition with samples discussed above from western Tethys. Some species range through the 2 formations, apparently from Triassic to Jurassic. In the palaeocontinental recontruction used here, Timor is situated on the southern margin of Tethys. Ostracod assemblages from eastern Tethys are so rare that the Timor data do not influence the argument as to whether the island was on the northern or southern side, nor do they allow at present any discussion about the differences in ostracod faunas between the two shores, or of faunal evolution and migration.

From Table 2 should be noted the absence of (a) bairdiids with strong surface morphology and/or ornamentation, so characteristic of many western Tethys Triassic sites, and (b) cytherac-

TABLE 2—SPECIES OCCURRENCE LIST FOR TIMOR.

Acratia sp.
?*Anisobairdia salisburgensis* Kollmann
Bairdia spp., including
B. cf. *B.* (*Akidobairdia*) *farinacciae* Oertli
B. cf. *B. rostrata* Issler
Bairdia sp. - puncatate surface
Bairdiacypris spp.
'*Bythocypris*' spp.
Fabalicypris sp.
'*Healdia*' 7 + spp.
?*Hiatobairdia arcuata* Kristan-Tollmann
Ogmoconchella/*Ogmoconcha*/*Hungarella*? spp.
Polycope cf. *P. cerasia* Blake
Polycope cincinnata Apostolescu

eans, as in Lower Jurassic Tethys assemblages, but in contrast to the Triassic material from China described by Kristan-Tollmann (1983).

LOWER JURASSIC OSTRACODS FROM SOUTH GERMANY AND FRANCE

Although vallate healdiids (*Hermiella*) have been recorded from various parts of France (Lord, 1982: fig. 7.2), the assemblages are generally rich with cytheracean species (see review by Donze 1985) and have much in common with Britain, The Netherlands, Denmark and north-west Germany. Material from south Germany is different and is reviewed for comparative purposes.

Vallate forms of *Ogmoconcha* were first described from south-west Germany and the area provides the best and most varied material available to date (Malz, 1975), but some Cytheracea also occur in the assemblages (Urlichs, 1977; Riegraf, 1984 — selected species only). Moorley (1974 MS) records full assemblages from the Upper Pliensbachian containing *Polycope* species (including *P. cincinnata*), *Bairdia* spp. (including *B. rostrata*), *Ptychobairdia aselfingenensis, P. hahni, Bairdiacypris, Liasina, Isobythocypris, Ogmoconcha* spp., *Ogmoconchella* spp., *Hermiella* spp. (see Malz *op. cit.*) and cytheraceans viz. *Bythoceratina seebergensis* (Triebel and Bartenstein, *Cuneoceratina amlingstadtensis* (T. & B.), *Gramannicythere aubachensis* Riegraf and *Nanacythere persicaeformis* Riegraf, although the cytheraceans are in relatively small numbers. In the Toarcian of southern Germany the assemblages can be diverse and are closely related to those described from elsewhere in northern Europe (Knitter, 1983; Knitter and Ohmert, 1983; Knitter and Riegraf, 1984). Thus, in the Pliensbachian, the area of southern Germany appears to lie in a transitional zone between Tethys and the north-west Europe shelf.

ORNAMENTED BAIRDIID OSTRACODS

The most impressive element in Triassic ostracod assemblages is without doubt the range of genera allied to *Bairdia* which have strong surface morphology and/or ornamentation. In the past 25 years our knowledge of Triassic faunas has greatly improved but, despite the growing number of taxa recognised and the special interest of cytheracean forms for post-Palaeozoic workers, the characteristic element of Triassic Tethyan assemblages remains the ornamented bairdiids. These ostracods are known primarily from the Alps, but recent accounts by Kristan-Tollmann (1980, 1983) describe material from Iran and China. It is easy to overlook the fact that these ostracods were not necessarily the most important element in the faunas, e.g. summaries of assemblage content for samples from the Zlambach-Schichten (Norian/Rhaetian) by Bolz (1974, figs. 1c, 2c, 2e) give a range of 5 to 20% for ornamented bairdiids, but they were never again so diverse and appear to be a characteristic Tethyan faunal element.

Ornamented bairdiid ostracods occur only sporadically during the rest of the Mesozoic. It is tempting to hypothesis that the cryptogenic appearances we encounter in younger levels in northern Europe are occasional migrants from Tethys; however, our knowledge of post-Triassic Tethyan ostracod faunas is very patchy and it is difficult to substantiate the idea. The species *Ptychobairdia* sp. A recorded above from eastern Spain, Morocco and Tunisia is not only a distinctive Pliensbachian marker, but is also morphologically very close to *Ptychobairdia kuepperi* Kollmann from the Rhaetian of Austria, an example of iterative evolution but in a purely Tethyan context.

TABLE 3—SUMMARY DIAGRAM FOR TETHYAN AND MARGINAL OSTRACOD ASSEMBLAGES.

		Smooth healdiids ①	Vallate healdiids ②	*'Bairdiacypris'*	*Polycope cincinnata*	*Ptychobairdia* sp. A ③	*P. hahni*/*P. aselfingenensis* ③	*Ektyphocythere champeauae* & allies ④	Cytheracea ⑤	Remarks
DSDP, 547	P	●		●			●		●	
	S	●							●	See Table 1
	H	●							●	
Portugal	T			●					●	*P. cincinnata* found
	P	●	●						●	in Grand Banks
	S									
Spain	P	●	●	●		●				Also *Ptychobairdia* sp. B and unornamented *Polycope*
Algeria	T			●				●	●	
	P	●	●			●			●	
Tunisia	P	●	●			●				
Italy/Sicily	T			●					●	
	P	●	●		●					
Italy/Apennines	P	●	●	●	●		●			
SW Germany	T							●	●	Cytheracea rare
	P	●	●	●	●		●		●	
Turkey	S	●								*Polycope* sp. present
Karakoram (L.J.)		●							●	
Timor (Tr.-L.J.)		●	●	●	●					See Table 2

Key: Tr. = Triassic, L.J. = Lower Jurassic, H = Hettangian, S = Sinemurian, P = Pliensbachian, T = Toarcian. ① *Ogmoconcha, Ogmoconchella, Ledahia*, etc.; ② *Hermiella*; ③ Bairdiacea with surface morphology and/or ornamentation; ④ *E. intrepida, E. debilis, E. furcata, E. bucki.* ① and ② Healdiacea, ③ Bairdiacea, ④ and ⑤ Cytheracea.

VALLATE HEALDIID OSTRACODS

The 'Vallate-*Ogmoconcha*' of Malz (1975), formalised as the genus *Hermiella* by Kristan-Tollmann (1977), were originally described from south-west Germany where they are a distinctive element in the Upper Pliensbachian. Fortuitously, these forms appear to be most diverse and well-preserved in the type area, but they seem to be characteristic of the Tethys rather than the north-west European shelf sea. Throughout the area covered by this discussion, from the 'Proto Atlantic' in the west (Portugal) to Timor in the east, the vallate forms are a characteristic Tethyan element.

Polycope cincinnata

Polycope cincinnata

This ornamentally distinctive species was described from the Paris Basin (Apostolescu, 1959), but is now known to range in time from the Triassic into the Lower Jurassic (Anisian-Pliensbachian; Urlichs, 1972: 696) and geographically in the Lower Jurassic from the Grand Banks to Timor. *P. cincinnata* thus originated in the Triassic in Tethys and became particularly cosmopolitan in the Lower Jurassic, together with the healdiids.

CYTHERACEAN SPECIES

From the site details discussed above (summarised in Table 3) it is clear that members of the Cytheracea are absent or at best uncertainly present in Hettangian to Pleinsbachian age sediments of the Tethyan area. In the Toarcian some representatives have been found, essentially only the widespread *Kinkelinella sermoisensis* and *Ektyphocythere* of species morphologically similar to *E. bucki*, viz. *E. intrepida*, *E. debilis*, *E. furcata*. Paucity of cytheracean species is thus a characteristic of Lower Jurassic Tethyan ostracod assemblages.

In marginal areas such as south-west Germany and Portugal, cytheraceans are relatively uncommon as compared with assemblages from north-west Europe. DSDP site 547 contains an interesting assemblage of species, with some large cytheraceans, small cytheraceans, healdiids and bairdiids including *Ptychobairdia*, with species known from north-west Europe, south-west Germany and Tethys (Apennines). The Tethyan element is most apparent at site 547 in the Pliensbachian, represented by healdiids and bairdiids, but is not especially strong.

Whatever the Palaeozoic origins of the Cytheracea may have been, it is clear that they were well-established and relatively diverse by the early Mesozoic. Kristan-Tollmann (1983) has described an Upper Anisian fauna from China containing 24 cytheracean species and subspecies and, interestingly, few unornamented healdiids and bairdiids. This example, together with other records of Triassic Cytheracea, supports Bate's (1977, p. 236) comment about the ancestral stock of new Lower Jurassic cytheracean lineages being introduced into north-west Europe from Tethys during the Rhaetian transgression. Once in the epicontinental seas of north-west Europe the cytheraceans rapidly diversified and from the early Toarcian onwards, following the extinction of the healdiids, dominated the ostracod faunas as they have continued to do to the present day. Thus, the north-west European shelf sea in Lower Jurassic times was the locus of evolution for the Cytheracea leading to the development of a large proportion of later Jurassic and Cretaceous genera and higher taxa.

CONCLUSIONS

A basic faunal pattern for Lower Jurassic ostracods seems evident, but it is important to remember the limitations of the data, which relate mostly to western Tethys and the north-west European epicontinental sea. Outside these areas, the faunas available for analysis are so scattered as to make their interpretation of little value at present. In addition, our knowledge of contemporary conditions is limited. Simulation of past climates is being carried out at present. Current patterns have been postulated (*e.g.* Ager, 1975, fig. 1) but are tentative and *reconstruct surface currents only*. The major marine feature of the Mesozoic world, 'eastern' Tethys, is almost unknown in terms of ostracods. We can at present only conjecture that there may have been a 'Pacific' Ostracod Province, distinct from that of Tethys.

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DISCUSSION

Colin: I have found *Kinkelinella* ex. gr. *K. sermoisensis* and *Praeschuleridea* spp. in the Toarcian of the Grand Banks (offshore Canada). Also, specimens of *Ptychobairdia* have been found in the Late Pliensbachian offshore Sicily and vallate *Ogmoconcha* are present in the basal Toarcian of SW France (Vendee).

Lord: I welcome Dr. Colin's three pieces of information, all of which confirm expected patterns. The Grand Banks records are a useful addition to the account given by Exton and Gradstein 1984.

McKenzie: Are there any deep-water facies?

Lord: Not to my knowledge, but how do you recognize with any certainty a deep-water assemblage from the early Jurassic?

Neale: I noticed that unlike the western seas of Tethys, the eastern seas in Timor and China appeared to lack highly ornamented "*Bairdia*". This could possibly suggest some sort of temperature barrier which would fit in with the margins of the "funnel" reconstruction shown on the map. I would welcome Dr. Lord's comment on this suggestion.

Lord: Professor Neale is almost certainly correct in thinking Triassic assemblages with ornamented bairdiids are from warmer water, more equatorial situations than the Timor and China materials that lack them. My placing of Timor in the southern hemisphere may be debatable, but even if it were placed on the northern margin of Tethys in a paleocontinental reconstruction, closer to China, the ostracod assemblage composition is quite different from the Anisian material from China described by Kristan-Tollmann (1983). It will be some time before we have enough data to begin to understand the constraints upon ostracod distribution patterns in the Triassic and, especially, in the Lower Jurassic of eastern Tethys.

IX
Speciation

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Geographical Isolation in Marine Species: Evolution and Speciation in Ostracoda, I

THOMAS M. CRONIN
U.S. Geological Survey, Reston, U.S.A.

ABSTRACT

This paper is the first of a series of studies investigating evolutionary processes in Ostracoda with emphasis on the relationship of speciation to climatic and tectonic events. Two types of geographical isolation and the resulting effects on ostracod populations are investigated: (1) Miocene to Holocene populations of *Hermanites transoceanica* from the Pacific and the Caribbean are examples of small, isolated founder populations; they were found to show a high degree of morphological stability despite frequent isolation of small populations on islands and atolls. (2) The formation of the Isthmus of Panama is a classic vicariant event and serves as a natural experiment to study rates of morphological divergence in large populations of ostracods of the same species, split from each other by a "dumbbell" type of allopatric separation. In species of many genera for which pre- and post-Isthmus material was examined (*Cativella, Occultocythereis, Touroconcha, Hermanites, Puriana,* and *Orionina*) morphological change has been minor or absent for 3.0 million years, since separation occurred. These studies indicate remarkable intraspecific stability under circumstances that, in theory, might have led to speciation. The results show ostracods are well-suited for studies of speciation due to the high degree of confidence that fossil species are equivalent to biological species.

INTRODUCTION

The processes of speciation lie at the heart of organic evolution. However, the various modes of speciation, particularly the geographical patterns and the rates of morphological change, are still debated by biologists (White, 1978; Templeton, 1980; Mayr, 1982; Charlesworth *et al.*, 1982) and paleontologists (Schopf, 1982; Gingerich, 1985; Gould and Eldredge, 1977). Furthermore, there is increasing interest in how extrinsic, abiotic factors might catalyze speciation events—what peculiar types of environmental change might cause speciation to occur and, significantly, when speciation does *not* occur. Understanding speciation will contribute to a host of unanswered questions including the controversy over the Red Queen hypothesis (Van Valen, 1973) and the stationary model of evolutionary change (Stenseth and Smith, 1984; Hoffman and Kitchell, 1984), and, in biogeography, dispersal versus vicariant theories of biological diversity and distribution (Nelson and Rosen, 1981; Young, 1984).

A PROSPECTUS FOR EVOLUTIONARY STUDIES IN OSTRACODA

This paper presents the background and initial results of a series of studies specifically designed to investigate speciation and morphologic stasis in marine Ostracoda. My ultimate objectives are 1) to assess the geographical classification of speciation by determining the relative frequency of types of allopatric, sympatric and parapatric speciation, 2) to estimate the relative frequency and circumstances of rapid and gradual morphological change, and 3) to assess the role of climate and tectonics in causing geographical isolation and speciation. The decision to conduct these studies stems from several trends emerging in evolutionary palaeontology. First, there are few case studies using fossil sequences that adequately address the question of speciation (Gingerich, 1985, Table 2). Of greater concern are questions about paleontologists' ability to identify species in fossil material (Schopf, 1980, 1982). It may be that Schopf's concern about fossil species reflects the approaches adopted by paleontologists, which may not be appropriate for answering current evolutionary questions, and not the fossil record itself. With few exceptions, paleontological studies of speciation have unnecessarily overemphasized stratigraphic completeness and high sampling resolution (Gingerich, 1985). Clearly, no stratigraphical sequence is complete, an idea known long before the comprehensive studies of Schindel (1980, 1982) and Dingus and Sadler (1982). Despite assertions by theorists that geographical coverage is of paramount importance (Eldredge and Gould, 1972; Schopf, 1982; Valentine and Jablonski, 1983), the apparent reluctance by paleontologists to delineate biogeographical patterns of speciation using fossils has been a major flaw in methodology. A stratophenetical approach is important, but in order to critically assess phylogenetic hypotheses, the geographical scope of a study should also be stated in the context of the paleogeography of the taxon (see Young, 1984). Climatically-induced shifts in species' biogeography,which form the empirical data for many paleoclimatologists, suggests that migration rather than evolutionary origination, accounts for the first stratigraphical appearances of most species in rock sections. It should therefore be stressed at the outset that comprehensive geographical coverage deserves as much priority as stratigraphical sampling interval.

Another topic is the question of abiotic, extrinsic factors and their effect on evolution. Widely divergent schools of evolutionary thinking hold that geographical isolation caused by climatic and tectonic events plays an important role in speciation. Some models of genetic changes during speciation postulate extrinsic events to initiate speciation (Carson, 1982). In advocating a cladistic approach, Eldredge and Cracraft (1980, p. 121) pointed out that isolation by geographical barriers is a mechanism for the disruption of "within species patterns of parental ancestry" but that isolation is not *prima facie* evidence for two species. Valentine and Jablonski (1983) discussed modes of speciation by small founder populations, large vicariant populations, and in clines and offered hypotheses about which mode might be more common in groups with various reproductive strategies and biogeographies.

Mayr (1982) has maintained that peripatric speciation is the most common type, but that speciation does not necessarily result from all founder events. However, we still cannot answer the question of which environmental events are more likely to result in speciation, which in extinction, and which in stasis. Is it true that a smaller population, when isolated, is more likely to "pass through the bottleneck of deleterious heterozygosity and reorganize itself genetically" (Mayr, 1982, p. 6)? If so, how can we identify such events in fossils and associate them with documented environmental changes? If sympatric and parapatric speciation are found to be common, do they support genetic models of speciation (Templeton, 1980) and relegate geography to a secondary role?

Climatic change represents an obvious candidate to explain evolutionary trends and has frequently been invoked as such (Cracraft 1982; Stanley, 1984; Valentine, 1984; Vrba, 1985). Indeed, it is almost always possible for a paleontologist to find a climatic event in the geological record to "associate" with a faunal or floral diversification or extinction. Yet simple age equivalence of a faunal and a climatic event does not imply a causal relationship. More rigorous testing of suspected abiotic influences on evolution is possible and necessary (Cronin, 1985 and below).

A third reason behind these studies is the unrealized potential of Ostracoda for understanding evolutionary processes. Ostracods have ideal characteristics for evolutionary research — sexual reproduction, abundantly fossilized carapaces with easily identified homologous features for morphometric study, and growth through moulting yielding a clear ontogeny (Cronin, 1985; Reyment, 1985). Many problems associated with assumptions of the "paleontologic approach" (see Eldredge and Novacek, 1985, p. 69, 70) are minimized by using ostracods. In addition to distinguishing ontogenetic and sexual dimorphism from other morphological variation, the ostracod carapace affords an opportunity to study the exoskeleton of the whole organism, not just a single part, such as the vertebrate tooth. Mention should also be given to important new studies, among them papers on ostracod histology and morphology (Okada, 1982), the relation between ecology, reproduction and morphology (Kamiya, this volume), and various aspects of polymorphism (Reyment, 1985; Abe, 1983; Ikeya and Ueda, this volume), that together boost our confidence that biological species can be recognized from carapace morphology. In an important paper, Kamiya (this volume) has demonstrated how distinct carapace shapes in two related extant species of *Loxoconcha* directly reflect different copulatory positions in different microhabitats. One species is phytal in habitat, and requires a rounded posterior shape and circular-oval lateral shape to copulate on the plants; the other species is flattened posteriorly and rectangular laterally to copulate on the sand bottom. Therefore, not only does carapace shape distinguish two species but it is functionally related to the primary means of distinguishing two species—the criterion of reproductive isolation.

TESTING EVOLUTIONARY HYPOTHESES USING FOSSILS

While some authors have emphasized species diversity and overall faunal patterns to test evolutionary laws (Hoffman and Kitchell, 1984), my approach focuses on species and monophyletic groups for which there is strong evidence for a common ancestor. I agree with Eldredge and Novacek (1985) that cladistic and paleontological methodologies of phylogentic analysis differ from one another more in style than in substance, and that both are confronted with similar subjective decisions. In my ostracod studies, relationships among species are known with varying degrees of confidence that will be stated in each case. While subjectivity and judgement will always play a role, testing genealogical hypotheses is treated as an iterative process, in which securing new modern and fossil material confirms or refutes suspected phylogenies.

Three points about the approach should be stressed: [1] As stated explicitly by more and more evolutionists (Stenseth and Smith, 1984; Vrba, 1984), the fossil record provides a unique, albeit imperfect, opportunity to test hypotheses about the influence of environment on organisms. Each study in this series of papers represents an effort to understand the evolutionary history of a species or monophyletic group of species, selected on the basis of their ecology, biogeography and exposure to known climatic or tectonic changes. One school of vicariance biogeography has criticized the role of fossils in biogeography and systematics, stating "recent distributions . . . provide the only unequivocal data of biogeography" (Patterson, 1981, p. 464). To test vicariance versus dispersal explanations of why a taxon lives in an area, some propose seeking concordant biogeographical trends in separate lineages subjected to the same vicariant events (Rosen, 1978).

However, different taxa will not necessarily respond in similar ways to the same extrinsic event (see Endler, 1982; Young, 1984). Although methodologically sound in trying to falsify hypothesized genealogies, this vicariant-cladistic approach tends to ignore valuable geologic evidence for environmental change.

The fossil record itself can be used both to test phylogenetic hypotheses (Young, 1984), and, more importantly, hypotheses about the causal relationships between organisms and their environments. In one example, I documented a period of speciation in the ostracod *Puriana*, which I hypothesized was caused by gradual climatic and oceanographical change along the eastern United States about 4 to 3 million years ago (mya) (Cronin, 1985). This idea was tested in three ways: 1) by examining *Puriana*'s response to cyclic climatic change, considered by palaeoclimatologists to be qualitatively distinct from gradual climatic change (no speciation events were found, Cronin, 1985); 2) by examining the entire endemic ostracod fauna off the eastern United States for evolutionary first appearances during the last 5 million years to see if other genera diversified when *Puriana* did (about 50% out of 127 ostracod species originated during this time, Cronin, in press a); 3) studies have been started on ostracods from the western north Pacific near Japan where a distinct ostracod fauna was subjected to similar climatic changes in temperate and subtropical climatic zones to those in the western North Atlantic. In summary, for some extant marine groups having a fossil record, paleobiogeography is known as well as modern distributions so that both hypotheses about genealogical relationships and hypotheses about the causal relationship between speciation (vicariant and dispersal) and extrinsic events can be tested and falsified.

[2] I do not share Schopf's (1982) pessimism about identifying biological species from fossilized hard parts. With the exception of sibling species, distinguishing among species of ostracods is possible as demonstrated by a growing literature (*e.g.*, Cronin, 1985, and below; Reyment, 1982, 1985; Abe, this volume; Ikeya and Tsukagoshi, this volume) provided one has adequate sample size and geographical coverage. [3] I place emphasis on intraspecific variability, particularly by comparisons among completely or partially isolated populations. Unless morphological variability within a species is understood over its geographical range, phylogenetic relationships among related species cannot be determined.

A wide range of environmental changes will be considered in these studies including: (1) cyclic and long-term, gradual climatic changes, (2) sea level changes, (3) vicariant geographic isolation of large populations, (4) founder events isolating small populations, (5) relict populations and others. The first set of studies will focus on shallow water marine taxa, and they will hopefully expand to deep water marine and fresh water forms in the future.

This first study, appropriately published in the Proceedings of the Ninth International Ostracod Symposium, whose theme was evolutionary biology, examines two major categories of geographical isolation. First, isolation during the Cenozoic of small populations of shallow water species on remote Pacific atolls and islands. In theory, such isolation could lead to peripatric speciation (sensu Mayr, 1982), which is equivalent to type 1b speciation of Bush (1975). Conversely, classic dumbbell isolation of large populations by the development the Isthmus of Panama about 3 mya might theoretically lead to allopatric speciation, type la of Bush (1975). This important distinction between types of allopatry was emphasised by Mayr (1982) because of his hypothesized inverse relationship between population size and rate of divergence.

GEOGRAPHICAL ISOLATION ON OCEANIC ISLANDS AND ATOLLS

Benthonic marine ostracods have no planktotrophic larval stage and therefore dispersal of shallow water species across deep water is almost certainly passive. This situation is similar to that of a terrestrial organism passively dispersed to small islands, but differs from that in some marine gastropods having larval dispersal and gene flow among dispersed populations (Scheltema, 1971). Study of the relationship between Atlantic/Caribbean and Pacific marine ostracods reveals interesting examples of taxa that disperse over long distances and show very little intraspecific variability in carapace morphology among widely separated populations. However, taxonomic studies of faunas from different regions have frequently not recognised the strong affinities of isolated populations. This may reflect an unfamiliarity with the literature from other regions or unstated assumptions by taxonomists about the endemic nature of shallow water ostracods. The evidence presented below shows the conspecific nature of many small, widely dispersed populations of a tropical species.

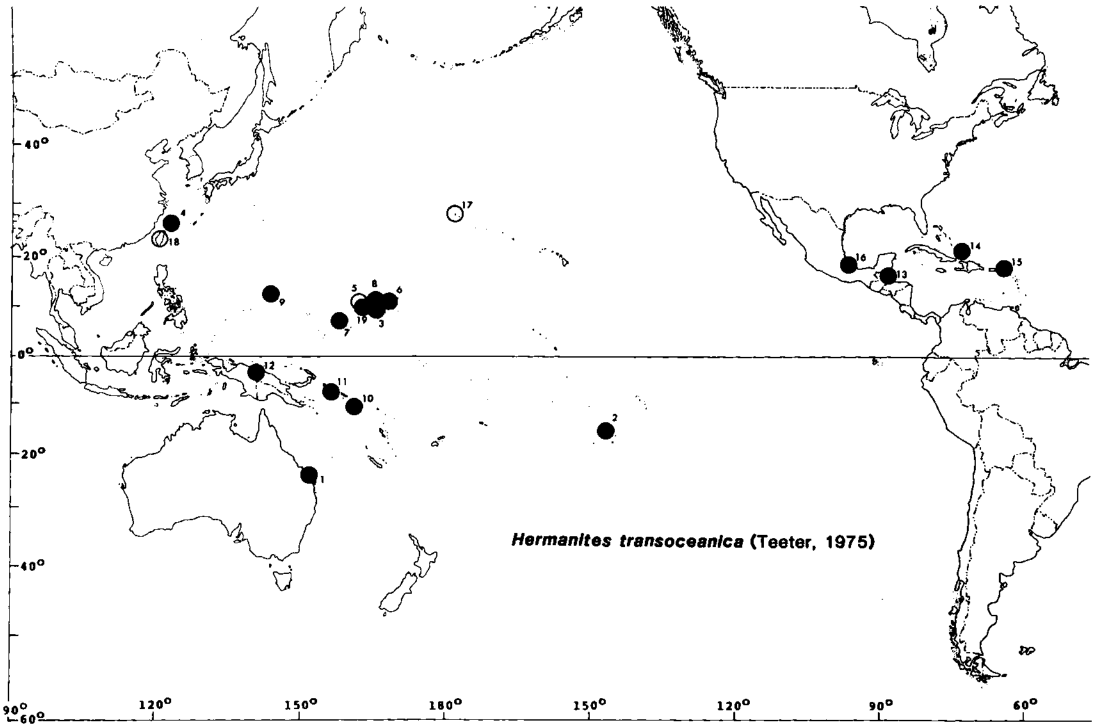
Hermanites transoceanica Teeter, 1975

Teeter (1975) described the extant species *Hermanites transoceanica* from the Belize carbonate platform near eastern Central America, and noted its wide distribution in the Pacific off New Guinea and Hawaii. Holden (1976) identified specimens of the same species from the Pleistocene of Midway Island as *Jugosocythereis lactea* (Brady, 1866), and Hartmann (1981) described the new extant species *Quadracythere insulardeaensis* from eastern Australia based on specimens that are also conspecific with Teeter's species. Bonaduce *et al.*, (1980) described *Quadracythere auricolata*

TABLE 1—LOCALITIES OF *Hermanites transoceanica* TEETER, 1975†

1. Eastern Australia (Hartmann, 1981)
2. Rangiroa Atoll (Tuamoto Archipelago) (Hartmann, 1984)
3. Kwajalein Atoll (Marshall Islands), this paper
4. Okinawa Island (Ryukyu Islands), this paper
5. Enewetak Atoll (Marshall Islands), this paper
6. Rongelap Atoll (Marshall Islands), this paper
7. Ponape, this paper
8. Bikini Atoll (Marshall Islands), this paper
9. Guam (Mariana Islands), this paper
10. Guadalcanal (Solomon Islands), this paper
11. Shortland Island (Solomon Islands), (Titterton, 1985)
12. New Guinea, (Teeter, 1975)
13. Belize (Central America), (Teeter, 1975)
14. Bahamas, this paper
15. Virgin Islands (St. Thomas), this paper
16. Vera Cruz (Mexico), (Krutak, 1982)
17. Midway Island (Hawaiian Islands), (Holden, 1976) Pleistocene
18. Taiwan (Hu, 1981) Pliocene-early Pleistocene
19. Enewetak Atoll, Marshall Islands, this paper, Miocene-Pleistocene
20. #Pinaki and Niau, (Tuamoto Islands), this paper
21. #Pago Pago, (Samoa Islands), this paper
22. #Gulf of Aqaba, Red Sea, (Bonaduce *et al.*, 1980)

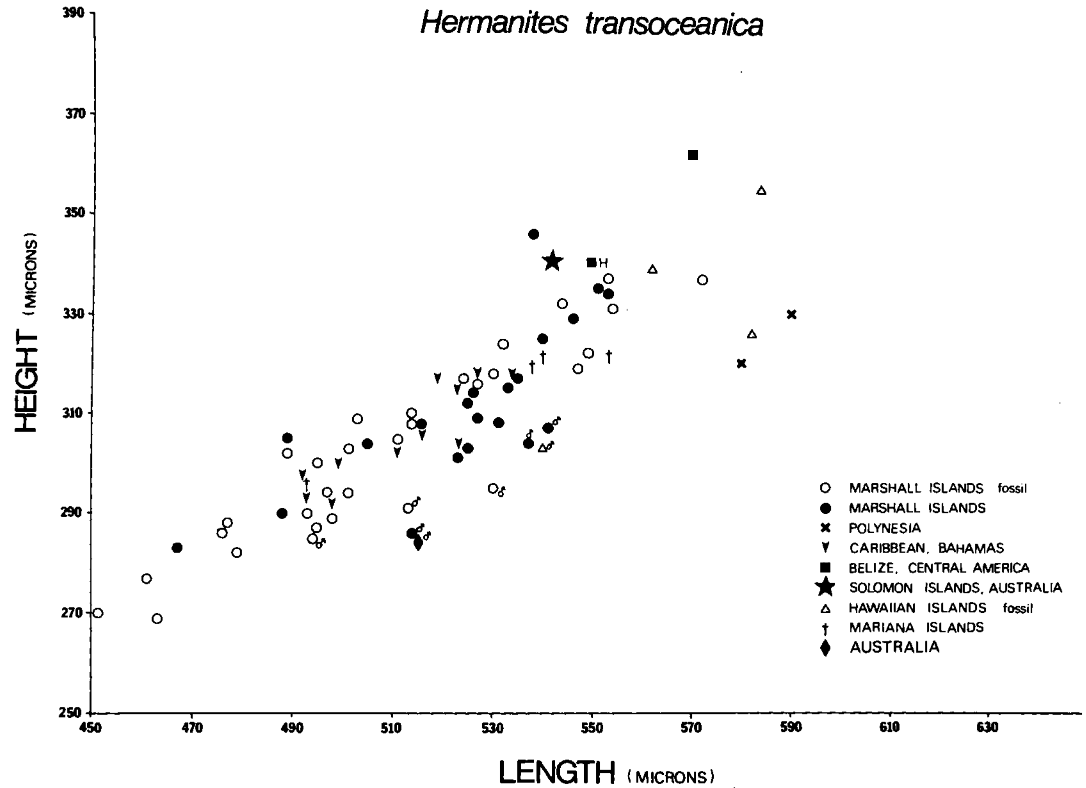
†: Numbers refer to map in Text-fig. 1. #: Not shown in Text-fig. 1. All samples are modern except 17, 18 and 19. Locality data can be obtained from the author.



TEXT-FIG. 1—Localities yielding *Hermanites transcoceanica* Teeter, 1975. Fossil samples are indicated by open circles, modern samples by solid circles (See Table 1 for list of localities). Since this paper was first written, this species has also been identified in samples from Pinaki and Niau, Tuamoto Islands, South Pacific, and from Pago Pago, American Samoa, from Truk, Majuro and Arno in Micronesia, and in the paper by Bonaduce *et al.*, (1980) on ostracodes from the Gulf of Aqaba, Red Sea.

from the Gulf of Aqaba in the Red Sea for a species that is conspecific with *H. transoceanica.* Similarly, Hu (1981) described the species *Radimella microreticulata* from the Maanshan Mudstone of southern Taiwan, and although citing Teeter (1975), Hu did not identify these Asian forms as conspecific with *H. transoceanica,* although they are clearly so.

To study *H. transoceanica* in detail, I assembled fossil and modern collections from shallow carbonate environments in the western equatorial Pacific and Caribbean and, where possible, examined material from published studies and theses. Selected localities yielding *H. transoceanica* are shown in Text-fig. 1 and are listed in Table 1. Text-fig. 2 plots carapace length versus height for measured specimens and plots length and height of holotypes using measurements given by Teeter (1975) and for Australian material from Hartmann (1981). As suggested by Teeter (1975), *H. transoceanica* includes widely dispersed populations from a single, morphologically well-defined species. The length/height plot shows the range of carapace sizes for fossil specimens (Miocene-Pleistocene) from the Marshall Islands is about the same as that from recent populations from the same region. Measurements taken from Holden (1976) for fossils from Midway, and from Hartmann (1984) for modern material from Polynesia show specimens slightly larger, but not outside the expected range for a species. Sexual dimorphism is weak in this species and the few specimens believed to be males are indicated. Carapace ornamentation shown in Plate 1 reveals a striking degree of morphological stability over time (at least 6 million years) and geographical area. The fossil record of this species shows that it lived in the Marshall Islands from the late Miocene until modern times, on Taiwan during the late Pliocene or early Pleistocene, and on Midway during the Pleistocene.

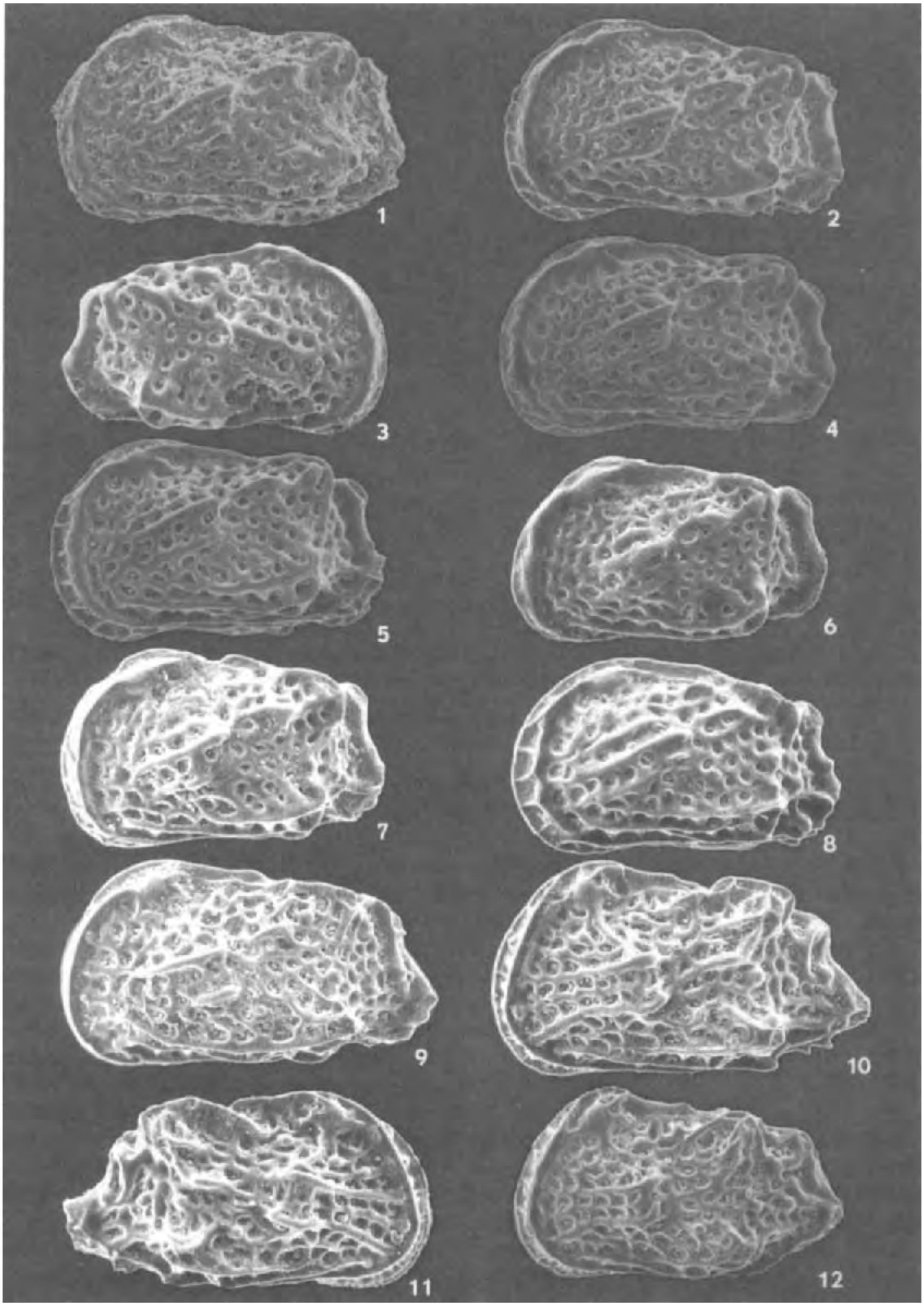


TEXT-FIG. 2—Plot of carapace length versus height of *Hermanites transoceanica* Teeter, 1975. Specimens presumed to be male are indicated with the male symbol. Measurements of the holotype of *H. transoceanica* from Belize were taken from Teeter (1975). Hartmann (1981) gives ranges of 500–530 microns and 280–290 microns as measurements for length and height for *Quadracythere insulardeaensis* from Australia, and the midpoint of these values was plotted.

The presence of this species in the Carribbean suggests it probably lived in this region before about 3.0 mya when the formation of the Isthmus of Panama separated Atlantic and Pacific populations. Specimens from Belize, the Virgin Islands and the Bahamas (Plate 1) cannot be distinguished from Pacific forms. Its presence in the Red Sea, however, leaves the remote possibility of westward migration across the Atlantic during the last few million years.

Populations of *H. transoceanica* were compared with two sympatric species, *H. parviloba* (Hu, 1981), believed to be a separate lineage, and *H. mooneyi* n. sp., the only known descendant species evolving from *H. transoceanica*. Text-figure 3 plots length versus height for these three species showing the similar dimensions of *H. transoceanica* and *H. mooneyi*. However, Plate1 shows *H. mooneyi* differing significantly from *H. transoceanica* in the development of surface ridges and reticulation.

The results for *H. transoceanica* show that at least 10 times during the Neogene, and probably dozens more, populations became established off remote islands or in isolated atolls, but maintained morphological stability for several hundred thousand to several million years. Since the Miocene, only one species has evolved from ancestral *H. transoceanica*. Although short-lived species may be as yet undiscovered, the evidence from well-studied fossil faunas from Midway (Holden, 1976), Enewetak (Cronin, unpublished), Taiwan (Hu, 1984 and references), and Okinawa (Nohara and Tabuki, 1985) shows no evidence for any. If new species had evolved during the Pliocene or Pleistocene, one would expect to find living representatives in the many well-known tropical Pacific faunas.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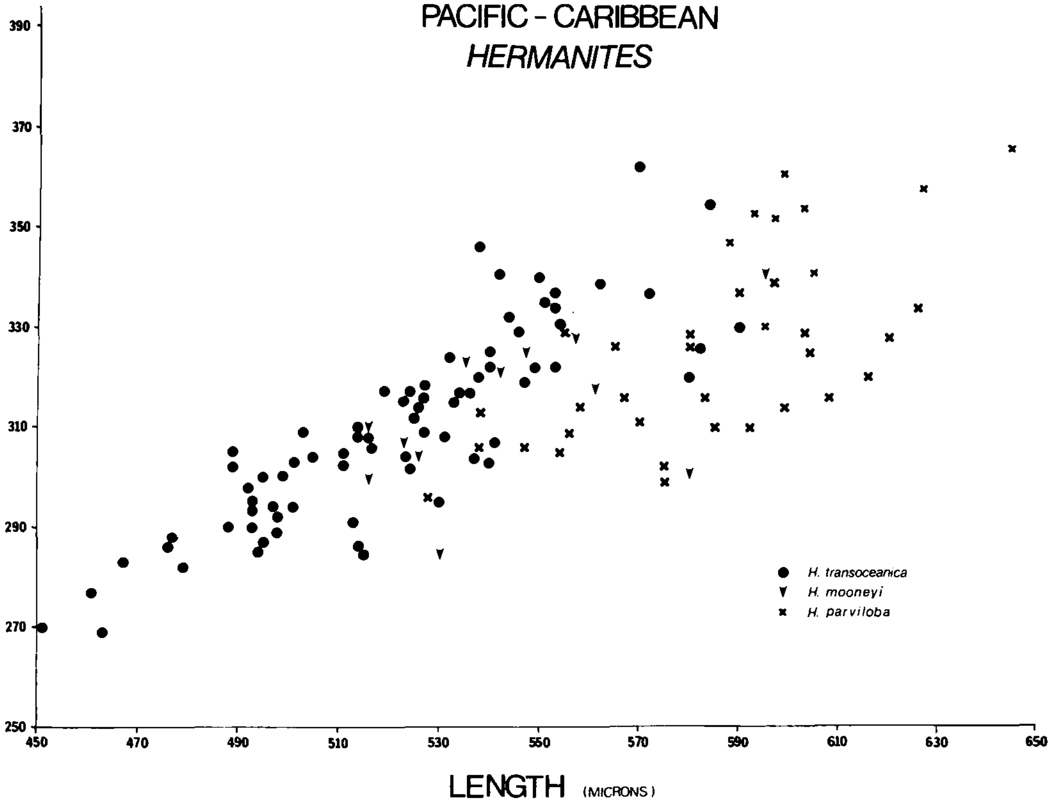


TEXT–FIG. 3—Plot of carapace length and height for three species of *Hermanites*. The plots of *H. transoceanica* are the same as in TEXT–FIG. 2. See text for discussion.

It is appropriate to consider mechanisms to account for the dispersal of *H. transoceanica*. This species could not have actively migrated across deep water barriers as it does not have a planktotrophic larval stage. Dispersal was almost certainly passive and there are several possible mechanisms which are summarized by Teeter (1973). The encysted (double-walled) eggs of fresh water ostracods can withstand dessication and therefore, have probably been dispersed by migratory birds, either on their feet, trapped in feathers or in the intestinal tract (Sandberg, 1964).

PLATE 1—Figs. 1–8. *Hermanites transoceanica* Teeter, 1975. 1. Lateral view, left valve, female carapace (USNM 401834, Holocene, Guam). ×99. 2. Lateral view, left valve, female (USNM 401835, Holocene, St. Thomas, Virgin Islands). ×99. 3. Lateral view, right valve, female (USNM 401836, Holocene, Rongelap Atoll, Marshall Islands). ×99. 4. Lateral view, left valve, female carapace (USNM 401837, Holocene, Acklins Island, Bahamas). ×99. 5. Lateral view, left valve, female carapace (USNM 401838, Holocene, Enewetak Atoll, Marshall Islands). ×99. 6. Lateral view, left valve, female (USNM 401839, Holocene, Bikini Atoll, Marshall Islands). ×99. 7. Lateral view, left valve, female (USNM 401840, late Pliocene, Enewetak Atoll, Marshall Islands). ×99. 8. Lateral view, left valve, female carapace (USNM 401841, middle to late Miocene, Enewetak Atoll, Marshall Islands). ×99.

Fig. 9. *Hermanites parviloba* (Hu, 1981). Lateral view, left valve, female (USNM 401842, early Pleistocene, Enewetak Atoll, Marshall Islands). ×99.

Figs. 10–12—*Hermanites mooneyi* Cronin n. sp. 10. Lateral view, left valve, female (Holotype, USNM 401843, Pliocene, Enewetak Atoll, Marshall Islands). ×99. 11. Lateral view, right valve, female carapace (Paratype, USNM 401844, Pliocene, Enewetak Atoll, Marshall Islands). ×99. 12. Lateral view, left valve, ?male (Paratype, USNM 401845, late Pleistocene, Enewetak Atoll, Marshall Islands). ×99.

Teeter (1973) considers avian transport unlikely for marine species because (1) eggs of marine species are single-walled and are not known to withstand dessication; (2) many species live in the subtidal zone and have a very small probability of contact with birds; (3) those tropical and subtropical ostracod species that are geographically widespread are latitudinally restricted over broad oceanic areas that are not related to north/south continental pathways of migratory birds.

Teeter (1973) similarly dismisses wind and fish as agents for widespread dispersal because of the vulnerability of the single-walled egg to destruction.

The possibility that transoceanic shipping is the cause of widespread distributions of some species has been discussed (Teeter, 1973), but an increasing number of species now have fossil records back to the Miocene and Pliocene showing they were widely dispersed millions of years ago. Teeter considers drifting on aquatic plants the most probable means of dispersal and notes the occurrence of living ostracods on the marine alga *Turbinaria,* which lives near tropical coasts, and on *Sargassum* near the Florida Keys. Sohn (1954) also reported benthonic marine ostracods living on *Sargassum* that had drifted near Cape Cod, Massachusetts. Surface water currents therefore could easily carry living ostracods on algae to new habitats on atolls and tropical islands. Another passive mechanism is transport on drifting pumice rafts (Newton and Bottjer, 1985), but there are no data on ostracods living on floating pumice. At present it is unclear how frequent these dispersal events were and whether they were frequent enough to postulate continued, albeit occasional, genetic interchange among seemingly isolated populations. In my opinion, the probabilities are low that significent genetic interchange occurred between Pacific atoll populations over the millions of years of the species history.

In summary, if the taxonomic literature from the last decade were taken at face value, populations of *H. transoceanica* would be recorded as five species in four separate genera, *Radimella, Jugosocythereis, Hermanites,* and *Quadracythere.* Actually, intraspecific stasis, both in the sense of species integrity over geographic range (Van Valen, 1982) and in terms of temporal stability (Eldredege and Gould, 1972) have characterised this single species despite many opportunities thought to be conducive to lineage splitting.

VICARIANT ISOLATION BY THE ISTHMUS OF PANAMA

During the middle Pliocene 4 to 3 mya, the Isthmus of Panama formed as a barrier preventing interchange between Pacific and Atlantic/Caribbean marine faunas (Keigwin, 1978; Quinn and Cronin, 1984). This event represents a classic dumbbell allopatric split of large populations of tropical species. Indeed, Vrba (1985) has cited it as a potential natural experiment for testing the punctuated equilibrium model and Valentine and Jablonski (1983) pointed out that identifying gradual patterns of change resulting from vicariant events such as the Isthmus would strengthen evidence for punctuational patterns found elsewhere.

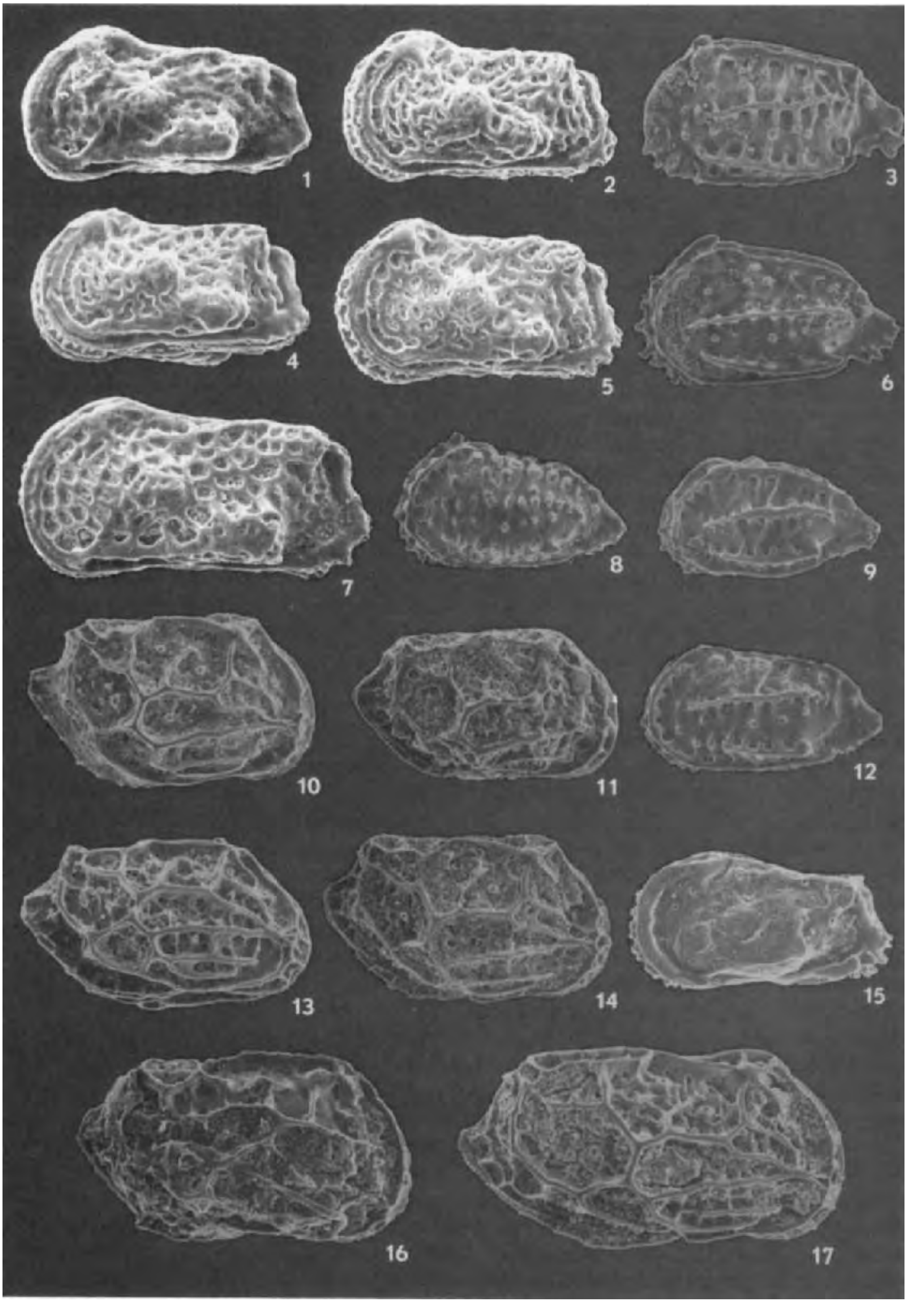
Ostracods from the Caribbean and western Atlantic are better known than are eastern Pacific faunas, but strong affinites between populations from the two sides have long been known. In a preliminary report, Swain et al. (1964) identified *Orionina vaughani* (an "Atlantic" species) from the Gulf of California, but later Swain (1967) renamed it *O. pseudovaughani* for Pacific populations. In a remarkable coincidence, Pokorny (1970) and Hazel (1977) independently identified a unique species of *Caudites* having asymmetrical ornamentation of left and right valves and both called it *asymmetricus* (Hazel's name was *nomen nudem*). Hazel's material was from the Pleistocene of South Carolina, Pokorny's was Holocene from the Galapagos. Subsequently, Hazel (1983) formally described the Atlantic form as *C. paraasymmetricus* citing slight differences in the location of the caudal process and position of the carinae. In ostracod faunas from the Clipperton Islands (Allison and Holden, 1971) and the Galapagos (Bate *et al.*, 1981) similarities with the Caribbean have also been noted for species of *Paracytheridea, Neocaudites, Cytherelloidea,* and *Caudites.* Carreño (1985) described Miocene-Pliocene ostracods from Maria Madre Island, Mexico and also noted strong affinites in species of *Loxocorniculum, Cativella, Puriana,* and *Triebelina.*

In the majority of cases, while acknowledging morphological affinities between Pacific and Atlantic populations, most authors either described new species based on relatively minor differences or postulated possible post-Isthmus faunal interchange to explain the similarities. I call this the "pacifica-atlantica" tendency and suspect it reflects a strong bias by many that geographical isolation should lead to allopatric speciation. There seems to be a reluctance to call populations from opposite sides conspecific. Yet on morphological grounds alone, splitter and lumper alike would not hesitate to call two populations conspecific if they were not separated by a land barrier and thousands of miles.

Resolving questions of species identification and rates of morphological divergences are extremely important. Consequently, to test whether many Pacific and Atlantic/Caribbean populations are really conspecific, I collected or obtained from colleagues Neogene material from numerous formations in southern California and Baja, Mexico to compare pre- and post-Isthmus populations of genera found on both sides of the Isthmus. In this way, the monophyletic relationships of descendant populations for each lineage can been demonstrated by establishing that a single contiguous (presumed "panmictic") population existed before the Isthmus formed. New Pacific material includes the Imperial Formation (Quinn and Cronin, 1984), a unit long known for containing mollusc and other macroinvertebrates with "Caribbean" affinities, the Santa Barbara and Pico Formations (Cronin *et al.*, 1983), and in Baja, the Loreto, Tirabuzon (Carreño, 1981), Salada, Ysidro, Boleo, and San Ignacio Formations. Material from 10 Caribbean formations and at least 20 more formations from the southeastern U.S. was examined. The following paragraphs briefly summarize the results for key species whose populations were split by the Isthmus, but which in most cases shown negligible morphological change during the last 3 mya.

Cativella navis Coryell and Fields, 1937: This species is known from late Miocene to Holocene deposits in numerous localities in the Caribbean, Central America, Atlantic Coastal Plain and Baja, Mexico (Bold, 1974). In addition to many published occurrences, *Cativella navis* was found in the Tirabuzon and Loreto Formations and modern sediments off La Paz (Baja, Mexico), the Gatun Formation (Panama), the subsurface Pliocene of south Florida, the "*Ecphora*" zone of the Jackson Bluff Formation (Florida), the Bowden Formation (Jamaica) and the Raysor Formation (South Carolina). It is characterised by its small size three longitudinal ridges, the ventral one sometimes having perforations. The medial ridge sometimes consists of a row of tubercles and can be slightly curved or straight (Pl. 2, fig. 8). This species is easily distinguished from *C. pulleyi* Teeter, 1975 and *C. semitranslucens* Couch, 1949 by its size, shape and ornamentation.

From examination of intra- and inter-population variability in Atlantic, Caribbean and Pacific forms, I consider the following forms conspecific with *C. navis: C. dispar* Hartmann, 1959; *C. semitranslucens* and *C. unitaria* of Carreño (1985); *C.* sp. A of Valentine (1976); *C. dispar* and *Costa*? *variabilocostata seminuda* of Swain (1967, Pl. 3, figs. 2a,b, 14). Plate 2 illustrates 5 specimens that show the similarity of widely distributed populations. *Cativella navis* therefore represents a cohesive group of populations showing very slight morphological variation among them. Before the Ithsmus of Panama formed, and during its formation, early-middle Pliocene populations lived in Baja, Mexico (Loreto, Tirabuzon Formations) and the Tres Marias Islands on the Pacific side, in Central America (Gatun Formation), and in the Atlantic/Caribbean/Gulf of Mexico (Bowden, Conception, Aquequexquite Formations, Pinecrest Member of the Tamiami Formation, and "*Ecphora*" zone of the Jackson Bluff Formation). Today, modern populations are still known from the Pacific in the Gulf of California, off the west coast of Baja, and off El Salvador, and in the Caribbean (see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Machain-Castillo, 1985). In summary, the formation of the Isthmus of Panama divided large, widespread populations of *Cativella navis*, but the resulting geographical isolation had little, if any, effect on carapace morphology in the ensuing 3.0 million years.

Occultocythereis angusta van den Bold, 1963: This species is widespread in the Caribbean from the Miocene to Holocene including many pre-Isthmus formations (see Bold, 1977; Teeter, 1975). New material from the Marshall Islands shows that this species inhabited the western Pacific from the late Miocene to Pliocene (Plate 2), indicating pre-Isthmus interchange between Caribbean and Pacific. Holden (1976, Pl. 12, figs. 22, 23) illustrated an *Occultocythereis* from the Miocene of Midway that is probably conspecific with *O. angusta.*

Touroconcha lapidiscola (Hartmann, 1959): From the literature, it would appear that the genus *Touroconcha* includes many species and has a confusing taxonomy (see Bate *et al.*, 1981 and Machain-Castillo, 1985). To clarify relationships among populations, I examined pre- and post-Isthmus specimens from the Pacific (Imperial Formation, California, Pliocene of Ecuador, off La Paz, Mexico) and Caribbean/Atlantic (modern near Hispañola and the Virgin Islands, Pleistocene subsurface of Florida, Bowden Formation of Jamaica). *T. lapidiscola* appears to be a species with significant interpopulation polymorphism in size and carapace ornamentation (Pl. 2, figs. 10, 11, 13, 14, 16, 17). As in the related genus, *Loxoconcha,* variability in carapace size and ornamentation is the rule and is probably related to evironmental conditions. I agree with Machain-Castillo (1985) that *T. mosqueraensis* Bate *et al.*, 1981 is conspecific with *T. lapidiscola*, but *T. emaciata* (Swain) is a distinct species endemic to the Gulf of California and the Pacific side of Baja, Mexico.

It is more difficult to assess morphological changes in *T. lapidiscola* during the last 5 million years due to its polymorphic nature. Most evidence points to a slow rate of morphological divergence since separation by the Isthmus. For example, Pliocene specimens from the east side of the Isthmus (Pl. 2, fig. 17 in Machain-Castillo, 1985) are virtually identical with modern specimens from the Gulf of Panama, the Galapagos, and off Hispañola. It should be noted that *T. emaciata* split from ancestral populations near the northern part of its Pacific range. This speciation, however, probably did not result from the formation of the Isthmus, but instead from "peripheral isolates" unrelated to main populations to the south and in the Caribbean.

Hermanites hornibrooki Puri, 1960: Bold (1983) has carefully documented the stratigraphical

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PLATE 2—Figs. 1, 2, 4, 5. *Hermanites hornibrooki* Puri, 1960. 1. Lateral view, left valve, male carapace (USNM 401846, early Pliocene, Maria Madre Island, Mexico). ×99. 2. Lateral view, left valve, female carapace (USNM 401847, Pliocene (subsurface), South Florida). ×99. 4. Lateral view, left valve, female carapace (USNM 401848, Holocene, north shore, Dominican Republic.). ×99. 5. Lateral view, left valve, female carapace (USNM 401849, Holocene, Belize). ×99.

Fig. 7—*Hermanites tricornis* Swain, 1967. Lateral view, left valve, ?female carapace (Specimen lost after photography, Holocene, La Paz, Baja Mexico). ×99.

Figs. 3, 6, 8, 9, 12. *Cativella navis* Coryell and Fields, 1937. 3. Lateral view, left valve, female carapace (USNM 401850, Pliocene, Tirabuzon Formation, Baja, Mexico). ×72.5. 6. Lateral view, left valve, female carapace (USNM 401851, Pliocene (subsurface), South Florida). ×72.5. 8. Lateral view, left valve, ?male carapace, morphotype showing rows of tubercles (USNM 401852, Pliocene (subsurface), South Florida). ×72.5. 9. Lateral view, left valve, female carapace (USNM 401853, late Miocene-Pliocene, Gatun Formation, Costa Rica). ×72.5. 12. Lateral view, left valve, female carapace (USNM 401854, late Miocene-early Pliocene, Loreto Formation, Baja Mexico). ×72.5.

Fig. 15. *Occultocythereis angusta* Bold, 1963. Lateral view, left valve, female carapace (USNM 401855, Pliocene, Enewetak Atoll, Marshall Islands). ×99.

Figs. 10, 11, 13, 14, 16, 17—*Touroconcha lapidiscola* (Hartmann, 1959). 10. Lateral view, right valve, female (USNM 401856, Pliocene, Ecuador). ×99. 11. Lateral view, right valve, ?female carapace (USNM 401857, Pleistocene (subsurface), Florida). ×99. 13. Lateral view, right valve, female carpace USNM 401858, Holocene, south shore, Dominican Republic). ×99. 14. Lateral view, right valve, female (USNM 401859, Pliocene, Bowden Formation, Jamaica). ×99. Fig. 16. Lateral view, right valve, female (USNM 401860, late Miocene, Imperial Formation, southern California). ×99. 17. Lateral view, right valve, male (USNM 401861, late Miocene-early Pliocene, Limon Formation, Costa Rica). ×99.

range of this common species to be Pliocene to Holocene throughout much of the Caribbean. I have recently found this species off Hispañola, the Florida Keys and for the first time in the Pacific, in Pliocene deposits from the Tres Marias Islands, Mexico (Pl. 2, fig. 1) in material kindly provided by Dr. A. L. Carreño. This latter occurrence demonstrates the existence of pre-Isthmus contiguous populations. Since the land barrier formed, populations in the Atlantic/Caribbean region have maintained morphological stability, but the Pacific populations are extinct. One apparent descendant from Pacific populations is *H. tricornis* (Swain, 1967) (=*Lucasocythere sanmartinensis* Swain and Gilby, 1974). Plate 2, figure 7 is a specimen of *H. tricornis* from modern sediments off Baja showing the morphological similarity to *H. hornibrooki.* Thus in this case, the ancestral species survived only on the Atlantic side while Pacific populations evolved to form a new species.

Other genera such as *Orionina,* (see Cronin and Schmidt, this volume) have species that lived in the Atlantic/Caribbean and Pacific before the Isthmus, but display no demonstrable change since separation. Although space does not allow discussion, two other species considered probable relicts of pre-Isthmus populations should be noted: *Paracytheridea tschoppi* Bold, 1946, and *Neocaudites subimpressus* (Edwards, 1944), (which is synonymous with *N. pacifica* (Allison and Holden, 1971); *N. scottae* Teeter, 1975).

Other genera are presently under more detailed study to contrast the effects of the Isthmus with other extrinsic events such as sea level and temperature changes. In the case of *Puriana* (Cronin, 1985; in press b.), the geographical ranges of some species extend north along the continental shelves off the western and eastern United States where the effects of climatic changes can be tested and compared with the effects of separation by land barriers.

SYSTEMATIC DESCRIPTION

Genus HERMANITES Puri, 1955

Type-species.—Hermania reticulata Puri, 1954

Remarks.—Because the muscle scars of the type species *H. reticulata* are not known, the distinction between this genus and *Quadracythere* Hornibrook, 1952 and the assignment to a subfamily are unclear. *H. transoceanica* differs from some other species of *Hermanites* in having four undivided adductor scars and two frontal scars, one of which is V-shaped. However, I have observed in single populations, specimens having a V-shaped frontal and others with a split "V" for a total of three frontal scars. Supraspecific taxonomic questions are beyond the scope of this paper.

HERMANITES TRANSOCEANICA Teeter, 1975
(Pl. 1, figs. 1–8).

Hermanites transoceanica TEETER, 1975, p. 450, figs. 11o–q, 12h; KRUTAK, 1982, p. 267, pl. 3, figs. 12, 13.
Jugosocythereis lactea (Brady, 1866): HOLDEN, 1976, p. F25, pl. 3, figs. 22, 23, pl. 12, figs. 15–17.
Quadracythere auricolata BONADUCE, MASOLI, MINICHELLI, and PUGLIESE, 1980, p. 152, pl. 5, figs. 1–4.
Radimella microreticulata HU, 1981, p. 90, pl. 1, figs. 4, 9, 10, text-figs. 8c, d.
Quadracythere insulardeaensis HARTMANN, 1981, p. 108, pl. 6, figs. 1, 2, text-figs. 21–25; HARTMANN, 1984 (partim), p. 126, pl. 5, figs. 1–5, text-figs. 37–41 (not pl. 5, figs. 6, 7 = *H. mooneyi* n.sp.)

Remarks.—Figure 1 shows some known localities of *H. transoceanica.* Holden (1976) also reported this species as *J. lactea* (Brady, 1866) from the Line Islands, Fiji, New Caledonia, the Pleistocene to Holocene of Funafuti, and Australia (Chapman, 1914).

HERMANITES MOONEYI n.sp.
(Pl. 1, figs. 10–12).

Quadracythere insulardeaensis HARTMANN, 1984 (partim), p. 126, pl. 5, figs. 6, 7.

Etymology.—After Glen Mooney (McClelland Engineers, Inc.), who drilled the cores at Enewetak from which the type material came.

Types.—Holotype, a female carapace, USNM 401843 (Pl. 1, fig. 10. L = 596 μm, H = 342 μm), from 692 ft (Pliocene) in a core from Enewetak Lagoon, Marshall Islands. Paratypes, a female carapace, USNM 401844 (Pl. 1, fig. 11) from the same sample as the holotype, and a male left valve, USNM 401845 (Pl. 1, fig. 12) from the late Pleistocene in a core XEN-3 from Engebi Island on the north end of Enewetak Atoll, Marshall Islands (see Ristvet *et al.*, 1978).

Diagnosis.—Carapace surface reticulate having two anteromedian ridges running from muscle tubercle; posterodorsal node raised, strongly overlapping dorsal margin; posterior end with sharp, pointed caudal process.

Description.—In lateral view, the carapace is subrectangular, tapering slightly posteriorly, having an irregular dorsal margin, a pointed and spinose posterior and an obliquely rounded anterior. The anterior margin has numerous small denticles, the posteroventral margin has 3 or 4 larger denticles. Primary surface ornamentation consists of reticulation; there are a few small tubercles at normal pores particularly in the posterior region. The posterodorsal and posteroventral nodes are strongly produced and overlap the margins. Two weak longitudinal ridges are developed on the subcentral muscle platform and extend anteriorly to the anterior marginal rim. The eyespot is well-developed in the anterodorsal region and raised above the dorsal margin. Males are slightly lower and longer than females. There are four almost vertical adductor muscle scars, the hinge is holamphidont and the radial pore canals are straight and simple. Juveniles are characterized by the extremely well developed posterodorsal and posteroventral nodes.

Remarks.—A specimen illustrated by Hartmann (1984) as a juvenile *Q. insulardeaensis* (Pl. 5, fig. 6) appears to be an adult of *H. mooneyi*. The two species are consistantly distinct in ornamentation and shape.

Dimensions.—Twelve specimens from Enewetak were measured (N = 12). Mean carapace length: 544.4 μm, standard deviation: 25.2, observed range: 516.3–596.0 μm. Mean carapace height: 314.0 μm, standard deviation: 15.5, observed range: 285.1–329.7 μm.

Occurrences.—Pliocene to Recent from Enewetak Atoll, Marshall Islands. Recent from Tuamatu Islands (Hartmann, 1984).

DISCUSSION AND CONCLUSION

The theme of this paper is relatively simple—the confident recognition of species in fossil and modern ostracods is possible using morphological, stratigraphical and biogeographical evidence. However, this seemingly routine task and the methodology by which it is accomplished should not be taken for granted if we are to be able to use fossil ostracods for micro- and macro-evolutionary studies. The data presented here and in cited references brings us a small step closer to delineating species as spacially and temporally bounded entities—individuals in the sense of Hull (1976) and Eldredge and Cracraft (1980). *Hermanites transoceanica* consists of highly integrated (and sometimes isolated) groups of populations having discrete geographical and stratigraphical ranges and no known morphological "intermediates" with related species. New recent and fossil occurrences will certainly be discovered which should add to the locality list, but not alter our understanding of the species as a morphologically cohesive unit.

With reference to the genetic cohesiveness of *H. transoceanica,* two apparently conflicting scenarios can be envisioned: (1) that genetic interchange among the many widespread populations of *H. transoceanica* occurred frequently due to passive dispersal events, or (2) that interpopulation genetic interchange was very infrequent and that the observed pattern of morphologic stability indicates the species changed very little despite this lack of gene flow. It is beyond the scope of this paper to suggest what mechanisms might contribute to maintaining species integrity (see Van Valen, 1982), but the ostracod data presented here at least help clarify the questions we need to ask.

The data also show that by using our knowledge of known geological events, we have the potential to delineate the environmental boundary conditions—including the locus of origin—of speciation events. Although we still cannot point to a specific population as the "peripheral isolate" that split from the ancestral range, we can constrain the location and the age of the evolution of *Tourococha emaciata* and *Hermanites tricornis* to the Gulf of California/Baja, Mexico regions, near the northern part of the range of the ancestral species *T. lapidiscola* and *H. hornibrooki.* Work in progress on species of several high latitude (*Finmarchinella, Baffinicythere*) and low latitude genera (*Puriana, Hermanites, Cletocythereis*) is yielding more details on the geography of speciation and its relation to climatic change. The overall results seem to indicate that there are a plurality of speciation mechanisms in marine Ostracoda, at least in the geographic sense, and that allopatric speciation should not be assumed in cases of geographic isolation of populations.

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DISCUSSION

Reyment: A few remarks on your statistical analysis as well as general analytical methodology. I was impressed by the degree of interpretability of your canonical variate analysis. The variables you have selected are all size-measures with minor information on shape. In such cases, the directly measured lateral area gives a good approximation to the first canonical variate scores. As a suggestion for expanding the scope of the study, it could be useful to consider using trellised variables in order to capture shape variation.

Cronin: I agree that your suggestion would be a useful expansion of the analysis and I believe that the particular type of morphological analysis depends on the shape and surface ornament of the taxon under study.

The Interspecific Relations between Three Close Species of the Genus *Cythere* O. F. Müller, 1785

NORIYUKI IKEYA AND AKIRA TSUKAGOSHI
Shizuoka University, Japan

ABSTRACT

The genus *Cythere* was first proposed by O. F. Müller in 1785, with the European *C. lutea* as the type species. Almost a century after this proposal, the genus had expanded to contain some 1,000 species. Hanai (1959) researched *Cythere,* but restricted it, however, to species that are closely related to *C. lutea,* the type species of this genus.

This communication deals with the interspecific relationships between *C. uranipponica* Hanai, 1959 and *C. nishinipponica* Okubo, 1976. These, both fossil and Recent, are distributed around the Japanese Archipelago and are very similar to each other. The two species were compared in detail, particularly with respect to morphological elements such as the size, outline, ridges, pits, distribution patterns of the normal pore and radial pore canals, muscle scars, hingement, chitinous appendages, and ecological elements as well as their geographical and stratigraphical distribution. The study has revealed that the morphology of the carapace is very similar in the two species, and that it is difficult to distinguish between them on this basis. In particular, the distribution pattern of the sieve-type normal pore canals, including both their number and position, which has been considered to be a criterion unique to each species, is not necessarily a very stable character in either of the two species studied, and the difference between them was found to be very small. The soft parts were also studied, but no significant difference was observed between the chitinous appendages, antennules, antennae, and legs. However, a striking difference was found in the copulatory organs of the males of the two forms.

The species reported by Schornikov (1974) as *C. uranipponica* was obviously different from *C. uranipponica* in the distribution pattern of the sieve-type normal pore canals and the morphology of the copulatory organs of the male, and therefore we propose it here as a separate species *C. schornikovi* n. sp.

INTRODUCTION

The genus *Cythere* O. F. Müller, 1785 is the oldest genus established for marine ostracods. For nearly a century most marine ostracods were referred to it, but most species which were once believed to belong to this single genus are now placed in other genera. The concept of the genus, as now generally adopted, was redefined by Hanai (1959). The genus *Cythere,* according to this definition, is restricted to the species that have a close genealogical relationship with *C. lutea* O. F. Müller, 1785, the type species. Six species (*C. japonica* Hanai, 1959; *C. golikovi* Schornikov, 1974;

C. urupensis Schornikov, 1974; *C. boreokurila* Schornikov, 1974; *C. nishinipponica* Okubo, 1976 and *C. simplex* Hu, 1977) and two subspecies (*C. lutea uranipponica* Hanai, 1959 and *C. lutea omotenipponica* Hanai, 1959) which were found in and around Japan have been proposed so far.

Two species, namely *C. uranipponica* Hanai, 1959 and *C. nishinipponica* Okubo, 1976, have been of particular interest to Japanese ostracodologists because, with their strong similarity in carapace morphology and geographical distribution, confusion has arisen as to whether they are two different species or merely one species with two subspecies.

When Hanai (1959) reported *C. uranipponica* from the Pliocene Sawane Formation, he called it *C. lutea uranipponica,* and regarded it as a subspecies of *C. lutea.* Hanai (1970) later compared the distribution pattern of radial pore canals of *C. lutea lutea* from Europe with that of *C. lutea uranipponica* from Japan, and on the basis of the strong similarity between them, he pointed out the close genealogical relationship between these two subspecies.

Schornikov (1974, 1975), on the other hand, observed the morphological differences between the chitinous parts in Hanai's two subspecies, and considered them as two independent species, *C. uranipponica* and *C. omotenipponica* Hanai, 1959, respectively.

Okubo (1976) recognized *C. nishinipponica* from the Inland Sea of Japan as a new species independent of *C. uranipponica* and *C. omotenipponica,* because of the differences in "general outline and the shape of the copulatory organs". In his observation of the differences in the chitinous parts, Okubo (1976) seems to have used sketches of the specimen of *C. omotenipponica* from the type locality by Hanai (1970) and sketches of the specimen of *C. uranipponica* from Southern Kurile Islands by Schornikov (1974). The specimen of *C. uranipponica* as used by Schornikov (1974), however, is obviously different from *C. uranipponica* from Japan.

Okubo (1976) regarded Schornikov's *C. uranipponica* as the same species as the Japanese counerpart, probably because Hanai, *et al.* (1977) referred to Schornikov's *C. uranipponica* and the closely related Japanese species called by the same name (which had often been called *C. lutea* or *C. lutea lutea*) as *C. lutea uranipponica.* The two species *C. uranipponica* and *C. nishinipponica* have been controversial not only because of great morphological similarity, but also because of taxonomic confusion. In addition to these difficulties, the fact that only a small number of specimens from a few places have been available has also remained an obstacle to the solution of this problem.

The ultimate purpose of our research project on the genus *Cythere* is to elucidate the process of evolution and speciation of the species belonging to this genus. In this communication, however, we restrict our attention to the two species that are morphologically similar, namely *C. uranipponica* and *C. nishinipponica,* in order to establish the basis for evolutionary research by clarifying their morphological differences and geographical distributions. The close similarity in carapace morphology of these two species first gave us the impression that they might be identical. To clarify this we collected as many specimens from as many places as possible, so that individual and geographical variations could be taken into account.

This paper deals with our comparative study of the morphological elements of the carapace, such as size, ornamentation, muscle scars, and pore canals, and the chitinous parts. We placed particular emphasis on the distribution pattern of the sieve type normal pore canals and the male copulatory organs. The number of specimens investigated totals about two thousand, including Recent samples from 45 localities and fossil samples from 19 horizons.

We conclude that *C. uranipponica* and *C. nishinipponica* are discrete species with distinct geological histories. In addition, through the kindness of Dr. Schornikov, we were able to study his specimen of *C. uranipponica.* We consider that *C. uranipponica* as interpreted by Schornikov (1974) differs from *C. uranipponica* s.s. and belongs in a new species which we here name *Cythere schornikovi* n. sp.

The method established in this study will be extremely useful in future attempts to clarify the process of evolution and speciation of the whole genus *Cythere.*

MATERIALS AND METHODS

Materials

The Recent material used in this research was collected at 45 localities: 33 localities along the Japanese coast, 9 along the Korean coast, 2 in the Yellow Sea and 1 on Iturup Island coast. About two thousand specimens were examined altogether.

Specimens from Iturup Is. (St. 1) were provided by E. I. Schornikov; those from Desaki-west coast (St. 33) were provided by I. Okubo; those from Mezaki (St. 40) were provided by Y. Iwasaki; those from the Korean coast (Sts. 24, 25, 37, 38, 39) and from the Yellow Sea (Sts. 36, 43) were provided by K. Choe.

Fossil material from 19 samples was investigated: 10 samples from the Pliocene and 1 from the Pleistocene/Pliocene of the Japanese Archpelago, 8 from the Pleistocene of Japan and Cheju Island. This included topotype specimens of *C. uranipponica* from the Sawane Formation (St. gl) provided by T. Hanai, samples from the Sawane Formation from ten localities (Sts. g2–5) provided by H. Kitazato, specimens from the Seoquipo Formation (St. j) provided by K. Choe and samples from the Sasaoka Formation (St. f) provided by T. Kamiya.

The occurrences of these samples are summarised in Table 1 and their geographical distributions are plotted on Text-fig. 1.

Methods

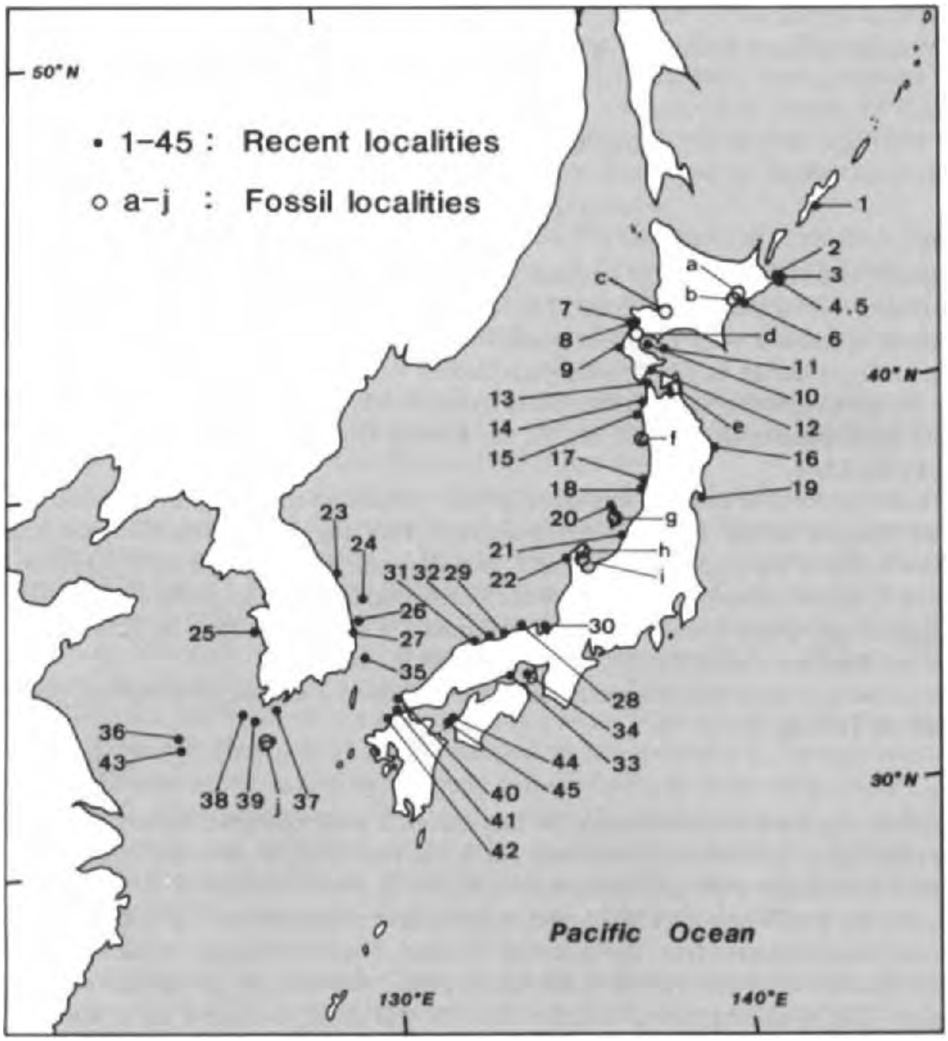
The Recent ostracod specimens used in this research were obtained mostly from calcareous seaweeds growing in tidal zones. These were cut at the root and placed in polyethylene bags with 5% formalin neutralized with hexamethylenetetramine, in order to preserve the chitinous parts of the ostracoda. In the laboratory, the samples were washed with water on a 200-mesh sieve, and the fine materials were separated from the seaweeds by hand. For identification of the seaweeds, a part of the fine material was fixed with 80% alcohol, together with a plant of the seaweed to which it was attached. The remaining part of the fine material was dried. Sediment materials were simply washed with water on a 200-mesh sieve and dried. After pre-drying, fossil materials were treated with hot water or 10% H_2O_2 solution in order to disaggregate the sediment, washed with water on a 200-mesh sieve, and then dried. Dry samples were picked under a stereo-microscope using a brush; wet samples, (alcohol) by means of a small pippette.

In order to observe the features, specimens with a dirty carapace surface were cleaned thoroughly with either water or H_2O_2 solution. Distribution patterns of the normal pore canals and the radial pore canals were observed under a binocular microscope by placing the specimen on a glass microslide and immersing it in glycerin.

Specimens of the chitinous parts were prepared, on a piece of slide glass under a stereo-microscope, by adding a small amount of water, separating the chitinous part from the carapace, dissecting the parts in Neo-shigaral, and then enclosing each part as a prepared specimen.

ECOLOGY

C. lutea is a species commonly found in the North Atlantic Ocean, and its geographical distribu-



Text-fig. 1—Occurrence of samples.

tion has been studied by several workers. They include Elofson (1941), who reviewed the known distribution of this species up to that time. He also produced a distribution map and made a number of excellent observations on the life cycle, ecological conditions and other features of this species. Hazel (1970), on the other hand, described the geographical distribution, temperature tolerance, and depth range of a number of species of ostracoda, including *C. lutea.* Whatley and Wall (1969, 1975) collected living specimens of *C. lutea* from the coast of Cardigan Bay, Southern Irish Sea, and showed the relationships between the seasonal change in the water temperature and the dissolved oxygen concentration and the number of living ostracod individuals in quantitative samples. Using the same samples, they pointed out the variations in distribution of the ostracod species on different seaweeds and the seasonal migration of ostracods between different sorts of habitats.

Schornikov (1974) collected samples of *C. alveolivalva, C. boreokurila, C. golikovi, C. uranipponica* (=*C. schornikovi* n. sp.), and *C. urupensis* along the coast of the Kurile Islands, and reported

TABLE 1—LIST OF SAMPLE LOCALITIES.

Recent materials

Sample Number	Localities	Lat. (N)	Long. (E)	Remarks
1.	Iturup Is. (Kurile Is.)			from Schornikov
2.	Tosamuporo (E. Hokkaido)	43°23.3′	145°47.2′	Alg. Rs. Tp.
3.	Nosappu Cape (E. Hokkaido)	43°22.8′	145°47.2′	Alg. Rs. Tp.
4.	Okenepu (E. Hokkaido)	43°19.9′	145°40.8′	Alg. Rs.
5.	Tomoshiri (E. Hokkaido)	43°18.8′	145°40.8′	Sed. Rs.
6.	Kushiro (E. Hokkaido)	42°56.6′	144°27.1′	Sed. Rs.
7.	Suttu Bay (SW. Hokkaido)	42°47.0′	140°16.5′	Sed. Ds.
8.	Suttu Bay (SW. Hokkaido)	42°47.0′	140°18.0′	Sed. Ds.
9.	Setana (SW. Hokkaido)	42°27.4′	139°51.0′	Alg. Rs.
10.	Hunka Bay (S. Hokkaido)	42°23.0′	140°25.0′	Sed. Ds.
11.	Hunka Bay (S. Hokkaido)	42°04.2′	141°25.0′	Sed. Ds.
12.	Kattoshi Cape (S. Hokkaido)	41°44.4′	140°36.5′	Alg. Rs.
13.	Imabetsu (N. Aomori Pref.)	41°10.9′	140°28.2′	Alg. Rs.
14.	Ōtosezaki (NW. Aomori Pref.)	40°46.1′	140°03.3′	Alg. Rs.
15.	Hukaura (SW. Aomori Pref.)	40°39.0′	139°55.9′	Alg. Rs.
16.	Ōtsuchi Bay (E. Iwate Pref.)	39°20.9′	141°56.9′	Sed. Ds.
17.	Yura (W. Yamagata Pref.)	38°43.4′	139°55.9′	Alg. Rs. Tp.
18.	Kobato (W. Yamagata Pref.)	38°41.7′	139°39.1′	Alg. Rs.
19.	Ayukawahama (Miyagi Pref.)	38°17.2′	140°30.7′	Alg. Rs.
20.	Iwayaguchi (Sado Is.)	38°15.2′	138°26.0′	Alg. Rs.
21.	Kujiranami (Niigata Pref.)	37°21.3′	138°31.2′	Alg. Rs.
22.	Sekinohana (Ishikawa Pref.)	37°12.6′	136°41.7′	Alg. Rs.
23.	South of Ōbun-Ri, Samcheog Eub, Samcheog Gun			Alg. Rs.
24.	Off Uljin	37°03.3′	129°59.0′	Sed. Rs. from Choe
25.	Shinheug-Ri, Daecheon Eub, Boryeong Gun			Alg. Rs.
26.	North of Uljin			Alg. Rs.
27.	Jigyeong-Ri, Songra Myeon, Yeongil Gun			Alg. Rs.
28.	Kagoshima (NE. Hyogo Pref.)	35°39.5′	134°46.8′	Alg. Rs.
29.	Moroyose (NW. Hyogo Pref.)	35°37.2′	134°26.2′	Alg. Rs.
30.	Momojima (N. Kyoto M. Pref.)	35°31.8′	135°16.2′	Alg. Rs.
31.	Nakanoumi (Shimane Pref.)	35°31.2′	133°11.7′	Sed. Ds.
32.	Nagawase (E. Tottori Pref.)	35°31.1′	133°58.8′	Alg. Rs.
33.	Dezaki (Okayama Pref.)	34°30.9′	133°59.8′	from Okubo
34.	Near Yoroizaki (Awaji Is.)	34°16.7′	134°39.8′	Alg. Rs.
35.	Off Ulsan	35°26.1′	129°59.0′	Sed. Ds. from Choe
36.	Yellow Sea	34°12.5′	126°00.3′	Sed. Ds. from Choe
37.	Off Wando	34°00.2′	127°03.3′	Sed. Ds. from Choe
38.	Off Geochado	34°12.5′	126°03.3′	Sed. Ds. from Choe
39.	Off Jindo	38°09.2′	126°22.5′	Sed. Ds. from Choe
40.	Mezaki (W. Yamaguchi Pref.)	34°04.8′	130°52.8′	from Iwasaki
41.	Dōyama (N. Hukuoka Pref.)	33°54.1′	130°27.7′	Sed. Ds.
42.	Tsuyazaki (N. Hukuoka Pref.)	33°47.5′	132°23.5′	Sed. Ds.
43.	Yellow Sea	33°39.3′	125°00.0′	Sed. Ds. from Choe
44.	Kikitsu (W. Ehime Pref.)	33°31.6′	132°23.5′	Sed. Sb.
45.	Takaura (W. Ehime Pref.)	33°27.4′	132°16.1′	Alg. Rs.

Alg.=Algae; Sed.=Sediments; Rs.=Rocky shore; Sb.=Sand beach; Ds.=Dredge sample; Tp.=Tidepool

Table 1—*continued*

Fossil Material

Sample Number	Formation (age)	Localities	Lat.(N),	Long. (E)	Remarks
a.	Harutori (1. Pleistocene.)	E. Hokkaido	42°58.3′	144°25.5′	
b.	Kushiro (1. Pleistocene.)	E. Hokkaido	42°59.0′	144°25.5′	
c.	Nopporo (1. Pleistocene.)	Hokkaido			
d.	Setana (e. Pleistocene./1. Pliocene.)	S. Hokkaido			Hayashi's sample
e.	Hamada (1. Pliocene.)	Shimokita Pen.			
f.	Sasaoka (m. Pleistocene.)	Oga Pen.			from Kamiya
g1.	Sawane (Pleistocene.)	Sado Is.			from Hanai
g2.	Sawane (Ppleistocene.)	Sado Is.	37°58.8′	138°16.5′	from Kitazato
g3.	Sawane (Pleistocene.)	Sado Is.	38°00.9′	138°16.6′	from Kitazato
g4.	Sawane (Pleistocene.)	Sado Is.	38°00.9′	138°16.6′	from Kitazato
g5.	Sawane (Pleistocene.)	Sado Is.	38°00.9′	138°16.6′	from Kitazato
g6.	Sawane (Pleistocene.)	Sado Is.	37°59.3′	138°16.4′	
g7.	Sawane (Pleistocene.)	Sado Is.	37°59.3′	138°16.4′	
g8.	Sawane (Pliocene.)	Sado Is.	37°59.3′	138°15.9′	
g9.	Sawane (Pliocene.)	Sado Is.	37°59.6′	138°15.6′	
h1.	Hiradoko (1. Pleistocene.)		37°27.0′	137°18.2′	
h2.	Hiradoko (1. Pleistocene.)		37°27.0′	137°18.2′	
i.	Miyainu (1. Pleistocene.)		37°20.2′	137°13.8′	
j.	Seoqwipo (1. Pleistocene.)				from Choe

1.=late; m.=middle; e.=early.

the water temperature, salt concentration and pH, dissolved oxygen concentration, as well as other information including the kinds of seaweeds which these ostracods inhabited. Valentine (1976) showed the relationships between the latitudinal ranges of distribution of *C. alveolivalva* and *C. maia, C.* sp. B and the temperature tolerance of these species.

As for *C. uranipponica,* little has been known about its geographical distribution and ecology, except that Hanai (1959) and Ueno and Hanai (1965) have pointed out a few localities where this species occurred. Okubo (1980) has shown the distribution of *C. nishinipponica* in the Inland Sea of Japan, and believed that this species generally inhabits seaweeds, rather than sediments.

In this communication, emphasis is placed on clarifying the geographical distribution of the two species, and the ecological aspects are left for future consideration. We restrict our attention here to some important elements observed in collecting the living specimens. Study of the geographical distributions of *C. uranipponica* and *C. nishinipponica* showed that the distribution areas of both *C. uranipponica* and *C. nishinipponica* are located within the area influenced by the Tsushima Warm Current. While these areas partially overlap each other, the former generally lies north of the latter. Thus, *C. uranipponica* seems to be slightly better adapted to a colder envoronment.

So far, samples collected by the same method show no significant difference between the two species with respect to their habitats. Both these species generally inhabit seaweeds growing in the tidal zone of rocky shores on open sea coasts, where the waves are relatively gentle. On the other hand, not many are found on seaweeds growing at the head of rocky shores exposed to strong waves. They do not occur at all on seaweeds in inner bays, where the salt concentration is low. Most of the living specimens were collected where the water depth is 0 to 50 cm at low tide, but some specimens were also obtained from seaweeds collected in the mid-littoral zones. In places where the range of tides is small, such as the coast of the Sea of Japan, it is usually possible to collect living specimens at water depths of 30–50 cm. It is not clear, however, whether significant numbers of these species inhabit greater depths.

We mainly collected seaweeds belonging to the subfamily Corallinoideae (Class Florideae) which have fine calcareous leaves. We found that these ostracod species are most abundant on seaweed species of the genus *Corallina* which grow where the waves are relatively gentle, but are rare on seaweeds of the genera *Joculator* and *Colliarthron,* growing where the waves are strong, and on those belonging to the genus *Amphiroa,* which grows on bare rocks with no sand on them.

From these observations, it appears that the habitat of these two ostracod species is restricted to coastal zones. Both these species are often found in samples of sediment obtained offshore, although never in large numbers. Living specimens, however, have never been found in these samples. Since they both have thick, strong carapaces, this suggests that they have survived being carried offshore along with the sediment and have been deposited where they are now found.

MORPHOLOGICAL STUDY

Dimensions of Carapace

The body size of ostracods varies even within the same species and depends on the sex and the locality, as well as on the fact that the right and left valves have different dimensions. Adult *C. uranipponica* and *C. nishinipponica* in the same population have, in general, longer left than right valves and the males have longer valves than the females. No significant difference in height was observed between the right and left valves and between males and females. The carapace width is also about the same for both sexes. Concerning the body size of Recent material, it was found that *C. uranipponica* tended to be larger in the northern districts where the water temperature is low, while in *C. nishinipponica* there was no significant variation among the individuals from different districts. Comparison of size showed that *C. uranipponica* is, in general, larger than *C. nishinipponica* in all three dimensions. In areas where both species coexist, *i.e.,* where the southern part of the *C. uranipponica* distribution area overlaps the northern part of the *C. nishinipponica* distribution area, *C. uranipponica* is larger than *C. nishinipponica.*

Carapace Outline

In proposing *C. nishinipponica,* Okubo (1976) observed that "*C. uranipponica* differs from them in its general outline," but gave no further details about the difference between the two species. In addition, *C. uranipponica* as recognized by Okubo seems to be the same as that of Schornikov (1974), which is different from the *C. uranipponica* s.s. that we are dealing with here. The carapace outlines of *C. uranipponica* and of *C. nishinipponica* are very similar and it is difficult to find any distinctive difference between them, except that both ends of the dorsal margin are slightly more angular in *C. nishinipponica* than in *C. uranipponica.* The outline generally differs between the two sexes; in both species, the dorsal margin of the female is gently rounded, while that of the male is linear.

Outer Valve Surface

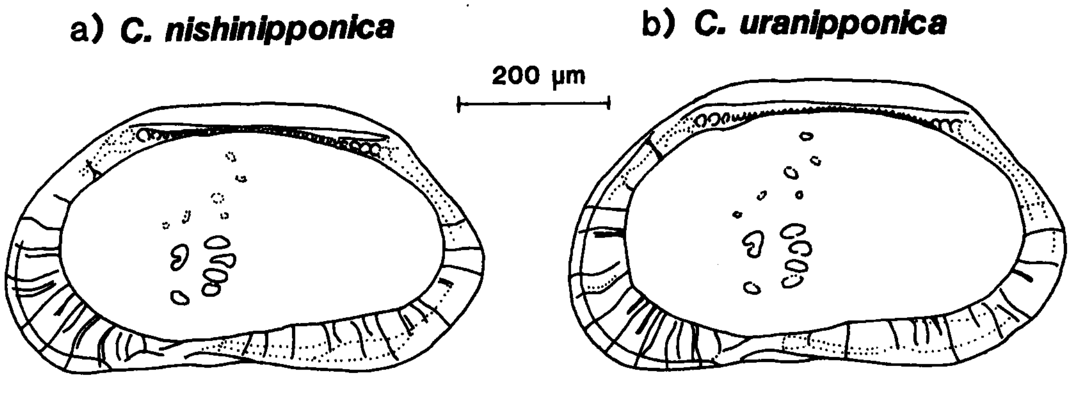
A) **Ridges:** Both species have ridges similar to those of *C. lutea,* the type species of this genus. Several weak ridges run radially from the median part of the valve to the marginal zone. A marginal ridge runs from the posterior to the ventral margin. In the postero-ventral area, this ridge splits into two branches which run parallel to each other along the ventral margin. Comparing specimens of both species from the type localities reveals that, in general, *C. nishinipponica* has stronger ridges than *C. uranipponica,* but the strength of the ridges varies even among individuals of the same species. *C. nishinipponica* shows relatively wide morphological variations from one locality to another; specimens from the western Inland Sea of Japan have weaker ridges than those from the eastern part, and those from the coast of the Sea of Japan have even weaker ridges.

B) Pits: Both species have a number of pits on the surface of the carapace. *C. nishinipponica* has larger, deeper and less densely distributed pits than *C. uranipponica*. As in the case of the ridges, *C. nishinipponica* shows relatively wide variation associated with the different localities. The pits tend to be smaller and shallower in individuals from the western Inland Sea of Japan than in those from the eastern part, and even smaller and shallower in those from the coast of the Sea of Japan. The density of the pits, however, is always lower in *C. nishinipponica* than in *C. uranipponica.*

C) Distribution pattern of radial pore canals: Hanai (1970) compared the distribution patterns of the radial pore canals of *C. lutea* and *C. uranipponica,* and pointed out a strong similarity between these two species. In the same paper, he showed the similarity in the distribution pattern among the individuals of a single species, using *Schizocythere okhotsukensis* as an example. He also pointed out that the distribution patterns vary markedly among different species of the same genus, using *Palmenella limicola* and *P. californica* as examples. Hanai (in Ruggieri, 1971) later expressed the view, probably based on these facts, that *C. uranipponica* is synonymous with *C. lutea.*

C. uranipponica and *C. nishinipponica* are also very similar to each other in the distribution pattern of their radial pore canals. Thus the three species, *C. lutea, C. uranipponica,* and *C. nishinipponica* have almost the same pattern and are therefore considered to be species that are very closely related to each other. The radial pore canals in *C. alveolivalva* and *C. schornikovi* n. sp., which have smooth surface ornamentation, and *C.* sp. B (Valentine, 1976), which has relatively strong ridges, also have a pattern similar to that of the three species mentioned earlier. Thus, in the genus *Cythere*, the distribution pattern of the radial pore canals is considered to be a stable character that shows little variation among individuals of the same species, and even between different species (Text-fig. 2).

D) Distribution pattern of normal pore canals: In ostracods, the distribution pattern of the normal pore canals has often been used as a basis for classification and identification. Morkhoven (1962) has pointed out that the distribution pattern of the pore canals is similar among individuals of the same species. Using *Schizocythere okhotsukensis* and *S. kishinouei* as examples, Hanai (1970) showed that the distribution patterns of the sieve type normal pore canals are not the same in different species of the same genus, but that the number and distribution pattern of these pore canals is very similar among individuals of the same species, indicating that these are conservative characters. Benson (1972, 1975) analysed the reticular patterns of the surface ornamentation, as-



Text-fig. 2—Comparison of radial pore canal distribution in right valve male of *Cythere nishinipponica* Okubo (IGSU-O-441, loc. 28) and *Cythere uranipponica* Hanai (IGSU-O-430, loc. 28).

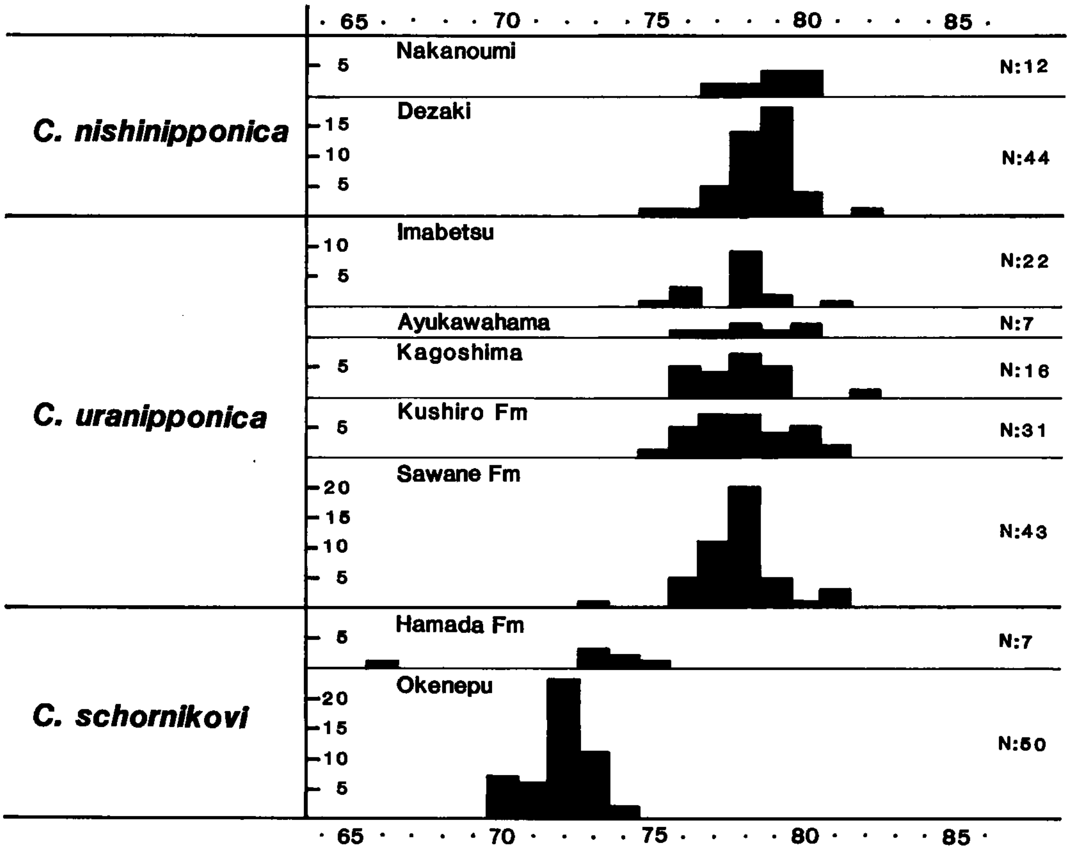
suming that the number and position of the single-type, normal pore canals are stable characters within the species, and using their positions as reference points. He also showed that the distribution pattern of the single-type pore canals is fairly stable, even between different species. Using *Cyprideis torosa* and *Loxoconcha elliptica* as examples, Rosenfeld (1982) revealed that slight interspecific variations exist in the number and locations of the sieve-type normal pore canals.

The normal pore canals on the carapace of *Cythere* are classified roughly into two categories, namely, single-type and sieve-type. The former is further divided into funnel-type (with a lip) and simple-type (without a lip).

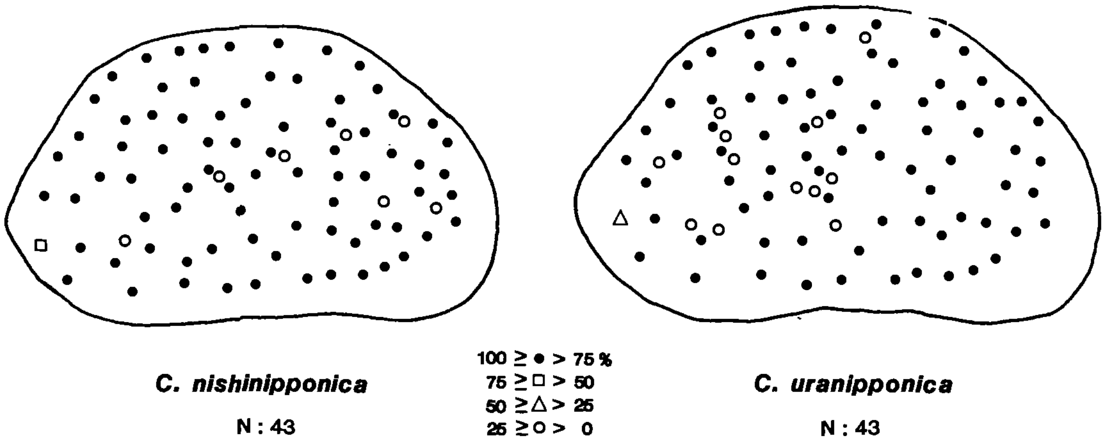
In this research, we studied the numbers and the distribution patterns of the normal pore canals of the adult stage right valves of the two species, *C. uranipponica* and *C. nishinipponica*, in order to clarify the intraspecific stability and interspecific variation in these elements.

The number of simple-type normal pore canals is about 5 in both species, and these canals are mainly distributed in the marginal zone of the valve. No significant variation was found in the number and locations of these canals, either within the same species or between these two species. The number of funnel-type normal pore canals is about 10, and they are almost constant within each of the two species and between these species. Single-type normal pore canals, as well as the radial pore canals, are considered to be very stable in specific and interspecific characters.

The total number of sieve-type normal pore canals per right valve of *C. uranipponica* and



TEXT-FIG. 3—Variation of total number of sieve-type normal pore canals on the right valve for several populations. abscissa: total number of pores, ordinate: number of specimens, and N: number of specimens examined.

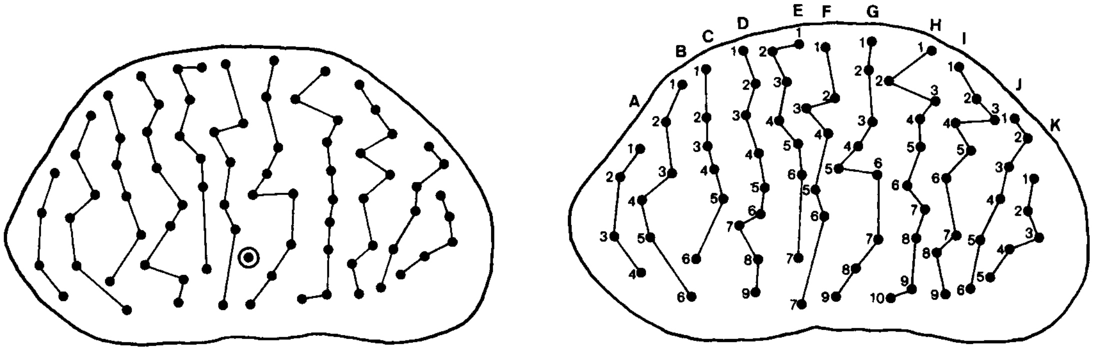


TEXT-FIG. 4—Comparison of probable occurrence of each sieve-type normal pore canal on the right valve. Black points: a pore exists at that location with 75 to 100% probability, square: with 50 to 75% probability, triangle: with 25 to 50% probability, white circles: with only 25% or less probability, and N: number of specimens examined.

C. nishinipponica were studied for each locality. The results show that the total numbers were about the same for both species and were between 75 and 82, with deviations between three and seven within each population. The deviations in the number of pore canals were also about the same for both species, and no significant geographical and geological differences were observed (Text-fig. 3).

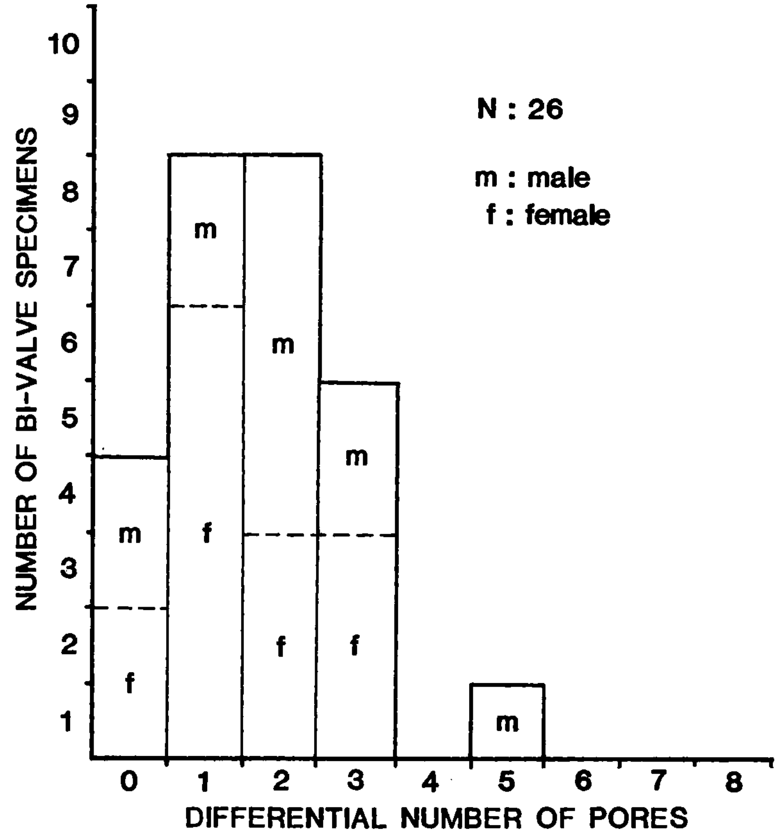
The distribution patterns of the sieve-type normal pore canals were studied in the 11 *Cythere* species—*C. alveolivalva, C. golikovi, C. lutea, C. nishinipponica, C. omotenipponica, C. schornikovi, C. uranipponica, C. urupensis, C.* sp. *α*, *C.* sp. S and *C.* sp. B (Valentine, 1976). The results revealed that the 11 species shared a common regularity in the distribution patterns of their pore canals on the carapace. The intraspecific variations in the distribution patterns were less significant than the interspecific variations. Therefore, it is possible to compare the locations of each pore canal, not only between individuals within the same species, but also between those belonging to different species. This regularity in the pore canal distribution pattern makes it possible to locate exactly each pore canal on the carapace. Examination of a large number of individuals of the same species also gives an estimate of the probability of occurrence of each pore. The probability of occurence of each sieve-type pore canal on the right valve was studied in *C. uranipponica* (43 specimens from Pliocene to Pleistocene Sawane Formation) and *C. nishinipponica* (43 specimens from Recent Dezaki), respectively (Text-fig. 4). It was found from the results that the probability of occurrence of each pore canal was either more than 90% or less than 5%. In other words, the pores fall into two extreme groups; some pores occur almost always, and the others occur only rarely. A few pores which were found to occur with a probability of between 25 and 75% are considered to be of variable stability.

The number of stable pore canals with high probability of occurrence (>75%) was 78 for *C. uranipponica*, and 79—one more than for *C. uranipponica*—for *C. nishinipponica*, respectively. Moreover, 78 out of the 79 pore canals of *C. nishinipponica* have exactly the same location as the corresponding canals of *C. uranipponica*. In both species most pores appear at the same site. The stability of the pore positions, however, differs between the two species: in *C. nishinipponica* instability of the pore positions lies in the anterior half, whereas in *C. uranipponica* it lies in the posterior half. The single pore canal that distinguishes the two species always occurs in the ventromedian zone of *C. nishinipponica*. With the exception of this single pore canal, the distribution



C. nishinipponica **C. uranipponica**

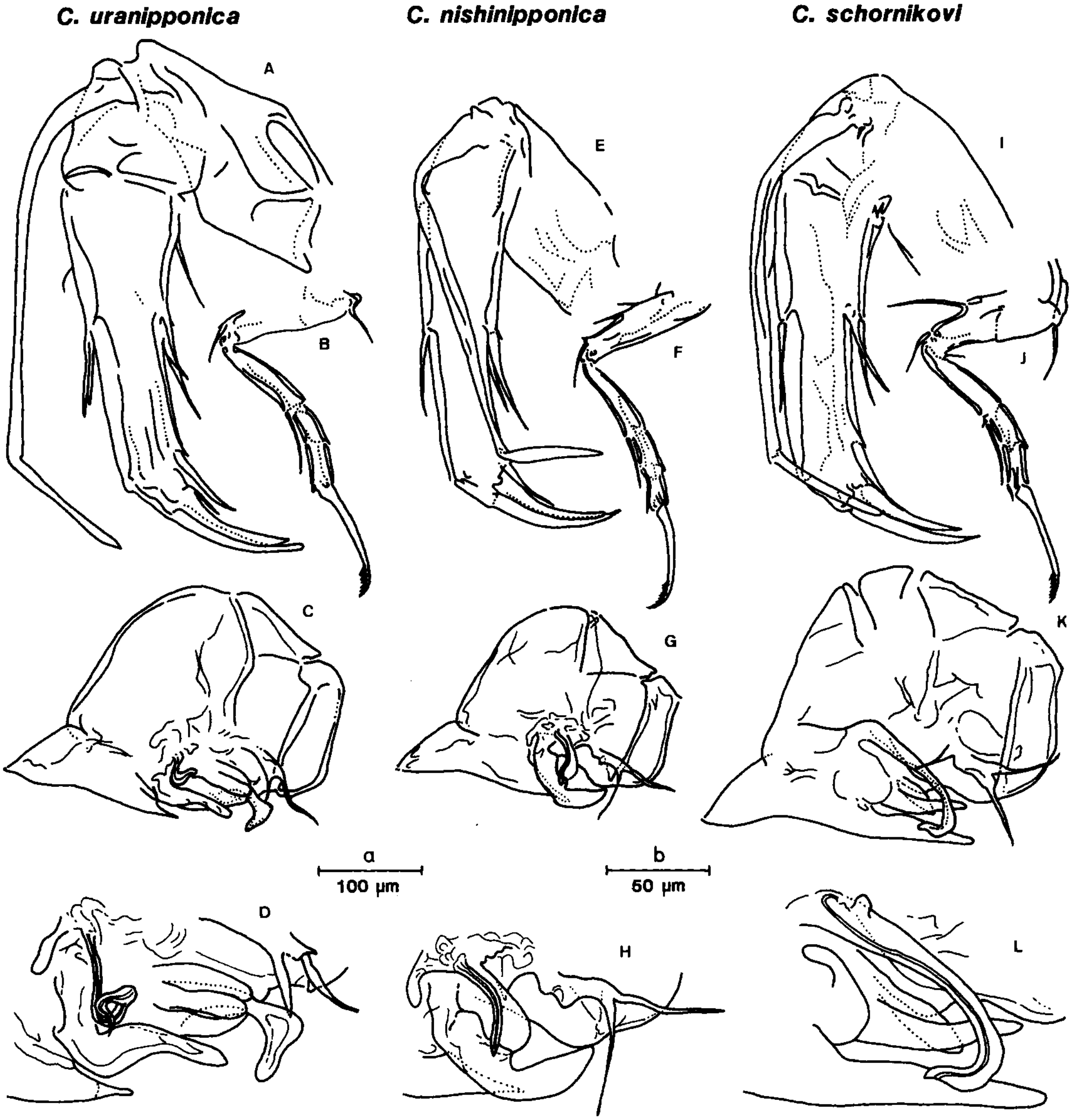
Text-fig. 5—Comparison of distribution patterns of each sieve-type normal pore canal on the right valve. Black points: sieve-type normal pore canals, and double circle: one sieve-type normal pore canal in the centro-ventral area appears with 100% probability in *C. nishinipponica*, but only with a probability of a few % in *C. uranipponica*. Combination of alphabet and arabic numeral shows the reference co-ordinate of a pore.



Text-fig. 6—The frequency distribution of the differential number of pores. The abscissa shows differential total number of sieve-type normal pores between left and right valves of the carapace.

patterns of the sieve-type normal pore canals of the two species are essentially identical (Text-fig. 5).

Prior to the study of the pore canals, we examined 26 bi-valve specimens of *C. schornikovi* to see if any differences could be found between males and females or between right and left valves with respect to the number and distribution pattern of the sieve-type normal pore canals (Text-fig. 6). The sex of the specimens used was determined beforehand by observation of the copulatory organs.



TEXT-FIG. 7—Comparison of chitinous parts of three *Cythere* species. A)–D)—*C. uranipponica* Hanai, male, from loc. 19. A), antenna IGSU-O-431; B), third thoracic leg IGSU-O-432; C) and D), copulatory organ IGSU-O:433. E)–H)—*C. nishinipponica* Okubo, male, from loc. 33. E), antena IGSU-O-442; F), third thoracic leg IGSU-O-443; G) and H), copulatory organ IGSU-O-444. I)–L)—*C. schornikovi* n. sp., male, from loc. 4. I), antenna IGSU-O-451; J), third thoracic leg IGSU-O-452; K) and L), copulatory organ IGSU-O-451. D), H) and L) show details of clasping apparatus and *ductus ejaculatorius*.

It was found that the pattern of the sieve-type pore canals on both valves, whether male or female, was not necessarily symmetrical (4 out of 26 individuals had symmetrical patterns). No pore canals were found that would characterise either the right or left valve or either of the sexes.

These facts may also be applied to *C. uranipponica* and *C. nishinipponica.*

Muscle Scars

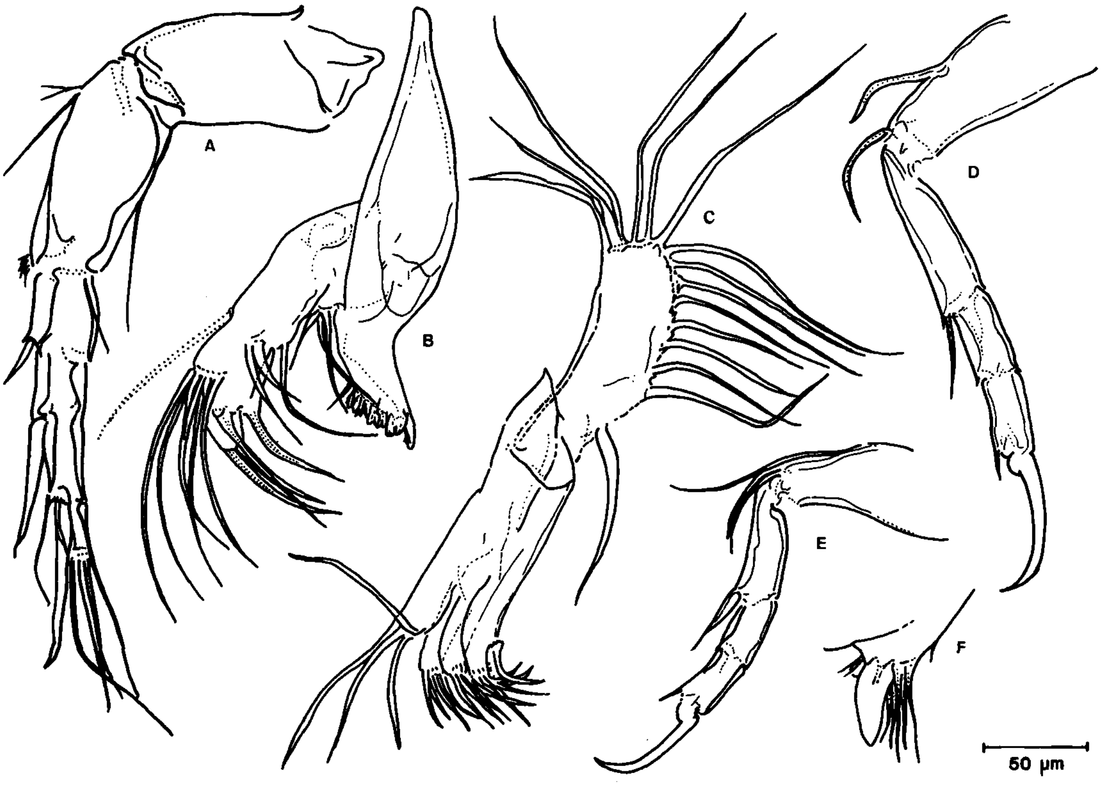
In both species, there are four adductor scars aligned perpendicularly to the ventral margin, with a frontal scar in front of the uppermost adductor scar and a mandibular scar in front of the lowest adductor scar. Three to five weak dorsal scars are located above the adductor scars and are difficult to see in some specimens (Text-fig. 2). No significant difference was observed between the two species with respect to the muscle scars.

Hingement

Both species have antimerodont hingement. The teeth are well developed and are larger at both ends and smaller in the middle of the hinge. Detailed comparison of both species revealed no significant difference between them (Pl. 1, figs. i, j; Pl. 2, figs. i, j).

Chitinous Parts

The chitinous parts of *C. lutea* have already been described, as well as those of other *Cythere*



TEXT-FIG. 8—Appendages of *C. uranipponica* Hanai, male, from loc. 19. A), antenule IGSU-O-434; B), mandible IGSU-O-435; C), maxilla IGSU-O-435; D), second thoracic leg IGSU-O-434; E), first thoracic leg IGSU-O-434; and F), caudal part IGSU-O-436.

species, such as *C. alveolivalva, C. omotenipponica, C. boreokurila, C. golikovi, C. urupensis.* Okubo (1976) described *C. nishinipponica* in detail. Hanai (1959) proposed *C. uranipponica* on the basis of his study of specimens from the Pliocene Sawane Formation. Chitinous parts of this species have not been previously described. The *C. uranipponica* whose chitinous parts were described by Schornikov (1974), differs from the type specimen of *C. uranipponica* as described by Hanai in the distribution pattern of the normal pore canals. It is also obviously different from Recent speciments of *C. uranipponica* from Honshu in several aspects of the copulatory organs. For these reasons, the "*C. uranipponica*" of Schornikov is considered to be a different species from the Japanese *C. uranipponica*, and we therefore propose the new species *C. schornikovi* to accommodate it.

We dissected male specimens of *C. nishinipponica* from two localities (Sts. 32, 33) and 20 specimens of *C. uranipponica* from three localities (Sts. 18, 19, 28), taking into account the individual and geographical variations. The dissections revealed that variations among individuals of the same species are not significant. The antennules, antennae, thoracic legs, etc. are very similar in the two species, and no significant difference was observed (Text-fig. 7). However, in the copulatory organ, the number and shape of the clasping apparatus, as well as the length and the shape of the *ductus ejaculatorius* differed in the two species. The clasping apparatus of *C. uranipponica* has a complicated, pleated structure, and is very different from that of *C. nishinipponica* (Text-fig. 7).

GEOGRAPHICAL AND GEOLOGICAL DISTRIBUTION

Recent (Text–fig. 9)

C. nishinipponica is distributed from the Yellow Sea to the southern Korean coast, along the Sea of Japan from northern Kyushu to Hokuriku, and along the coast of the Inland Sea of Japan.

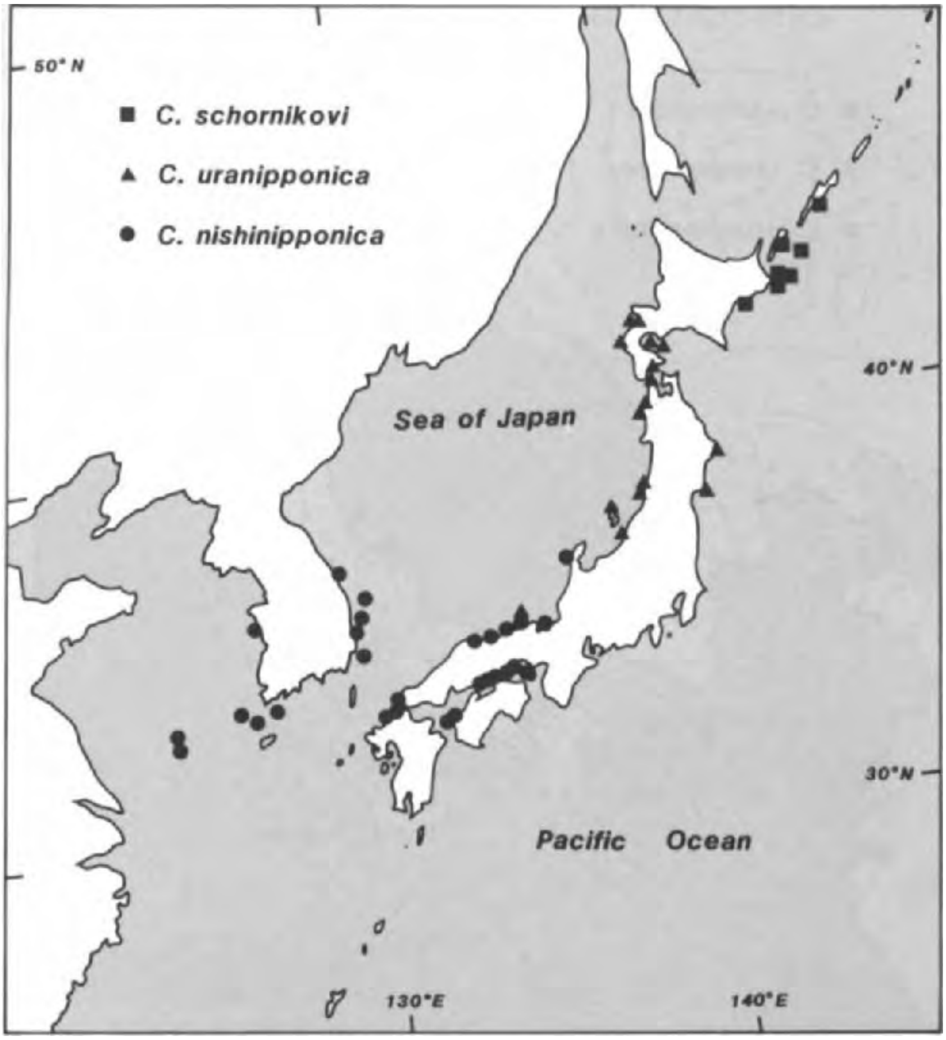
C. uranipponica, on the other hand, is distributed along the coast of the Sea of Japan from San-in to Hokkaido and along the Pacific coast from Sanriku to southern Hokkaido. Both species are typically found along the coasts that are under the influence of the Tsushima Warm Current. The former is distributed nearer the source current than is the latter. The two species, however, co-exist in the area from Hokuriku to eastern San-in. At Kagoshima (St. 28), specimens of both *C. nishinipponica* and *C. uranipponica* have been found in the same sample.

C. nishinipponica co-exists with *C. japonica* and *C. omotenipponica* in the northern part of its distribution area (Hokuriku), and also with *C. omotenipponica* along the coast from San-in to Hokuriku, and along a smaller part of the coast (Iyonada) of the Inland Sea. However, *C. nishinipponica* does not co-exist with species of *Cythere* in other areas such as the coasts of the Yellow Sea, Korea, and the greater part of the Inland Sea. *C. uranipponica,* on the other hand, co-exists with *C. japonica* in almost all its distribution area, with *C. omotenipponica* in Sanriku and with *C. golikovi* in southern Hokkaido.

Fossil (Text–fig. 10).

Fossil *C. nishinipponica* have been found, so far, only in a few Pleistocene formations within the distribution area of the Recent specimens, but not in older formations. Moreover, no other *Cythere* species have been found together with *C. nishinipponica* in these localities.

According to Ishizaki (1966), *C. uranipponica* has been found in the Miocene (Hatatate For-Formation), the oldest formation from which it has ever been recorded. The oldest specimens dealt with here were from the Early Pliocene Sawane (St. g), Harutori (St. a) and Kushiro (St. b) Formations, which occur in eastern Hokkaido and are slightly to the north of the Recent distribution area of *C. uranipponica.* This area, where the Oyashio Cold Current prevails, is surrounded by the

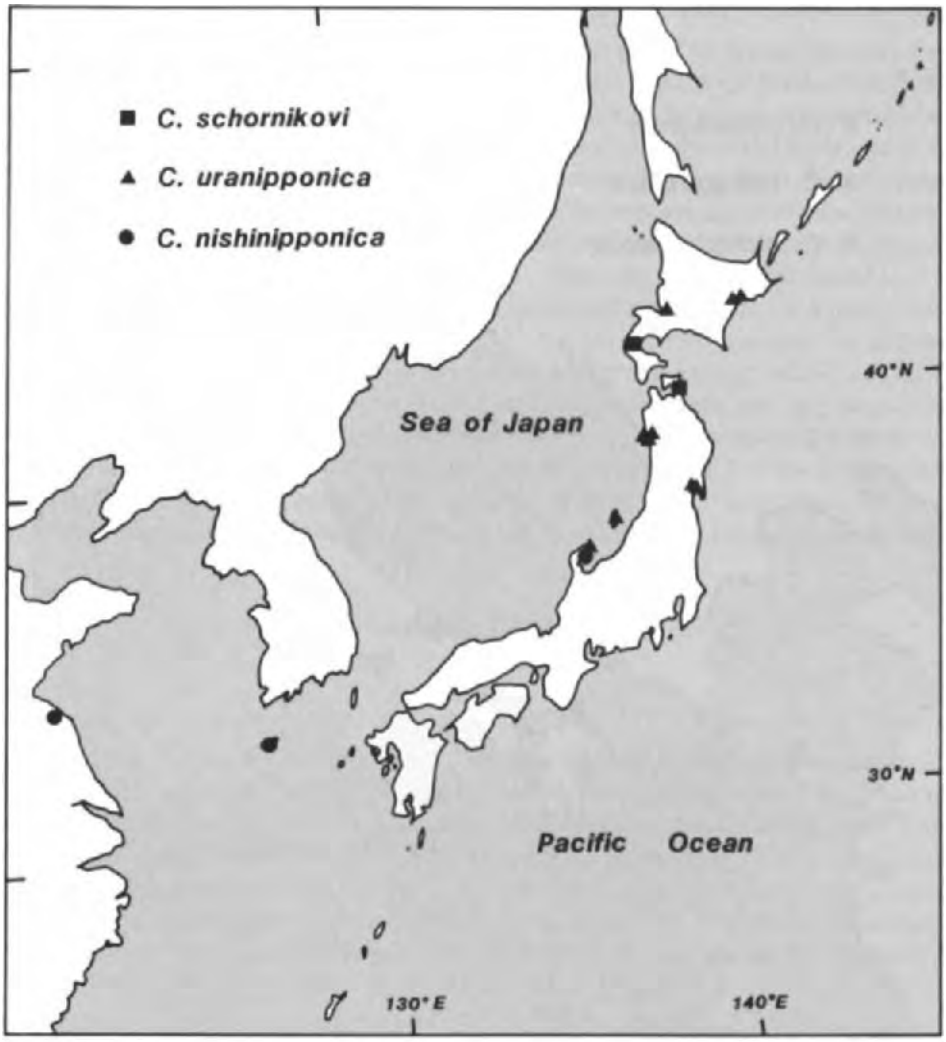


TEXT-FIG. 9—Geographical distribution of three Recent *Cythere* species.

distribution area of the Recent *C. schornikovi.* Geologically, *C. uranipponica* has been found together with *C. omotenipponica* in the Miocene Hatatate Formation; with the four species *C. golikovi, C. japonica, C.* sp. S, *C.* sp. *α* in the Pleistocene Sawane Formation; with *C. japonica* in the Pleistocene Sasaoka (St. f) Formation; with *C.* sp. B in the Pleistocene Nopporo (St. c) Formation and with *C. golikovi* in the Pleistocene Hiradoko (St. h) Formation. Okada (1979) reported that *C. lutea,* as he called it, was found together with *C. japonica* in the Pleistocene Shibikawa Formation.

DISCUSSION

At first we were not able to distinguish between *C. uranipponica* and *C. nishinipponica* on the basis of the carapace morphology. These species showed almost no significant differences with re-

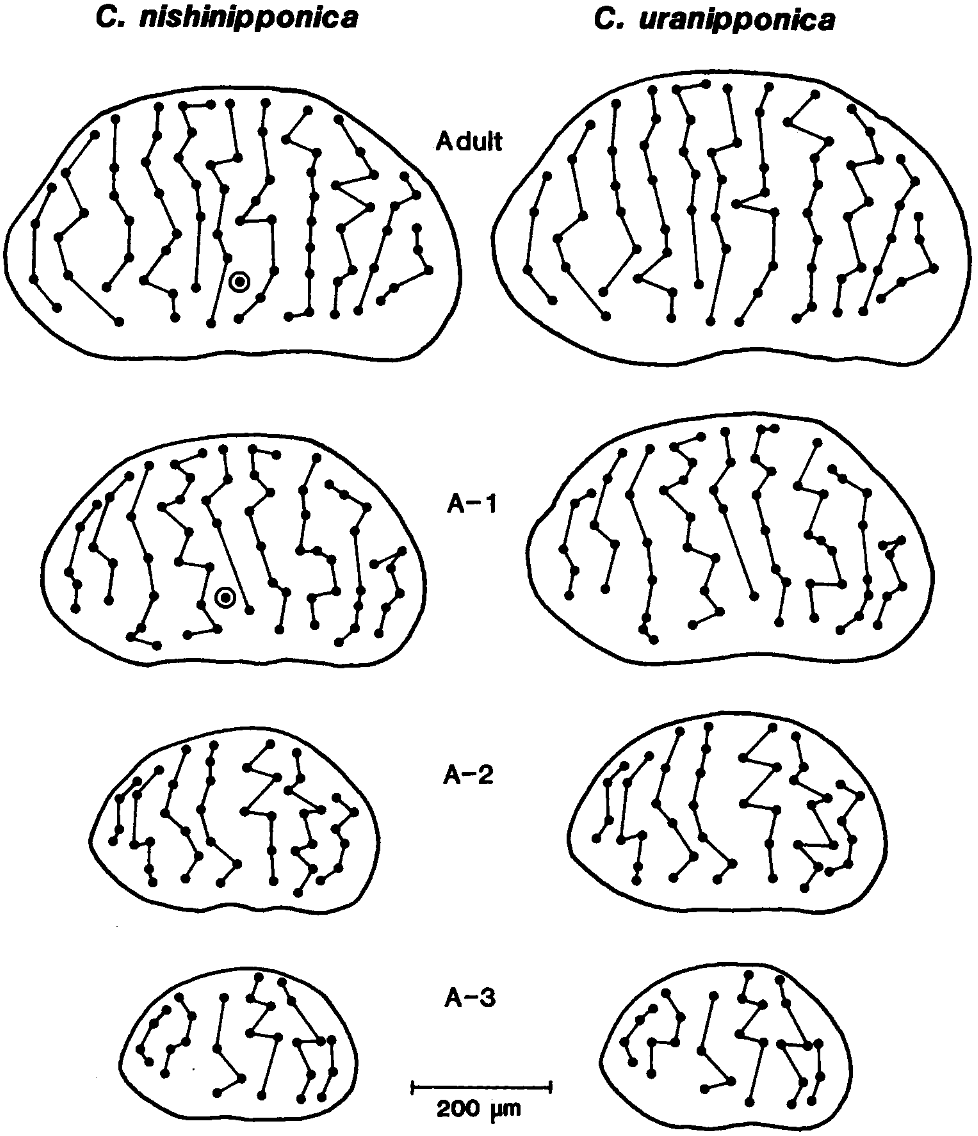


TEXT-FIG. 10—Geographical distribution of three fossil *Cythere* species.

spect to some morphological characters that are routinely used as the bases for ostracod classification. In each species there are some morphological variations among the populations from different geographical areas. Some of these variations in one species, however, overlap with those of the other. The ridges on the carapace surface, for example, are one such character. *C. nishinipponica* from the Inland Sea and the coast of the Korean Peninsula has well developed ridges, whereas the same species from the Sea of Japan has weak ridges and in this respect resembles *C. uranipponica*, which also has weak ridges.

Distinction between the two species on the basis of carapace morphology is possible in most cases based on the pore canal pattern. The difference between the coarse pits of *C. nishinipponica* and the fine ones of *C. uranipponica*, as well as the angular outline which is characteristic of *C. uranipponica* are useful for differentiation between the two species.

We compared in detail the distribution patterns of the normal pore canals of four moult stages, adult to the A-3, of *C. uranipponica* with those of the corresponding stages of *C. nishinipponica*.



TEXT-FIG. 11—Ontogenetical distribution patterns of the sieve-type normal pore canals of four moult stages in *C. nishinipponica* and *C. uranipponica*.

These comparisons revealed that there is almost no difference in the distribution patterns of the pore canals between the two species in the A-2 and A-3 stages. However, a clear difference was found in the adult and A-1 stages in that *C. nishinipponica* has one more pore canal in the ventro-median zone than *C. uranipponica* (Text-fig. 11). It was also observed that in the younger stages, the morphological characters that help distinguish between the two species, such as those of the pits and ridges, are less prominent, making it even more difficult to distinguish one species from the other.

Our main theme in this research lies in the taxonomic closeness of the two species, *C. uranipponica* and *C. nishinipponica*, as seen in the similarity of carapace morphology. It is certainly true, as we have emphasized repeatedly, that the two species are extremely similar as far as carapace morphology is concerned. It is surprising, however, that the structures of their copulatory organs have such obvious and outstanding differences. We dissected specimens of several other *Cythere* species in order to observe the copulatory organs. Comparisons revealed that in this respect *C. uranipponica* is more similar to *C. schornikovi* than to *C. nishinipponica,* and *C. nishinipponica* is similar to *C. lutea* and *C. urupensis.* These relationships are radically different from those we have established on the basis of observations of the carapace morphology, and this discrepancy poses a question that calls for careful investigation: in which element does morphological similarity reflect the phylogenic closeness most directly?

Our observations of *C. uranipponica* and *C. nishinipponica* suggest that two distinct species may possess almost identical carapace morphologies. This raises a problem, particularly in taxonomic studies on dead specimens without chitinous parts and fossil specimens, in which even a subtle difference in carapace morphology calls for careful attention. The interspecific relations illustrated here are found in some other *Cythere* species as well. We are contemplating applying the methods used here to the whole genus *Cythere,* in order to clarify the interspecific relationships and, hopefully, the speciation process within this genus.

SYSTEMATICS

Order PODOCOPIDA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDAE Baird, 1850
Subfamily CYTHERINAE Dana, 1852
Genus CYTHERE O. F. Müller, 1785

CYTHERE URANIPPONICA Hanai, 1959
(Pl. 1, figs. a–n, text-figs. 2b, 7A–D, 8A–F)

Cythere lutea uranipponica: HANAI, 1959, p. 142, 143, Pl. 28, figs. 2, 6a, b, Text-figs. 2a, b. (except for "Recent specimens from the mouth of the Onga River"); HANAI, 1961, p. 366, Text-fig. 9, figs. 2a, b; HANAI, 1970, p. 704, Textfigs. 5c, d; HANAI, 1971 (in RUGGIERI, 1971), p. 293; ISHIZAKI AND MATOBA, 1985, p. 12, Pl. 2, fig. 19, not fig. 20.

Cythere lutea: UENO and HANAI, 1965, p. 455, figs. 420–1, 2, not 3; OKADA, 1979, p. 159, Fig. 14, b, p. 169, Pl. 21, figs. 2, 7, 8.

Cythere lutea lutea: ISHIZAKI, 1966, p. 137, Pl. 17, figs. 1, 2.

not Cythere uranipponica: SCHORNIKOV, 1974, p. 143–145, Pl. 1, figs. 1a-c, Text-fig. 4.

Diagnosis.—Several weak ridges running radially from the centre of the carapace to the margin. A marginal ridge runs from the posterior to the ventral zone. Fine pits densely distributed over the carapace except on the normal pore canals. The number of the normal pore canals per valve is

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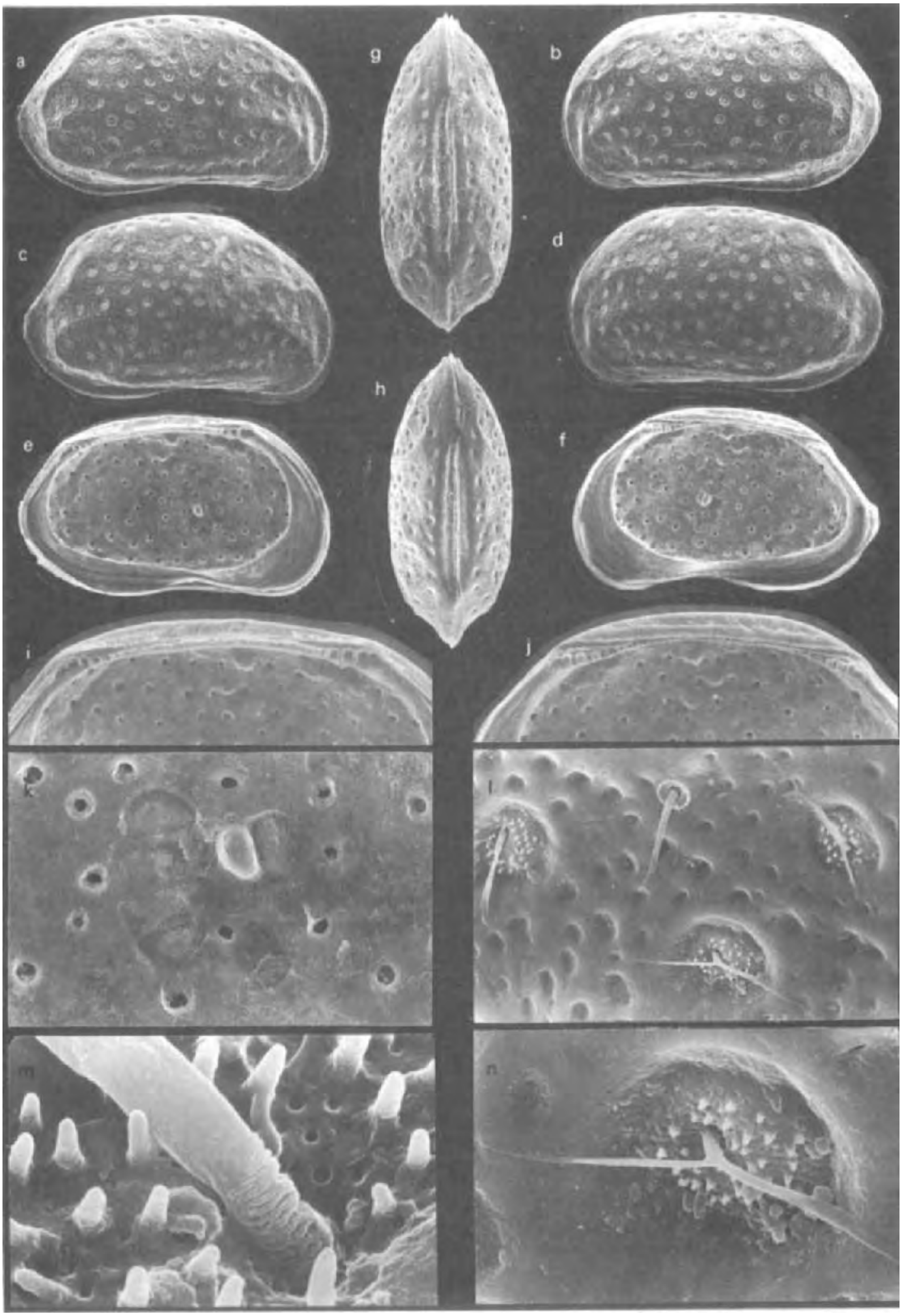
PLATE 1—*Cythere uranipponica* Hanai, 1959
a, b. External lateral view of male right and left valve (×72), IGSU-O-437. c, d. External lateral view of female right and left valve (×72), IGSU-O-436. e, f. Internal lateral view of female left and right valve (×72), IGSU-O-438. g. Dorsal view of male carapace (×72), IGSU-O-439. h. Dorsal view of female carapace (×72), IGSU-O-440. i. Hingement of female left valve (×120), IGSU-O-438; j. Hingement of female right valve (×120), IGSU-O-438. k. Distribution of the adductor, frontal, mandibular scars (×320), IGSU-O-438. l. Sieve-type and funnel-type normal pore canals (×720), IGSU-O-436. m. Root of seta on sieve-type normal pore canal (×6600), IGSU-O-437. n. Sieve-type normal pore canal (×2000), IGSU-O-436.
a–n: all loc. 19. Ayukawa-hama (38°17.2′N, 140°30.7′E).


a
g
b
c
d
h
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i
j
k
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n

mostly between 75 and 84. Copulatory organ with four pairs of clasping apparatus and a pair of fine spermic tubes.

Description.—Carapace subreniform in lateral outline. Anterior margin showing smooth infracurvature. Dorsal margin slightly curved. Ventral margin forming a gentle arch, with its peak somewhat anterior to the centre. Posterior margin with a slight angle in the middle; the lower half gently curved, the upper half linear. The male usually longer than the female and with a straighter dorsal margin. Carapace oval in dorsal outline, with the maximum thickness at about one-quarter the length from the posterior end; ovoid in anterior outline, with the maximum thickness at about one-third the height from the bottom. The right valve projects over the left along the dorsal margin; the left valve projects over the right along the anterior margin and the upper half of the posterior margin. Several weak ridges run radially from the centre to the margin. A marginal ridge runs from the posterior to the ventral area where it splits into two branches which run parallel to each other. Numerous fine pits distributed over the carapace except on the normal pore canals. The pits are finer and more densely distributed in the marginal zone. Duplicature of almost constant width developed along the free margin. Vestibule less developed. Radial pore canals, some long and reaching the margin, others short, total about 30. Most are straight but some are curved. Three types of normal pore canals are recognized: simple-, funnel-, and sieve-types, the diameters being about 2 μm, 5 μm, 15 μm, respectively. Numerous coniform processes were observed on the sieve plates of the sieve-type normal pore canals of a living specimen. The number of the sieve-type, normal pore canals per valve mostly between 75 and 84, of which 78 are stable. A regularity is found in the distribution pattern as shown in Text-fig. 5. Muscle scar pattern of four adductor scars aligned perpendicular to the ventral margin in the centre of each valve with a V-shaped frontal scar anterior to the uppermost adductor scar and a mandibular scar anterior to the lowest adductor scar. Mid-dorsal and dorsomedian zones spotted with several inconspicuous dorsal scars. Hingement anti-merodont. Anterior and posterior ends of the right valve have well developed teeth; the medium part forms a loculate groove. The left valve has a complementary arrangement. Male copulatory organ with almost square proximal shield, four pairs of clasping apparatus, fine and fairly short *ductus ejaculatorius*.

Dimensions.—Listed below are the measurements of *C. uranipponica* from the Pliocene to Pleistocene Sawane Formation (st. g) and Recent specimens from Imabetsu (St. 13), Ayukawahama (St. 19) and Kagoshima (St. 28).

Occurrence.—Recent: Coasts from San-in to southwestern Hokkaido, from Sanriku to Southern Hokkaido. Fossil: Pliocene/Pleistocene Sawane Formation(Sado Is.), Pleistocene Shibikawa and Sasaoka Formations (Oga Peninsula), Pleistocene Nopporo Formation (southwestern Hokkaido), Pleistocene Kushiro and Harutori Formations (eastern Hokkaido), Pleistocene Hiradoko Formation (Noto Peninsula).

Remarks.—Okada (1979) discussed the difference between what he called "well preserved" and "poorly preserved" fossil specimens of the species "*C. lutea*". What he called "poorly preserved" specimens turned out to be *C. uranipponica* and the "well preserved" specimens were identified as *C.* sp. *α* (We are going to propose *C.* sp. *α* as a new species in a future paper).

CYTHERE NISHINIPPONICA Okubo, 1976
(Pl. 2, figs. a–n, Text-fig. 2a, 7E–H)

Cythere lutea uranipponica: HANAI, 1959, p. 413 (Restricted to those labelled "Recent specimens from the mouth of the Onga River").

Cythere lutea omotenipponica: ISHIZAKI, 1969, p. 215, 216, Pl. 26, fig. 9.

	Length (mm)		Height (mm)		
	Av.	OR	Av.	OR	N
Sawane F.					
R. (M)	0.72	0.68–0.81	0.42	0.37–0.46	14
R. (F)	0.71	0.67–0.75	0.42	0.40–0.45	22
L. (M)	0.75	0.65–0.81	0.44	0.41–0.48	10
L. (F)	0.73	0.67–0.81	0.43	0.38–0.48	12
Imabetsu					
R. (M)	0.77	0.72–0.80	0.45	0.42–0.47	11
R. (F)	0.74	0.71–0.76	0.44	0.42–0.46	13
L. (M)	0.76	0.72–0.80	0.43	0.41–0.46	9
L. (F)	0.74	0.71–0.80	0.43	0.40–0.45	17
Ayukawa-hama					
R. (M)	0.73	0.69–0.75	0.42	0.40–0.44	17
R. (F)	0.70	0.66–0.72	0.42	0.40–0.43	6
L. (M)	0.74	0.70–0.76	0.40	0.40–0.43	18
L. (F)	0.71	0.67–0.73	0.41	0.39–0.42	9
Kagoshima					
R. (M)	0.69	0.66–0.70	0.40	0.39–0.41	3
R. (F)	0.68	0.67–0.70	0.41	0.40–0.42	5
L. (M)	0.71	0.71	0.40	0.40–0.41	2
L. (F)	0.69	0.68–0.70	0.40	0.39–0.41	7

Cythere nishinipponica: OKUBO, 1976, p. 113–119, figs. 1a–m, 2a–h′, 3a–m; MALZ AND IKEYA, 1983, p. 141, Text-figs. 4, 5.

Cythere lutea lutea: HOU, *et al.*, 1982, p. 158, 159, Pl. 71, figs. 1–3, Text-fig. 22.

Diagnosis.—Ridges in posterior zone of carapace surface better developed than those in other parts. Deep pits distributed all over the carapace surface. Distribution pattern of sieve-type normal pore canals almost the same as in *C. uranipponica*, except for one additional pore canal in the ventromedian zone. In the male copulatory organ, each hemipenis has two clasping apparatuses, one nearly circular, thin and difficult to distinguish. *Ductus ejaculatorius* thin and short.

Description.—Carapace surface ornamentation almost identical with that of *C. uranipponica*. Some major differences are listed in the "Diagnosis" section for this species. Ornamentation more prominent in specimens from the Inland Sea than in those from the Sea of Japan. Surface of the latter relatively smooth.

Dimensions.—Listed below are the measurements of the Recent specimens from the Inland Sea of Japan, western coast of Desaki (St. 33), Kagoshima (St. 28) and Nakano-umi (St. 31).

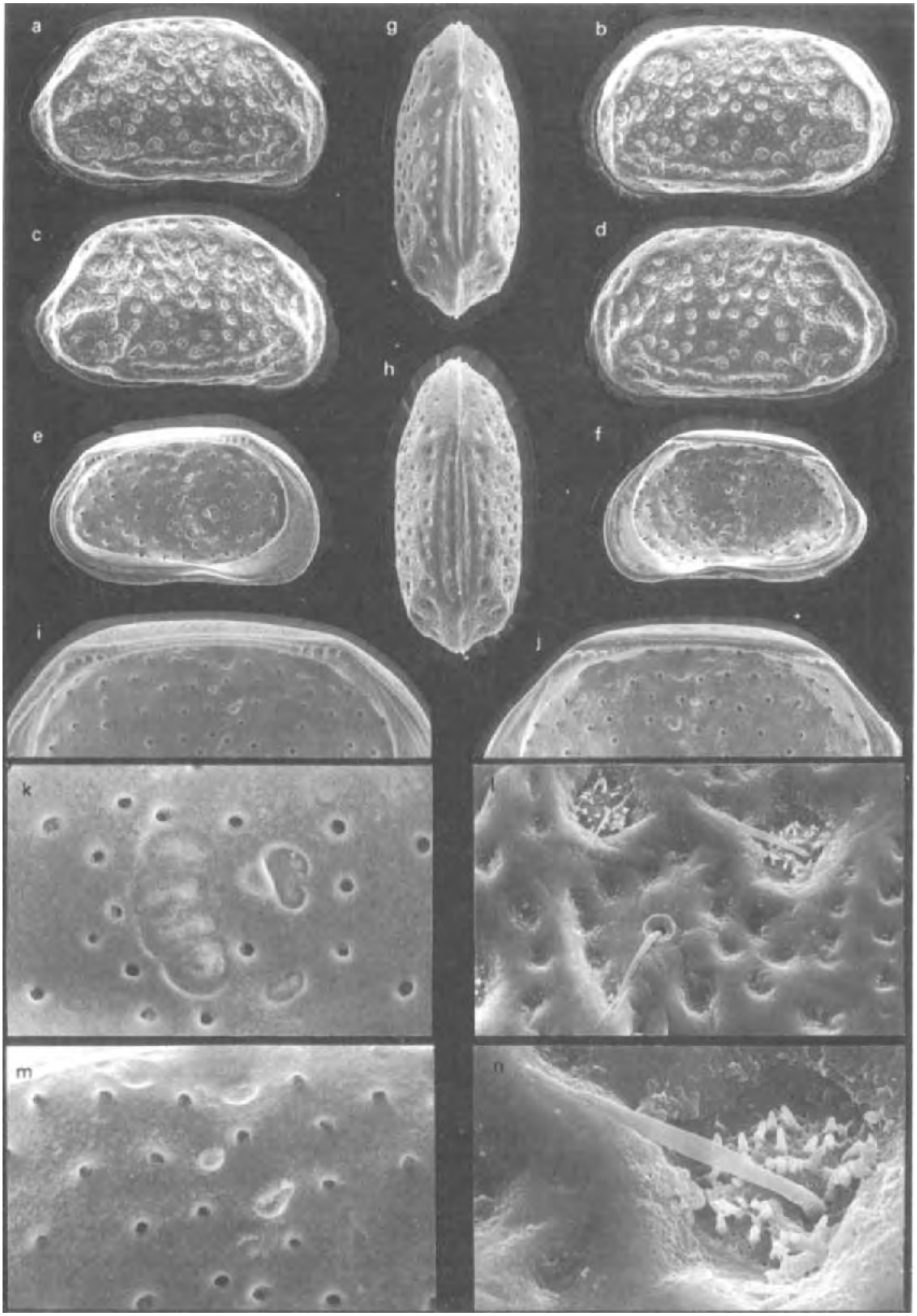
Occurrence.—Recent: The Yellow Sea, southern coast of Korean Peninsula, coast of northern Kyushu to Hokuriku. Fossil: Pleistocene Seoquipo Formation (Cheju Is.), Pleistocene Miyainu Formation (Noto Peninsula).

CYTHERE SCHORNIKOVI n. sp.

(Pl. 3, figs. a–n, Text-figs. 7I–L)

Cythere uranipponica: SCHORNIKOV, 1974, p. 143–145, Pl. 1, figs. 1a–c, Text-fig. 4.

Type.—Holotype (a male carapace) IGSU-O-453 (Pl. 3, figs. a, b; a: right valve, length = 0.68 mm, height = 0.40 mm, b: left valve, length = 0.70 mm, height = 0.39 mm). Paratype (a female carapace) IGSU-O-454 (Pl. 3, figs. c, d; c: right valve, length = 0.64 mm, height = 0.39 mm,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	Length (mm)		Height (mm)		
	Av.	OR	Av.	OR	N
Desaki West Coast					
R. (M)	0.68	0.67–0.71	0.40	0.38–0.41	23
R. (F)	0.65	0.62–0.68	0.39	0.37–0.41	23
L. (M)	0.69	0.68–0.71	0.39	0.38–0.41	24
L. (F)	0.66	0.63–0.68	0.39	0.37–0.40	22
Kagoshima					
R. (M)	0.65	0.64–0.65	0.36	0.36–0.37	3
R. (F)	0.63	0.57–0.65	0.37	0.34–0.39	9
L. (M)	0.65	0.63–0.67	0.37	0.35–0.39	8
L. (F)	0.63	0.60–0.66	0.37	0.35–0.39	11
Nakano-umi					
R. (M)	0.68	0.62–0.72	0.38	0.36–0.41	17
R. (F)	0.67	0.61–0.72	0.39	0.36–0.41	37
L. (M)	0.69	0.61–0.73	0.38	0.34–0.41	31
L. (F)	0.68	0.63–0.71	0.39	0.35–0.41	45

d: left valve, length = 0.65 mm, height = 0.38 mm). Paratype (a female carapace) IGSU-O-455 (Pl. 3, figs. e, f; e: left valve, length = 0.67 mm, height = 0.41 mm, f: right valve, length = 0.67 mm, height = 0.40 mm). Paratype (a male carapace) IGSU-O-456 (Pl. 3, fig. g, width = 0.32 mm, right valve, length = 0.72 mm, height = 0.43 mm, left valve, length = 0.73 mm, height = 0.42 mm). Paratype (a female carapace) ISGU-O-457 (Pl. 3, fig. h, width = 0.33 mm, right valve, length = 0.68 mm, height = 0.43 mm, left valve, length = 0.70 mm, height = 0.42 mm). Paratypes IGSU-O-451,452.

Type locality.—Okenepu, Nemuro-shi, Hokkaido, Japan (43° 20.2′N, 145° 45.5′E), Recent, marine tidal zone of rocky shore.

Etymology.—In honour of Dr. E. I. Schornikov, who has studied many *Cythere* species from the Kurile Islands and provided specimens of this species from Iturup Island.

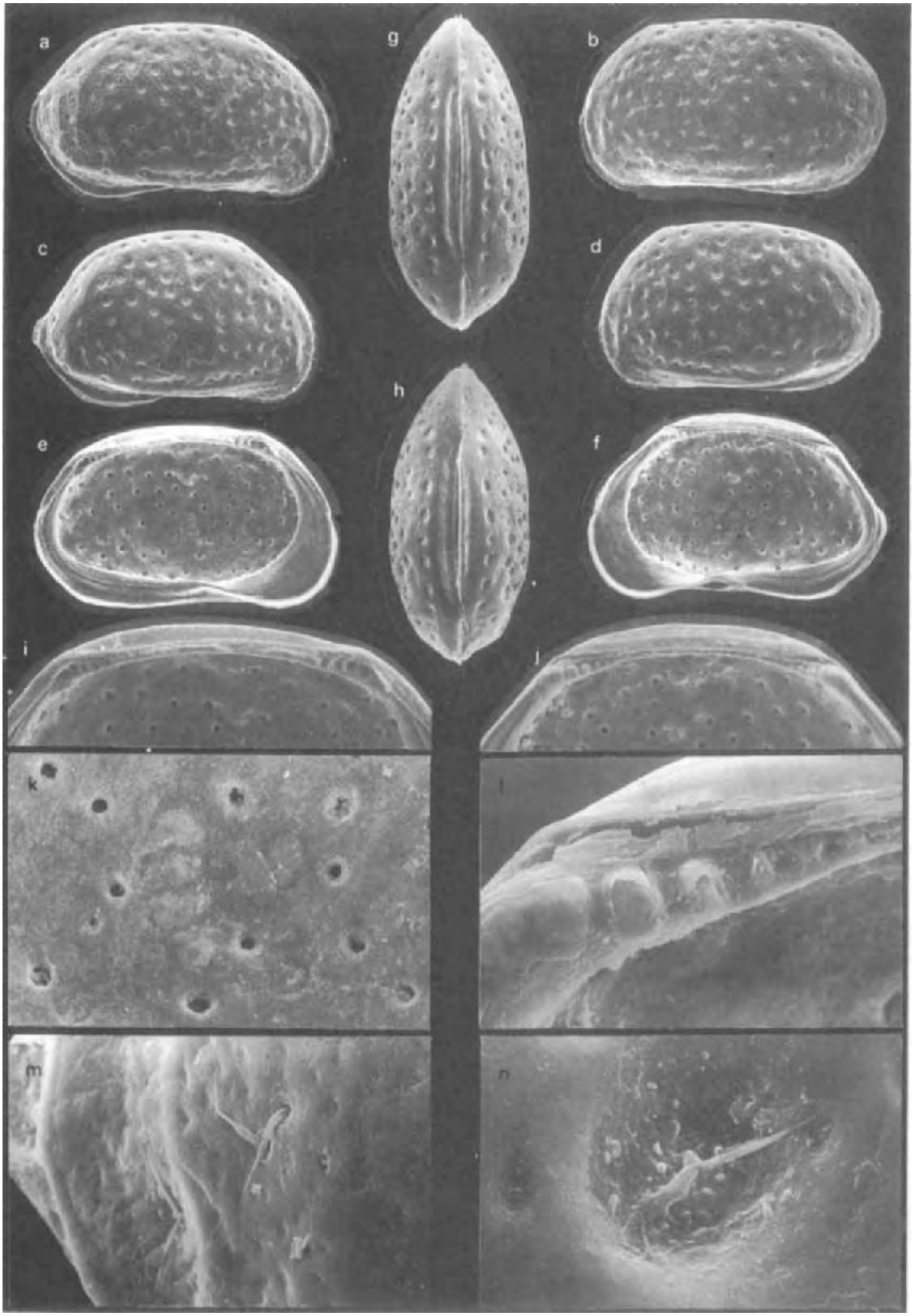
Diagnosis.—Carapace surface very smooth, with blunt ridges and numerous fine pits. The number of sieve-type, normal pore canals per valve between 70 and 74, relatively less in genus *Cythere*. The male copulatory organs characterized by marked asymmetry in the posterior processes on the outer lobes on the hemipenises on both sides. The left process, about twice as long as the right one, extends posteriorly.

Description.—Morphological characteristics of this species generally similar to those of *C. uranipponica*. Carapace subreniform in lateral outline, as typically observed in *Cythere* species. Obliquely rounded anterior margin crosses gently arched dorsal margin at a relatively sharp angle. Ventral margin curved gently. Posterior margin straight in the upper one-third and gently curved in the lower two-thirds. Carapace surface, though generally smooth, has a relatively well-developed ridge on the ventral margin, with a wide, blunt ridge parallel to it inside the margin.

PLATE 2—*Cythere nishinipponica* Okubo, 1976

a, b. External lateral view of male right and left valve (×72), IGSU-O-445. c, d. External lateral view of female right and left valve (×72), IGSU-O-446. e, f. Internal lateral view of female left and right valve (×72). e. IGSU-O-447. f. IGSU-O-448. g. Dorsal view of male carapace (×72), IGSU-O-449. h. Dorsal view of female carapace (×72), IGSU-O-450. i. Hingement of female left valve (×120), IGSU-O-447. j. Hingement of female right valve (×120), IGSU-O-448. k. Distribution of the adductor, frontal, mandibular scars (×320), IGSU–O-447. l, Sievetype and funnel-type normal pore canals (×720), IGSU-O-446. m. Dorsal scars of left valve (×320), IGSU-O-447. n. Sieve-type normal pore canal (×2000), IGSU-O-446.

a–d, l, n: loc. 33, Dezaki (34°30.9′N, 133°59.8′E); g: loc. 30, Momojima (35°31.8′N, 135°16.2′E); h: loc, 45, Takaura (33°27.4′N, 132°16.1′E); i, j, k, m: loc. 28, Kagoshima (35°39.5′N, 134°46.8′E).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In some rare individuals, several blunt radial ridges run from the centre toward the margin, or marginal ridges develop in the posterior zone. Numerous pits distributed all over the carapace except on the normal pore canals, particularly dense in the marginal zone. The number of sieve-type, normal pore canals per valve between 70 and 74, which is always four to six less than the average in *C. uranipponica*. The pores found in *C. uranipponica*, but not in this species are A-3, D-6, E-1, F-2, G-5, and K-1 (Text-fig. 5).

In the copulatory organs, the posterior process of the supporting lobe of the left hemipenis is markedly longer than that on the right, and extends posteriorly. Each hemipenis has three clasping apparatuses, which are almost symmetrical on both sides. A thick *ductus ejaculatorius* usually extends long to the supporting lobe.

Dimensions.—Listed below are the length and height measurements of adult specimens from the type locality (St. 4).

	Length (mm)		Height (mm)		
	Av.	OR	Av.	OR	N
R. (M)	0.70	0.68–0.74	0.41	0.39–0.43	21
R. (F)	0.67	0.63–0.70	0.40	0.39–0.44	26
L. (M)	0.71	0.69–0.74	0.41	0.39–0.42	23
L. (F)	0.68	0.64–0.71	0.39	0.38–0.42	21

Occurrence.—Recent: Southern Kurile Islands (Kunashir Is., Iturup Is., and Shikotan Is.) and eastern Hokkaido (Nemuro Pen. and Kushiro). Fossil: Pliocene Hamada Formation (Shimokita Pen.) Pliocene/Pleistocene Setana Formation (southern Hokkaido).

Remarks.—There are close similarities in carapace ornamentation between this species and *C. alveolivalva* Smith, 1952. The number and distribution pattern of the sieve-type normal pore canals are almost the same as those of *C. alveolivalva*. The two species differ in that the pits covering the carapace surface are shallower and denser in *C. schornikovi* and the duplicature is wider than in *C. alveolivalva*. In the copulatory organs, the supporting lobes are shorter than in *C. alveolivalva*, the difference being particularly marked in the right hemipenis. While *C. schornikovi* has three pairs of independent clasping apparatuses, one of the three pairs is incomplete in *C. alveolivalva*.

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PLATE 3—*Cythere schornikovi* n. sp.

a, b. External lateral view of male right and left valve (×72), holotype, IGSU-O-453. c, d. External lateral view of female right and left valve (×72), paratype, IGSU-O-454. e, f. Internal lateral view of female left and right valve (×72), paratype, IGSU-O-455. g. Dorsal view of male carapace (×72), paratype, IGSU-O-456. h. Dorsal view of female carapace (×72), paratype, IGSU-O-457. i. Hingement of female left valve (×120), paratype, IGSU-O-455. j. Hingement of female right valve (×120), paratype, IGSU-O-455. k. Distribution of the adductor, frontal, mandibular scars (×320), paratype, IGSU-O-455. l. Anterior part of hingement of female right valve (×600), paratype, IGSU-O-455. m. Sieve-type and funnel-type normal pore canals (×720), paratype, IGSU-O-454. n. Sieve-type normal pore canal (×2000), paratype, IGSU-O-454.

a–n: all loc. 4, Okenepu (43°19.9′N, 145°40.8′E)

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DISCUSSION

Cronin: Do you have any idea on the Miocene ancestor of the genus *Cythere*?

Ikeya: While we can trace *Cythere* back to the Pliocene with certainty, we are not in a position to point to a potential ancestor in the Miocene with any confidence.

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Speciation Completed?
In *Keijella bisanensis* Species Group

KATSUMI ABE
University of Tokyo, Japan

ABSTRACT

Since the whole life of *Keijella bisanensis* (known in East Asia, Pliocene to Recent) is restricted to the muddy bottoms of shallow inner bays, the local populations are essentially isolated, and consequently we can expect geographical variation of species characters to have developed among the spatial isolations. Along the margin of the East China Sea four different forms are actually recognized. They differ in size and in the H/L ratio of carapace. These forms represent different stages of divergence, ranging from local genetic races to full species. Their distribution pattern is largely allopatric, but partly sympatric along the southern coast of Korea and Southwest Japan. The *K. bisanensis* species group is therefore one of the most suitable marine animals for the study of speciation. The origin of the disparity between sympatric forms is discussed based on knowledge of population structure. The author suggests breaking the *K. bisanensis* complex into two completed species based on carapace size.

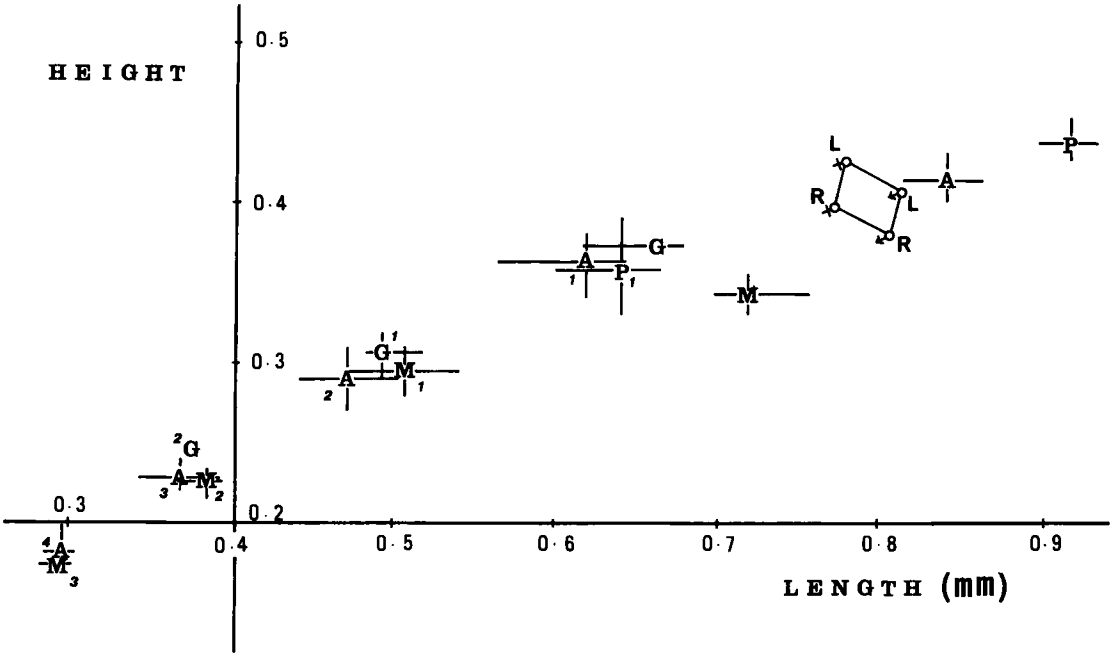
INTRODUCTION

Every local population of podocopid ostracods living on the muddy bottom of a shallow sea is reproductively isolated from adjacent populations. This is because their true habitat, flocculent mud, is restricted to embayments and because these ostracods, unlike many other marine invertebrates, do not have a planktonic stage in their early life. Such ostracods have every qualification which Mayr (1963) put forward as necessary for the development of speciation research. Mayr also pointed out that population structure is the key to the problem of speciation.

Keijella bisanensis inhabits the muddy bottom of inner bays, and its population structure has been clarified in some detail by Abe (1983). Thus it should be an ideal taxon for the study of speciation. The taxonomy of this ostracod is not firmly settled yet and it is known under two names, *Keijella* Ruggieri and *Bicornucythere* Schornikov and Shaitarov. This study deals with only one species group and therefore we can leave the question of proper generic assignment to another time.

CLASSIFICATION OF LIVING AND FOSSIL *K. bisanensis* SPECIES GROUP

K. bisanensis (Okubo) was first described from the Inland Sea of Japan. The occurrence of both



Text-fig. 1—Comparison of the mean values of the carapace size (left valve of adult males) among four forms. Form A, form G and form P are represented by samples from Gamagyang Bay. The parallelogram is based on the population of Aburatsubo Cove (cf. Abe, 1983). Specimens of form M are from Misumi-machi, Kyushu. Suffix number ($n = 1, 2, 3, 4$) indicates adult-n juveniles.

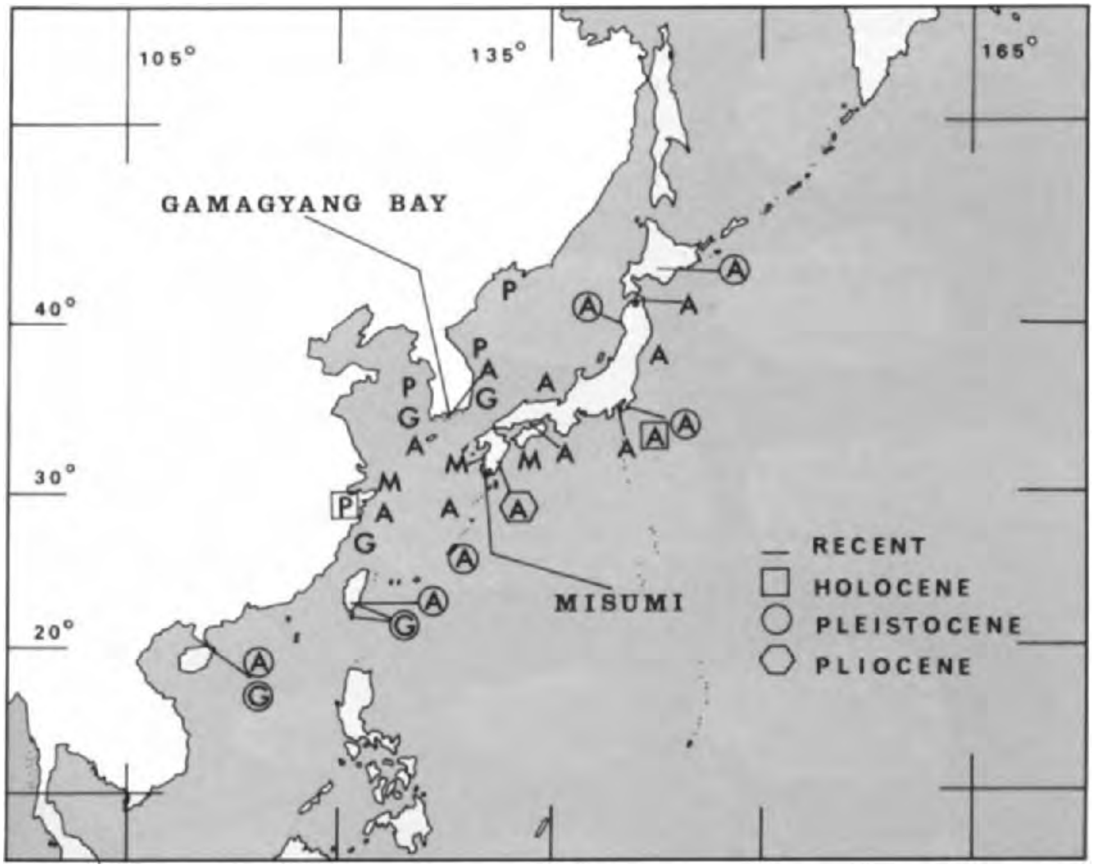
living and fossil specimens has been widely reported from Recent inner bays and post-Miocene shallow marine deposits of East Asia.

Recent specimens of *K. bisanensis* include four morphs. Text-fig. 1 compares the mean values of carapace size with the observed range. Each population is represented by the last several moulting stages. For discussion of sexual dimorphism, see Abe (1983). We now know that populations fall into two distinct groups based on carapace size. The size difference between the two groups can be expressed in a generalized fashion such that adult-n ($n = 0, 1, 2, \ldots$) of the smaller group corresponds to adult-($n + 1$) of the larger group. For instance, adults from the smaller group are almost equivalent to the adult-1 from the larger group. Here a judgement of maturity is based on the marginal infold of the carapace and, in living material, on the degree of development of the copulatory organ.

The second criterion is the ratio of carapace height to length. The smaller value of H/L is due to the elongation of the posterior half of the carapace. Thus, specimens from various local populations are divided into four forms, using two classifying criteria (see Text-fig. 4 of Abe and Choe's paper in this volume). All fossil specimens of *K. bisanensis* in the literature were also found to correspond to one of the four forms. To simplify the following discussion, the four forms are called A, P, M and G after the names of the representative places of their occurrence.

Distribution of the Four Forms

Text-fig. 2 illustrates the distribution of the four forms in east Asia during the last several million years. Insufficiency of the fossil record does not allow us to determine when and where each



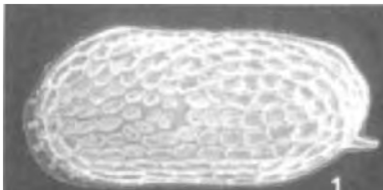
TEXT-FIG. 2—Classification of the four forms. Forms A, P, G and M are named after Aburatsubo Cove, Great Peter Bay, Gamagyang Bay and Misumi-machi respectively.

form originated. The distribution patterns of living populations are principally allopatric but sympatric in part: for instance form A, form G and form P coexist in Gamagyang Bay, Korea and form A and form M around Misumi in Kyushu, Japan.

PERSPECTIVES ON SPECIATION

Of the two primary criteria, the carapace size may be more meaningful and significant than the H/L ratio, because the former divides a population more discretely, while the latter occasionally yields some intermediates. The difference in carapace size should not be attributed to seasonal changes. There are two pieces of evidence for this point; first, as the author reported in 1983, reproduction in Aburatsubo Cove takes place within a limited interval and seasonal difference in size, if any, is negligible. The second line of evidence is the fact that in Misumi, live specimens of both form M and form A are commonly present in the same sample. Thus it seems natural to think that the two groups at first differed in terms of carapace size, and that each of these two groups divided again into two subgroups in terms of H/L ratio. Consequently, a total of four groups have so far been produced and can be recognized at present.

The fact that the distribution pattern of the four forms is essentially allopatric and sympatric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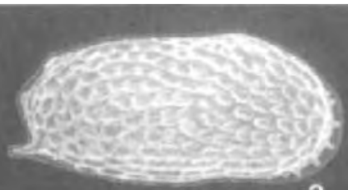
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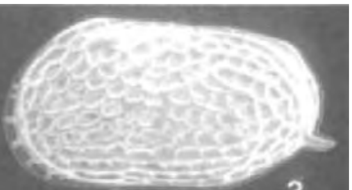
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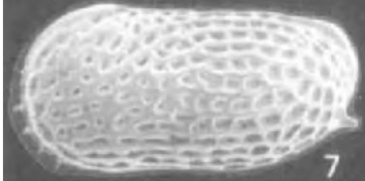
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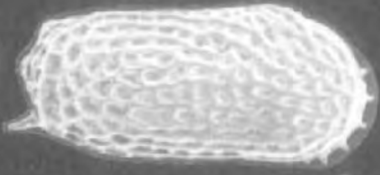
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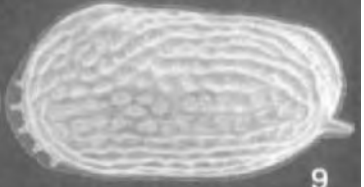
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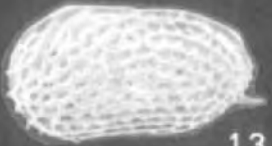
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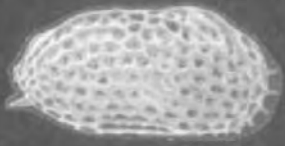
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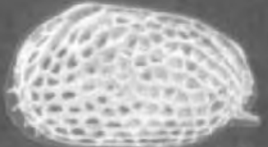
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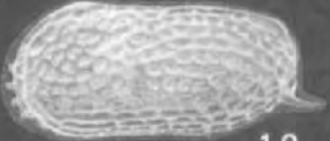
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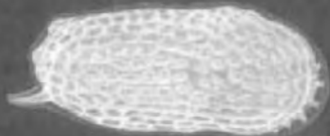
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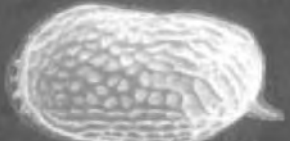
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in a limited area allows us to call them a species group, though it has not yet been decided whether they are a full species or not.

What is, then, the process by which the species group of the four components has speciated? Because differentiation in carapace size is independent of the change in H/L ratio, the following discussion will be focused on the problem of the carapace size only. To generate and fix the larger and smaller group, two independent and serial steps are required to have occurred in the past. The first step is the origin of a new group which has a significantly different phenotype from the existing group. The next step is to subject a variety of new groups to natural selection, so that only successful groups can find their own habitat. They were distributed at first allopatrically and subsequently sympatrically, in part.

We must explain the origin of two sizes of the ostracod body in the first step of speciation. What mechanism could produce such a pair? Because the chronological order of appearance of the two groups is unknown due to an insufficient fossil record, three kinds of answers are possible to the above question; heterochrony, polyploidy and geographical variation within the normal range.

Those who would like to attribute the process to heterochrony have only to point out that the size difference between the two groups corresponds just to the difference between the two successive moulting stages in the group. They can explain that the small group has been produced from the large group by some mechanism like paedomorphosis in which development in two moulting stages had occurred during only one moulting stage in early ontogenical development. This interpretation, however, has two defects. One is that the ostracods of the small-size group have probably as many instars as those of the large-size group. The other defect is that the developmental change in the number and distribution pattern of the reticules and thus the epidermal cells is exactly the same between the two groups, at least in the last four stages.

The second answer, polyploidy, is not faced with any negative evidence. Polyploidy in animals is less commonly reported than in plants, yet some cases are known in crustaceans, including ostracods. Karyotype analysis should be applied, but it is questionable whether chromosomes of this ostracod are amenable to such analysis. Since polyploidy generally produces a larger form than the original one, if this answer is correct, the larger group will be the descendant of the smaller group.

Geographical variation may be the simplest answer. Here the fact which favoured the first answer turns into a defect. Indeed it is likely that the body size has changed little by little, but isn't the actual change beyond the normal range?

Since the change of carapace size and the change of H/L ratio occurred independently, it is most reasonable to suggest that the origin of the two different sizes of the species group is due to polyploidy, and that the variation of H/L ratio was produced by long-term interaction of ostracods with a variable environment.

Next, the second step in speciation may be mentioned. The pattern of distribution of natural populations should reflect the pathway of geographical speciation. The occurrence of two or more species in an isolated habitat is the result of multiple invasions (Mayr, 1963). As for the history of the distributional isolation, changes in the coastline and the ocean currents of East Asia will be important, but at present we have only limited data. When discussing the selection pressure in the

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Plate 1—Figs. 1–6. Form A. 1. Left valve of adult male. 2. Right valve of adult male. 3. Left valve of adult female. 4. Left valve of adult-1. 5. Left valve of adult-2. 6. Left valve of adult-3. Figs. 7–12. Form P. 7. Left valve of adult male. 8. Right valve of adult male. 9. Left valve of adult female. 10. Left valve of adult-1. 11. Left valve of adult-2. 12. Left valve of adult-3. Figs. 13–18. Form G. 13. Left valve of adult male. 14. Right valve of adult male. 15. Left valve of adult female. 16. Left valve of adult-1. 17. Left valve of adult-2. 18. Left valve of adult-3. Figs. 19–24. Form M. 19. Left valve of adult male. 20. Right valve of adult male. 21. Left valve of adult female. 22. Left valve of adult-1. 23. Left valve of adult-2. 24. Left valve of adult-3. (all figures ×50)

local environment, we should not pay much attention to the present-day situation. It should not be assumed that species have originated where they are now found. It is more reasonable to consider that the same group once existed widely in the East China Sea and that the descendants are now living in the limited peripheral regions such as the southern coast of Korea and western Kyushu. An embayment or an inward curve of the coastline is an outward protrusion from the viewpoint of marine dwellers. Therefore, each of the local populations can be regarded as a kind of peripheral isolate.

Although it is not known when and where the diversification of large and small groups occurred, this may be clarified with sufficient knowledge of the fossil record. However, we can say that at present, the larger group is living to the north and the smaller group to the south in the East China Sea, and that here they are in part sympatric. The zonation in distribution pattern of the three forms in Gamagyang Bay (see Text-fig. 5 of Abe and Choe's paper in this volume) may be attributed to two different events. I suppose that a minor change—variation in the H/L ratio—occurred secondarily within a larger group while the two groups of different size coexisted.

Now I conclude that speciation of the *K. bisanensis* species group is almost completed at least with regard to the two major groups of different size. And herewith can we not find another attractive theme of study? The two subgroups based on the difference in H/L of the carapace were produced independently in these two full species. Were they produced by chance or of necessity?

Recognising that what evolves is a population and what selection acts on are the organisms or some unit at the lower level, we should distinguish sharply between the two problems of the population and the individual. Before going on to discuss the evolution of ostracods at the level of populations, we should accumulate more knowledge at the level of individuals. One question must be considered in evaluating the second step in speciation: how can benthonic ostracods extend their distributional range, when their whole life is essentially limited to a bottom habitat without any planktonic stage in early life? The eustatic change of sea level will be the key to this problem. The other question is whether the speciation is truly completed. Culturing experiments can answer whether fertile offspring can be produced by a pair of different forms. In general, culturing of shallow marine benthonic ostracods is not easy, but since I have just succeeded in keeping mud dwelling ostracods alive for more than one year, research in this direction will be possible in the future.

ACKNOWLEDGEMENTS

I thank Professors Tetsuro Hanai, Itaru Hayami and other colleagues at the University of Tokyo for their discussion and advice. I am indebted to Dr. Paul M. Frydl for reading the manuscript.

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DISCUSSION

Adamczak: Did you follow up the variability of the reticulation in your material? Your material looks to me to be an excellent basis for study of pattern analysis.

Abe: Yes, I have examined the variability of the reticulated pattern before, and pointed out in some cases when and where a variation pattern had been produced. I have also clarified the microgeographical cline in the frequency of occurrence of variant forms. Please refer to Abe (1983).

Cronin: Could you please comment on the possibility of sympatric speciation with "ecological" isolation in this group?

Abe: All the components of this species group are considered to crawl in the same manner on the surface of flocculent mud. Therefore such a possibility is extremely rare.

Reyment: Dr. Abe has provided us with an excellent account of variational patterns in ornamental features. With respect to the comment on eustatic effects as a migrational driving force, I can mention that under special, rather rare, circumstances, such as the spread of shallow, narrow epicontinental seas (the Trans-Saharan seaways of the Late Cenomanian, Early Maastrichtian, and the Early Paleocene), the relatively rapid advance of the sea in relation to increasing depth of the encroaching inland sea, can have been a force to be reckoned with, notwithstanding secondary effects such as algal transport (for phytal species) and episodic spreading by strand-wading birds in the case of marine ostracods with eggs able to survive for at least some hours in the free air (*i.e.* withstand dessication). Nonetheless, even if such transport of eggs, and isolated mud-encapsulated individuals etc. is a possibility, the chances of new demes becoming established by avian agencies is slight indeed for bisexual organisms. The basic tenets of quantitative genetics (Falconer, J. (1981) *Quantitative Genetics* [2]; Oliver and Boyd, Edinburgh) tell us that there is a minimum population size below which new populations cannot have a reasonable likelihood of becoming established. A single female or male, or just a few individuals, is insufficient for bisexual organisms, but the chance of success becomes greater for parthenogenetic (hence non-marine) ostracods. Reyment and Brannstrow (1962; *Stocht. Dontri. Geol.* Vol. 3) found something like a $<10\%$ chance of success for eggs of a parthenogenetic ostracod species to succeed in establishing a new deme.

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Evolution and Biogeography of *Orionina* in the Atlantic, Pacific and Caribbean: Evolution and Speciation in Ostracoda, II

THOMAS M. CRONIN AND NANCY SCHMIDT
U.S. Geological Survey, Reston, Virginia and
University of Arizona, Tucson, Arizona U.S.A.

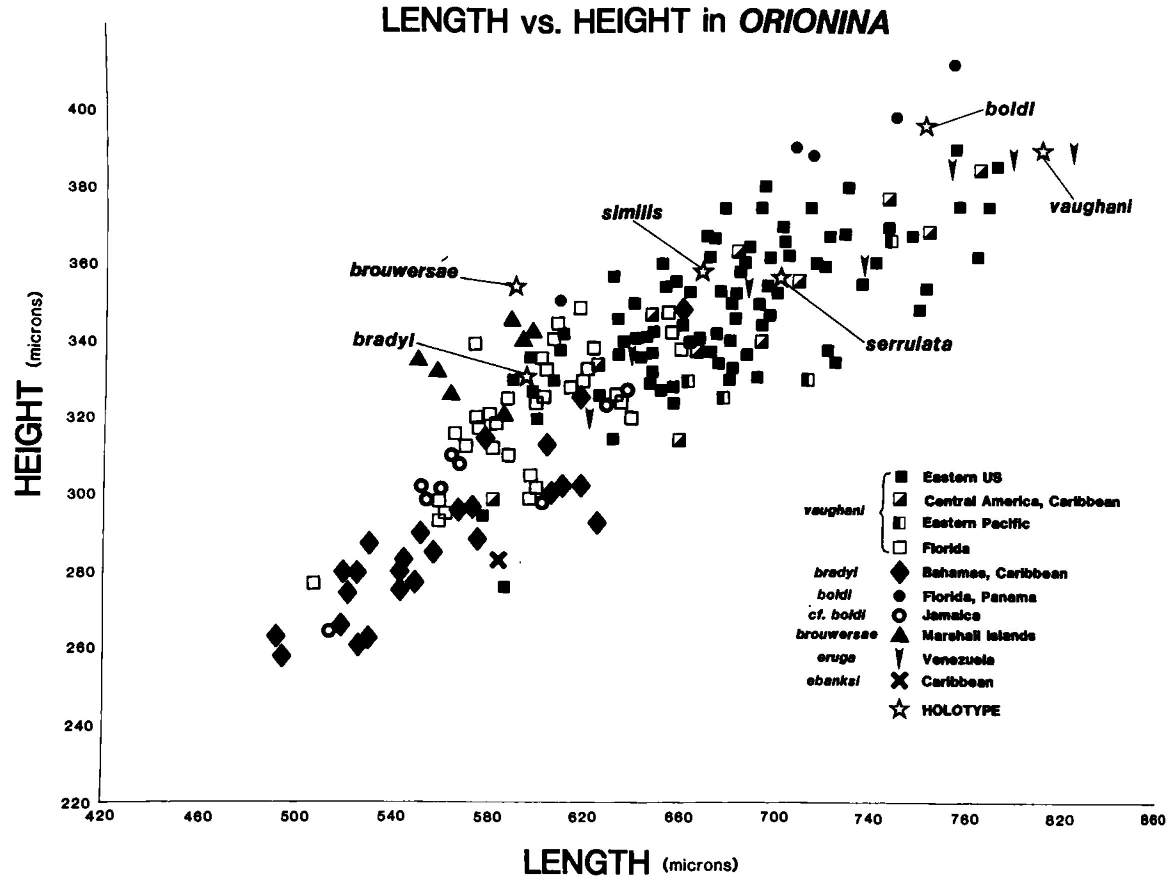
ABSTRACT

We studied the evolution and paleobiogeography of the marine ostracod genus *Orionina* Puri, 1953 by examining specimens from 23 Neogene and Quaternary formations and Holocene material from the Atlantic Coastal Plain, the Caribbean, Central and South America, and the central and western Pacific. Inter- and intraspecific variation in carapace length, surface ornamentation and internal features obtained by morphometric analysis and scanning electron microscopy showed post-middle Miocene *Orionina* can be grouped into 7 species, including two new species, *O. boldi* and *O. brouwersae*. Biostratigraphical and biogeographical data show that geographical isolation of large populations by the Isthmus of Panama since the Pliocene did not result in morphologic divergence, but that the isolation of small populations on remote central and western Pacific islands and atolls resulted in the differentiation of the species *O. flabellacosta* Holden, 1976 and *O. brouwersae* n. sp. Inter-and intraspecific variation in *Orionina* carapace morphology is illustrated with scanning electron photomicrographs.

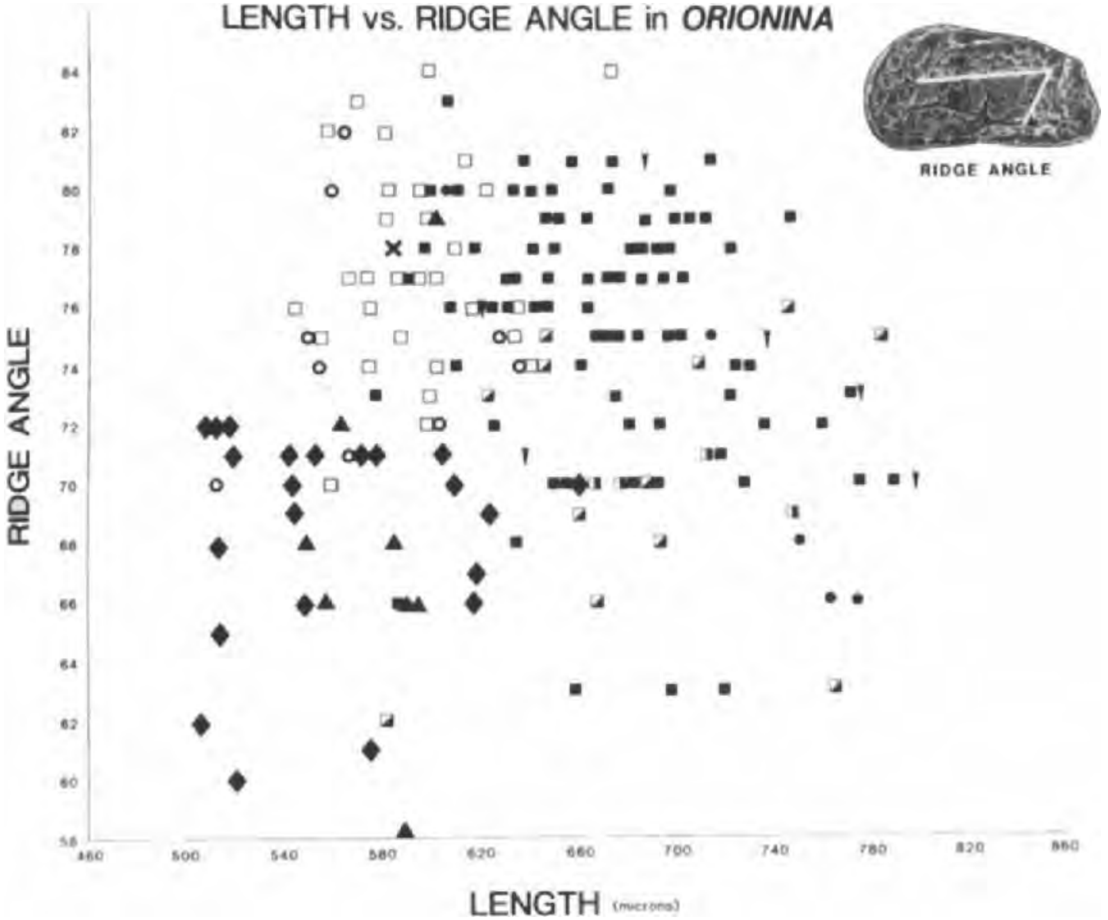
INTRODUCTION

Recognizing biological species in marine ostracods requires identification of a consistent range of morphotypes in time and space, such that intraspecific variation is distinguishable from interspecific variation. In addition, biogeographical patterns should be consistent with the known ecology and dispersal capabilities of the taxon and the geological and climatic history of the taxon's range. This paper is the second in a series of studies designed to investigate speciation and evolutionary patterns in Ostracoda with emphasis on the geography of speciation and the abiotic factors influencing the speciation process. In Part I, Cronin (this volume) outlines in detail the rationale and methodology behind these studies. The present paper focuses on the genus *Orionina,* a monophyletic group of species which, with two important exceptions, has been endemic to tropical, subtropical, and warm temperate regions of the Western Hemisphere from the Oligocene to the Holocene. *Orionina* was selected for detailed study because populations were subjected to two kinds of geographical isolation: "dumbbell" isolation of large populations by the Isthmus of Panama during the Pliocene, and "founder" type isolation of small populations on remote central and western Pacific islands and atolls thousands of miles from the range of ancestral populations.

After its original description based on species from Florida by Puri (1953), Bold (1963) redescribed *Orionina* in detail, giving a comprehensive list of occurrences from the Caribbean and Central America. The type species, *O. vaughani* was described in 1904 by Ulrich and Bassler based on material from the Pliocene of Virginia. Although our results and interpretations of some of the relationships among species differ slightly from those of van den Bold, his work stands as the underlying framework for all subsequent study of this genus. Gunther and Swain (1976) provided important occurrence data from the Gulf of Panama and postulated some evolutionary relationships in *Orionina*. Other important occurrences of *Orionina* from the eastern Pacific are found in Swain (1967, 1969), Swain and Gilby (1967), and Valentine (1976). Holden (1976) described *Orionina flabellacosta* from the Miocene of Midway Island, Hawaii. A new species closely related to Holden's species is proposed below.



Text-fig. 1—Plot of carapace length versus height for *Orionina* from various localities. The *vaughani* group, designated by squares, includes specimens assigned by other authors to *O. pseudovaughani* and *O. serrulata*. Holotype specimens are indicated by open stars (measurements of *O. bradyi*, *O. similis*, *O. serrulata*, and *O. vaughani* holotypes are taken from Bold, 1963).



TEXT-FIG. 2—Plot of carapace length versus angle between median longitudinal ridge and oblique ridge in posterior part of the carapace. See Text-fig. 1 for explanation of symbols.

MATERIAL AND METHODS

Table 1 lists the formations and recent material from which specimens of *Orionina* were examined. Pre-late Miocene species *O. armata* Poag, 1972 and *O. butlerae* Bold, 1965 were not examined, nor was *O. fragilis* Bold, 1963. One hundred and sixty one specimens from our collection were photographed with a scanning electron microscope and using a digitizer, measurements were taken of carapace length, anterior and posterior height, and distance from the anterior margin to the muscle platform. We also measured the angle between the median longitudinal ridge and the oblique ridge (see Text-fig. 2). These data were subjected to various bivariate analyses of which two plots are presented here.

INTERSPECIFIC VARIATION

Table 2 lists the fourteen proposed species of *Orionina* and the taxonomic assignment given in the present paper. We recognize ten species including the three unstudied species *O. armata, O.*

TABLE 1—*Orionina* MATERIAL STUDIED.†

MIOCENE		PLIOCENE	
Formation	*Region*	*Formation*	*Region*
Manzanilla	Trinidad	Yorktown	Virginia
Gatun	Panama	Duplin	North Carolina
Cubagua	Venezuela	Raysor	South Carolina
Cueva de Angostura	Ecuador	Goose Creek	South Carolina
Undescribed	Marshall Islands	Bear Bluff	South Carolina
		Tamiami	Florida
		Pinecrest	Florida
		Jackson Bluff	Florida
		Bowden	Jamaica
		Gurabo	Dominican Republic
		Limon	Costa Rica

PLEISTOCENE		HOLOCENE
Formation	*Region*	*Region*
James City	North Carolina	Bermuda
Chowan River	North Carolina	Acklins Island, Bahamas
Canepatch	South Carolina	Florida Keys
Waccamaw	South Carolina	St. Thomas, U.S. Virgin Islands
Caloosahatchee	Florida	Dominican Republic, North Shore
Bermont	Florida	Dominican Republic, South Shore
Fort Thompson	Florida	Payardi Island, Panama
Undescribed	Marshall Islands	Gulf of Panama
		Campeche Banks, Mexico
		Corinto Bay, Nicaragua
		Fiji

†, Exact locality information is available from T. M. Cronin.

TABLE 2—DESCRIBED SPECIES OF *Orionina*.

Species	This Paper
† *O. armata* Poag, 1972	*O. armata*
Cythere bermudae Brady, 1880	*O. bradyi*
O. bradyi van den Bold, 1963	*O. bradyi*
O. brouwersae new species	*O. brouwersae* n. sp.
† *O. butlerae* van den Bold, 1965	*O. butlerae*
O. ebanksi Teeter, 1975	*O. ebanksi*
O. eruga van den Bold, 1963	*O. eruga*
O. flabellacosta Holden, 1976	*O. flabellacosta*
† *O. fragilis* van den Bold, 1963	*O. fragilis*
O. boldi new species	*O. boldi* n. sp.
O. pseudovaughani Swain, 1967	*O. vaughani*
Cythereis reticulata Hartmann, 1956	*O. vaughani*
Cythere serrulata Brady, 1869	*O. vaughani*
O. similis van den Bold, 1963	*O. similis*?
Cythere vaughani Ulrich and Bassler, 1904	*O. vaughani*

†, Not Studied.

fragilis, and *O. butlerae,* and the seven studied for this paper—*O. boldi, O. bradyi, O. brouwersae, O. ebanksi, O. eruga, O. flabellacosta,* and *O. vaughani.* Each species consists of populations having a distinct morphotype consistently distinguishable from the other species in populations examined from most of their stratigraphical and geographical ranges. Plate 1 illustrates the seven species and Text-fig. 1 plots their carapace lengths and heights. These figures should be referred to in the following summaries of the characteristics of each species.

Orionina vaughani is comprised of a complex of populations all having relatively large carapaces, strong sexual dimorphism, well-developed ridges and surface reticulation, and, in some populations, variable radial pore patterns. The intraspecific variation and synonymy of *O. vaughani* with other species is discussed below. *O. bradyi* has a small carapace, lacks the vertical posterior ridge present in other species, and has a low angle between the medial and oblique ridges (see Pl. 1, fig. 1). Sexual dimorphism is not as pronounced as in other species of *Orionina*. *O. eruga* displays a very large, elongate carapace, a strongly convex dorsum and less-tapered posterior end. The murae forming the reticulum are not as sharp as in *O. vaughani*. *O. ebanksi* is very similar to *O. bradyi*, especially in its small size and evenly reticulate ornamentation. It differs in having its dorsal ridge merge gradually with the dorsum in contrast to the sharper intersection in *O. bradyi* and in the curved shape of the dorsal margin. *O. brouwersae* is quite distinct from other members of the genus and is characterized by a very high carapace (Text-fig. 1) and a distinct pattern of longitudinal ridges. Also, the anterior ridge runs through the eyespot continuing to the dorsal margin in contrast to the ridge position in other species. *O. flabellacosta* lacks the prominent medial and vertical ridges typical of Caribbean and Atlantic *Orionina*, but has the characteristic curved ventral ridge and reticulate surface. Gunther and Swain (1976) illustrated a large, strongly calcified species, which they designated as *Orionina* n. sp. 2, from the Gulf of Panama. We have found this form in the Pliocene of Costa Rica, and in modern sediments off the Florida Keys. We describe this new species as *O. boldi* below.

INTRASPECIFIC VARIATION

We gave considerable attention to the relationships between *Orionina vaughani* and the species *O. serrulata*, *O. pseudovaughani*, and *O. reticulata*, each long recognized as closely related, but usually separated on the basis of minor differences. Specimens that have been identified as *O. serrulata* are said to be identical to *vaughani* in external appearance, differing only in the presence of indentations in the line of concrescence and bundling of radial pores, whereas *O. vaughani* has numerous parallel, straight pores (Bold, 1963). In a preliminary study of Gulf of California ostracods, Swain *et al.* (1964) identified *O. vaughani* for the first time from the Pacific, but later Swain (1967) redescribed these populations as *O. pseudovaughani*, which he characterized as differing from *O. vaughani* in having three rather than four pillars in the anterior vestibule. Swain also pointed out that these populations might be conspecific with *O. serrulata*, but he considered *O. serrulata* to have a confused taxonomic history.

We regard *O. serrulata*, *O. pseudovaughani*, and *O. reticulata* as conspecific with *O. vaughani* and believe that the minor differences among them represent interpopulational variation, perhaps related to local environmental conditions. We don't consider the variation in radial pores a specific level character because we have observed populations from the Limon of Costa Rica that have individuals with both the straight, parallel pattern and the bundled pattern. Similarly, Gunther and Swain (1976) illustrate these two types of pore pattern in populations from the Gulf of Panama and they assign them to two species (*O. vaughani* and *O. pseudovaughani*). It is our opinion that these two morphotypes belong to a single species. Many other shallow marine genera, such as *Proteoconcha* (Plusquellec and Sandberg, 1969; Hazel and Cronin, this volume) show strong variation in radial pores. Text-fig. 1 shows the similarity in carapace length and height of *Orionina* populations from the eastern United States, Central America and the Caribbean, the eastern

Pacific and Florida. The SEM photographs in Plate 2 show the similarity in surface ornamentation of populations from different regions. The evidence shows that intraspecific variation is substantially less than interspecific variation within the genus. Plate 2 illustrates this point with four specimens of *O. boldi* n. sp. This species almost certainly descended from Caribbean populations of *O. vaughani* but the two species are consistently distinct from one another in all the populations studied. There are no gradational populations between the two species.

GEOGRAPHICAL ISOLATION IN *ORIONINA*

The formation of the Isthmus of Panama during the Pliocene, about 3 to 4 million years ago, represents a major barrier to the genetic interchange of eastern Pacific and Caribbean populations that were formerly contiguous with each other. That *Orionina* lived on both sides before the Isthmus developed and was not artifically introduced into the Pacific is demonstrated by Miocene and early Pliocene occurrences throughout the Caribbean and southeastern North America (Bold, 1963), in the Pacific at Midway Island (Holden, 1976), and reported here for the first time, in Ecuador and the Marshall Islands. Evidence from the two species known as fossil and/or Holocene from both sides indicates minor morphological divergence of populations since separation several million years ago. *Orionina vaughani* is known pre-and post-Isthmus on both sides and comparison of specimens illustrated in Plate 2 show a strong morphological similarity between Pacific and Atlantic/Caribbean forms. *O. boldi* occurs in Holocene sediments on the Pacific side in the Gulf of Panama and off southern Florida. As a fossil, it is known from the Pliocene of Costa Rica. Although much less common than *O. vaughani,* there are no consistent differences in carapace morphology in populations from the different regions (Pl. 2).

A second type of barrier isolating shallow water populations is deep water. Deep water separates many populations of *Orionina* living off Caribbean Islands from shelf populations off the coasts of the Americas and from each other. However, the distances across these barriers is relatively small and they were even less during the numerous glacial periods when sea level was 100 to 150 metres lower that its present level. Consequently, there is a much higher probability of passive dispersal of ostracods (possibly on drifting seaweed, see Teeter, 1973; Cronin, this volume) among western Atlantic, Caribbean and Gulf of Mexico populations than there is among more distant islands such as the Hawaiian Islands, the Marshall Islands and off Fiji, where *O. flabellacosta* and *O. brouwersae* occur. In the case of these two Pacific species, alternative hypotheses might explain the seemingly anomalous occurrence of *Orionina,* a genus otherwise restricted to the eastern Pacific, western Atlantic and Caribbean. One alternative is that these species are not phy-

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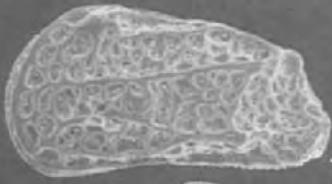
PLATE 1—Fig. 1. *Orionina bradyi* Bold, 1963. Lateral view, left valve, female (USNM 403818, Holocene, Bahamas), ×78 Figs. 2, 4. *Orionina brouwersae* n. sp. 2. Internal view, left valve, female (USNM 403819, Recent, Fiji), ×78 4. Lateral view, left valve, female (Holotype, USNM 403820, early Miocene-late Pliocene, Marshall Islands), ×78 Fig. 3. *Orionina* cf. *O. brouwersae* Cronin and Schmidt n. sp. Lateral view, left valve, female (USNM 403821, early Miocene-late Pliocene, Marshall Islands), ×78 Figs. 5, 6, 9, 10. *Orionina vaughani* (Ulrich and Bassler, 1904). 5. Lateral view, left valve, female (USNM 403822, Pliocene, Costa Rica), × 78 6. Lateral view, left valve, male (USNM 403823, Pliocene, Costa Rica), ×78 9. Lateral view, left valve, female (USNM 403824, Pliocene, North Carolina), ×78 10. Lateral view, left valve, male (USNM 403825, Pliocene, North Carolina), ×78 Figs. 7, 8. *Orionina boldi* n. sp. 7. Lateral view, left valve, female (Holotype, USNM 403826, Holocene, Florida), × 78 8. Lateral view, left valve, male (USNM 403827, Holocene, Gulf of Panama), ×78 Figs. 11, 12. *Orionina* cf. *O. eruga* Bold, 1963. 11. Lateral view, left valve, female (USNM 403831, Pliocene, Venezuela), ×78 12. Lateral view, left valve, male (USNM 403832, Pliocene, Venezuela), ×78 Fig. 13. *Orionina ebanksi* Teeter, 1975. Lateral view, left valve, female (USNM 403833, Holocene, St. Thomas, U. S. Virgin Islands), ×78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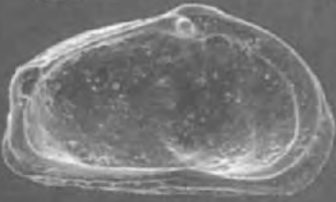
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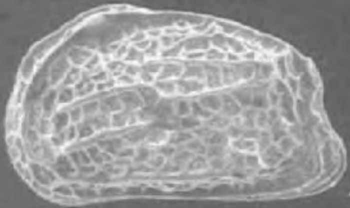
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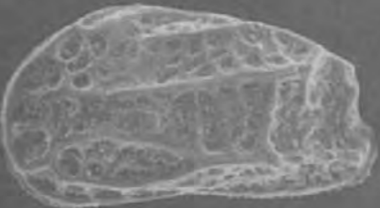
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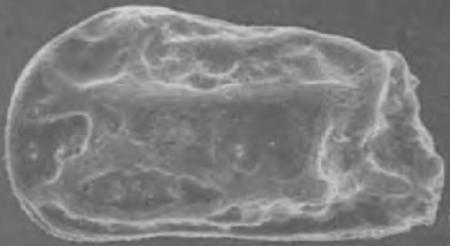
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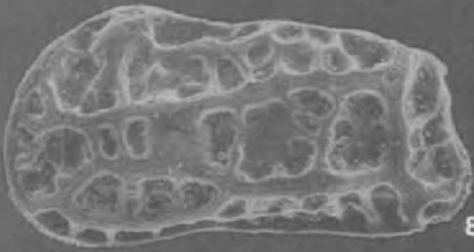
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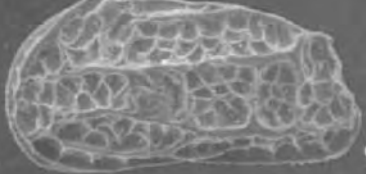
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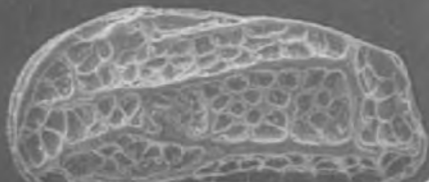
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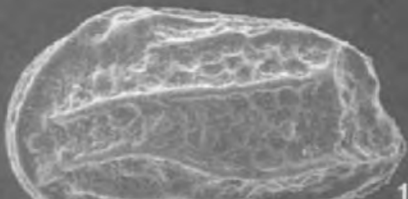
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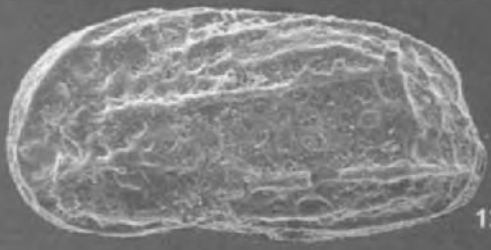
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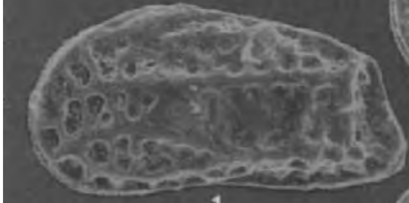

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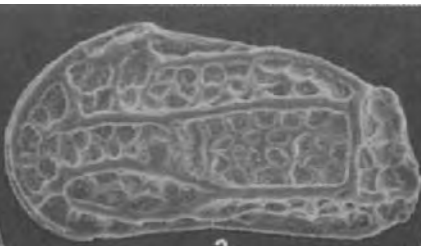

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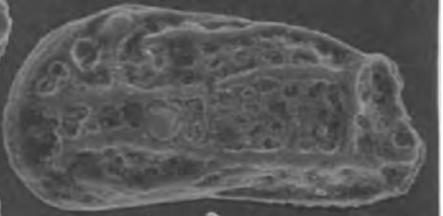

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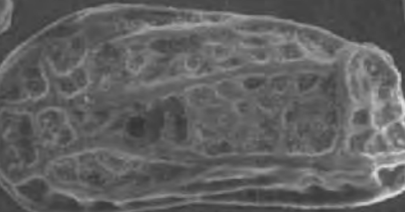

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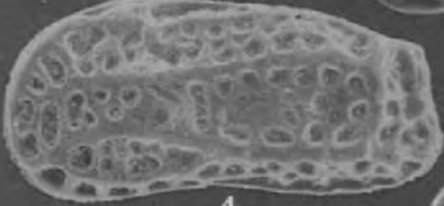

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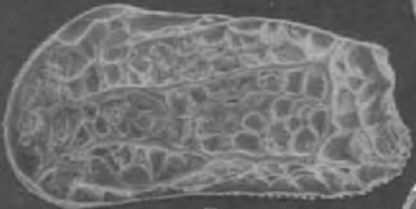

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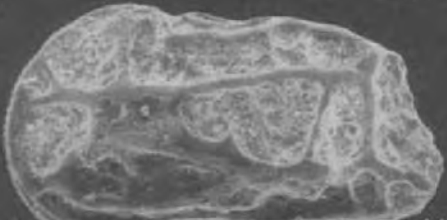

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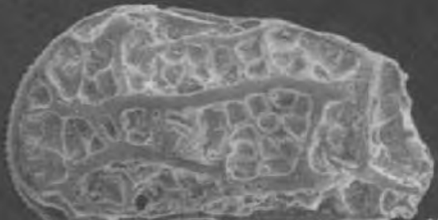

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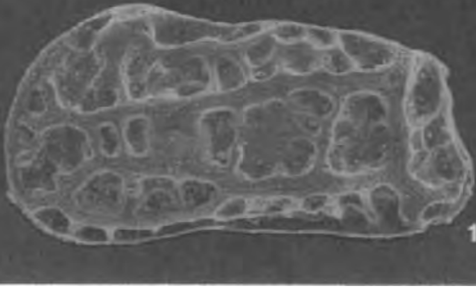

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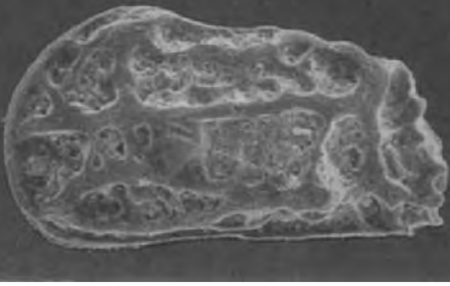

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logenetically related to Caribbean *Orionina,* but are descended from another western Pacific hemicytherine lineage. At present, well-documented Miocene to Holocene faunas from Midway (Holden, 1976) and the Marshall Islands (Cronin, unpublished data) do not show any likely candidates. Further, as recognized by Holden, external and internal carapace features are clearly *Orionina*-like, although these central and western Pacific forms have evolved so that they are distinct from other species in details of carapace ornament. We consider the most reasonable interpretation to be that *O. flabellacosta* split from early Miocene populations of *Orionina* that became isolated in the Hawaiian Islands, and that during the middle or late Miocene, *O. brouwersae* split when populations became dispersed farther west in the Marshall Islands. Although the Pacific data are still sparse and phylogenetic relationships unclear, the evidence indicates at least two speciation events occurred when relatively small populations became isolated on small islands, probably through passive dispersal on seaweed (Teeter, 1973). These speciation events contrast with the lack of speciation or even intraspecific morphologic divergence that resulted from isolation by the Isthmus of Panama.

The patterns observed in *Orionina* are, of course, subject to different interpretations. For example, Gunther and Swain (1976) hypothesized that major barriers existed between Jamaica and Florida and between Venezuela and the eastern Pacific such that "three more-or-less isolated evolving groups" (p. 141) of *Orionina* can be recognized. Based on our distribution data and the inferred dispersal capabilities of tropical ostracod genera (see also Teeter, 1973), we do not believe there were effective barriers east of Central America within the Caribbean, Gulf of Mexico, and western Atlantic regions. Although *O. ebanksi* and *O. boldi* probably evolved within this region, there is no direct evidence for geographic isolation having been the cause. Further, considering the 25 million year history of the genus, surprisingly few species have evolved. Even the land barrier formed by the Isthmus of Panama has not yet led to divergence within *Orionina.* We believe the preliminary evidence from the central and western Pacific shows isolation of small populations led to the formation of at least two new species and the most significant morphological divergence within the genus. Overall, the results support the hypothesis of Valentine and Jablonski (1983) that geographical isolation of large populations of benthic invertebrates results in slow rates of morphological change. Conversely, rapid morphological change accompanying speciation events occurs when small populations become isolated.

SYSTEMATIC PALEONTOLOGY

Our study was designed to investigate the effects of types of geographical isolation on the genus *Orionina.* A major taxonomic revision is beyond the scope of this paper. Further, the phylogenetical relationships of some species remain unclear, so an abbreviated systematic section is given.

PLATE 2—Figs. 1–10. *Orionina vaughani* (Ulrich and Bassler, 1904). 1. Lateral view, left valve, (USNM 403834, Holocene, Gulf of Panama), ×78 2. Lateral view, left valve, (USNM 403835, early Pleistocene, North Carolina), ×78 3. Lateral view, left valve, (USNM 403836, early Pleistocene, North Carolina), ×78 4. Lateral view, left valve, (USNM 403837, Holocene, Gulf of Panama), ×78 5. Lateral view, left valve, (USNM 403838, middle Pleistocene, South Carolina), ×78 6. Lateral view, left valve, (USNM 403839, early Pliocene, South Carolina), ×78 7. Lateral view, left valve, (USNM 403840, Miocene, Ecuador), ×78 8. Lateral view, left valve, (USNM 403841, Pliocene, Panama), ×78 9. Lateral view, left valve, (USNM 403842, middle Pleistocene, Florida), ×78 10. Lateral view, left valve, (USNM 403843, late Miocene, Venezuela), ×78 Figs. 11–14. *Orionina boldi* n. sp. 11. Lateral view, left valve, (USNM 403828, Pliocene, Costa Rica), ×78 12. Lateral view, left valve, (USNM 403829, Pleistocene, Florida), ×78. 13. Lateral view, left valve, (USNM 403827, Holocene, Gulf of Panama), ×78 14. Lateral view, left valve, (USNM 403830, Holocene, Florida Keys), ×78.

Van den Bold (1963) discussed early studies of *Orionina* and should be consulted for Caribbean occurrences, synonymies, and detailed descriptions of most species. We concentrate here on the two new species and their distinction from other *Orionina.* As mentioned above, we did not examine *O. armata, O. fragilis* and *O. butlerae,* but we consider at least the first two as valid species distinct from those illustrated here. *Orionina butlerae* we believe to be in need of further study.

Genus ORIONINA Puri, 1954

ORIONINA BOLDI Cronin and Schmidt n. sp.

(Pl. 1, figs. 7, 8; Pl. 2, figs. 11–14)

Etymology.—Named for Dr. W. A. van den Bold, Louisiana State University, in honor of his pioneering work on *Orionina.*

Types.—Holotype, a female left valve from the Holocene off the Florida Coast, USNM 403826 (Pl. 1, fig. 7). Sample 1554 of Hathaway (1971), 55 m water depth 26° 31.1′N, 80° 01.4′W.

Illustrated specimens.—USNM 403827 (Pl. 1, fig. 8; Pl. 2, fig. 13); USNM 403828 (Pl. 2, fig. 11); USNM 403829 (Pl. 2, fig. 12); USNM 403830 (Pl. 2, fig. 14).

Diagnosis.—Very large and heavily calcified, having very thick longitudinal ridges and two subvertical ridges in the posterior region that connect the longitudinal ridges.

Description.—Carapace slightly more rectangular and less tapered posteriorly than other *Orionina,* valve walls very thick and heavily calcified. Lateral surface of valves having two prominent longitudinal ridges that converge near the muscle node and that diverge anteriorly and posteriorly from the anterocentral region. Posteriorly, there is a strong nearly vertical ridge and anterior of this, a distinct oblique ridge connecting the longitudinal ridges. Postero-ventral ridge is sometimes nodose. Between the ridges the surface is variably reticulate to almost smooth. Internal features are typical for the genus and there are many straight, parallel, evenly spaced radial pore canals.

Remarks.—Some female specimens resemble large males of *O. vaughani,* but differ in their larger size, and the presence of the well-developed oblique ridge, anterior to the posteroventral ridge, that connects the longitudinal ridges. Some specimens resembling *O. boldi* were found in the Bowden Formation of Jamica, but they were much smaller and require additional study.

Occurrence.—Recent off South Florida and Gulf of Panama; Bermont Formation, middle Pleistocene, subsurface of South Florida; Limon Formation, Pliocene, Costa Rica.

ORIONINA BRADYI Bold, 1963

(Pl. 1, fig. 1)

Remarks.—This widespread species is well-known throughout the Caribbean (Bold, 1963). Dias-Brito *et al.* (this volume) has also found it in Sepetiba Bay, Brazil. Bold (1963, p. 45–47) considers some specimens described by Brady (1880) as *Cythere bermudae* to be synonymous with *O. bradyi* and discusses the taxonomy of these species in detail.

ORIONINA BROUWERSAE Cronin and Schmidt n. sp.

(Pl. 1, figs. 2, 4)

Etymology.—Named for Dr. Elisabeth M. Brouwers, U. S. Geological Survey.

Types.—Holotype, a female carapace, USNM 403820, from the Pliocene (a depth of 498 feet in a core) from Enewetak Atoll, Marshall Islands (Pl. 1, fig. 4).

Illustrated specimens.—USNM 403819 (Pl. 1, fig. 2).

Diagnosis.—Relatively low length/height ratio, valve surface evenly reticulate, having two short parallel anterior ridges, two fine posterior ridges, an anterior marginal ridge running through the eye tubercle.

Description.—Carapace arched, convex dorsally, evenly rounded anteriorly, surface ornament consisting of reticulation and polygonal fossae. An anterior marginal ridge runs through eye tubercle continuing along dorsal margin. Longitudinal ridges differ from those in other *Orionina,* consisting of two short anterior ridges, two fine, posterodorsal ridges and a long ventral ridge. Ridges and murae are relatively thin compared to Caribbean species.

Remarks.—Plate 1, figure 3 shows a morphotype that is tentatively assigned to this species based on its size shape and reticulate surface. However it clearly differs from the Holotype illustrated in Plate 1, figure 4 in the development and orientation of posterodorsal and to a lesser extent in the anterocentral ridges. Both these specimens come from the subsurface Miocene-Pliocene of Enewetak Atoll. Specimens from recent sediments of Fiji are more similar to the holotype specimen and are confidently placed in this species. *Orionina flabellacosta* Holden 1976, differs from *O. brouwersae* in having a curved ventral ridge, lacking the short anterior ridges and having larger male carapaces.

Occurrence.—Miocene to Pleistocene of Enewetak Atoll; Recent off Fiji.

ORIONINA cf. O. ERUGA Bold, 1963
(Pl. 1, figs. 11, 12)

Remarks.—The specimens illustrated in Plate 1 from the Pliocene Cubagua Formation of Venezuela have a stronger ridge than those illustrated by Bold (1963) from the Miocene of Trinidad.

ORIONINA FLABELLACOSTA Holden, 1976

Orionina flabellacosta HOLDEN, 1976, p. F20, Pl. 3, figs. 5–7; Pl. 11, fig. 6.

Remarks.—Holden (1976) described and illustrated this species from the Miocene of Midway, Hawaiian Islands.

ORIONINA VAUGHANI (Ulrich and Bassler, 1904)
(Pl. 1, figs. 5, 6, 9, 10; Pl. 2, figs. 1–10)

Cythere serrulata BRADY, 1869, p. 153, Pl. 18, figs. 11, 12.
Cythere vaughani ULRICH AND BASSLER, 1904, p. 109, Pl. 38, fig. 25.
Cythereis reticulata HARTMANN, 1956, p. 37, figs. 45–52.
Orionina pseudovaughani SWAIN, 1967, p. 86, Pl. 3, figs. 5a, b; Pl. 4, figs. 6a-c; Text-figs. 50d-g, 54c.

Remarks.—As discussed in detail above, we believe *Orionina vaughani, O. serrulata, O. pseudovaughani* and *O. reticulata* constitute different populations and morphotypes of the same species. Although *serrulata* was described by Brady in 1869, Bold (1963) was not able to find its holotype and Swain (1967) expressed concern over the confusing status of this species. We therefore use *vaughani* to refer to this well known species.

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Polymorphism and Speciation
Medoc Ostracods at the Eocene/Oligocene Boundary
(Aquitaine, France)

O. DUCASSE, C. LÉTÉ AND L. ROUSSELLE
Institut de Géologie du Bassin d'Aquitaine, Université de Bordeaux, Talence, France

ABSTRACT

Wet drilling and numerous outcropping sections at the northwestern Aquitaine basin (Medoc) yielded continuous sedimentary records of the Eocene/Oligocene boundary within shallow and unstable marine and laguno-marine environments.

Successive ostracod assemblages ranging from the upper Eocene to the basal Oligocene revealed five stratigraphic stages. Significant ostracofaunal modifications appear to have occurred between the late upper Eocene (horizon 4) and the basal Oligocene (horizon 5). Populational transformations recorded in nine polymorph species belonging to the genera *Cytheretta, Hammatocythere, Pokornyella, Quadracythere* and *Schuleridea* were studied. After a markedly significant polymorphism stage corresponding to the late upper Eocene phase, a structural populational readjustment occurs at the base of the Oligocene, accompanied by a reduction in polymorphism and/or number of individuals; only three morphs show inflated demographic characteristics. For instance, the "strangled" *Hammatocythere oertlii* form (Ducasse) becomes the initial bud of *H. hebertiana trituberculata* (Reuss) s.s. Keen: a polymorph well-represented species in the Aquitaine Oligocene.

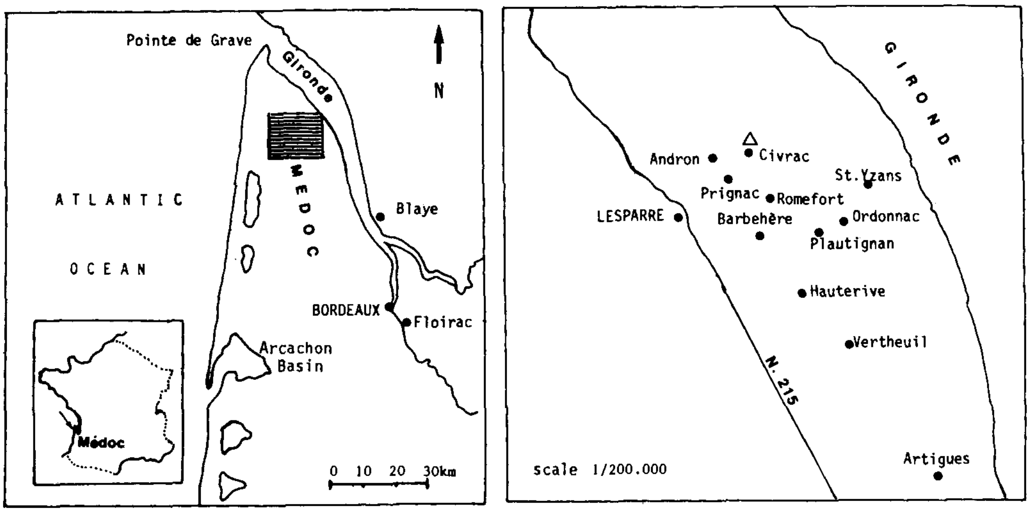
Aspects of monomorphic speciation are studied within a context of Eocene/Oligocene climatic crisis and against a background of fluctuating paleogeographic conditions in the Paleogene northern Aquitaine.

The contribution of polymorphism to speciation poses a number of problems not yet solved. The geographic isolation of a morph could be accounted for by environmental selection; this implies the existence of a close relationship between morphs and environment. The genetic drift could then only affect a fragment of the genetic pool governed by only one morph, rather than a hazardous sampling of the genome species.

This type of speciation is congruent with both the Darwinian principle because of the importance of selection, and the punctualist because of diagram the limited impact it has (only one fraction) on the motherspecies.

INTRODUCTION

Dorst (1974) postulated, on the basis of observations on modern birds, that transitory polymorphism is responsible for the differences noted in certain local forms and for the appearance of a new secondary monomorphism that gives rise first to the fixation of a subspecific, and later specific,



Text-fig. 1—Location of the zone studied. ●, outcrops; △, drillings.

stock of population. He also assumed that geographic isolation can separate fractions of polymorphic populations within which a morph becomes—under the pressure of various factors—dominant and later unique, the other morphs disappear or occur sporadically. Dorst also advanced that evolutionary trends are observable beyond the subspecific stage, thereby implying that polymorphism is, at least theoretically, the origin of speciation.

Isolation of morphs is often observed with fossils; their development through time contributes, in fact, to a better understanding of evolution. Rousselle (1978) showed that outside a large Iberian/Moghrebin polymorphic group of *Stolmorhynchia bouchardi* (Dav.) s.l. (Toarcian Brachiopoda Rhychonellacea) the segregation of two populations (one in France and Great Britain and the other in Morocco, South Rif domain) had led to the individualization of two newborn species, both borrowing their characteristics from one of the morphs of the major species.

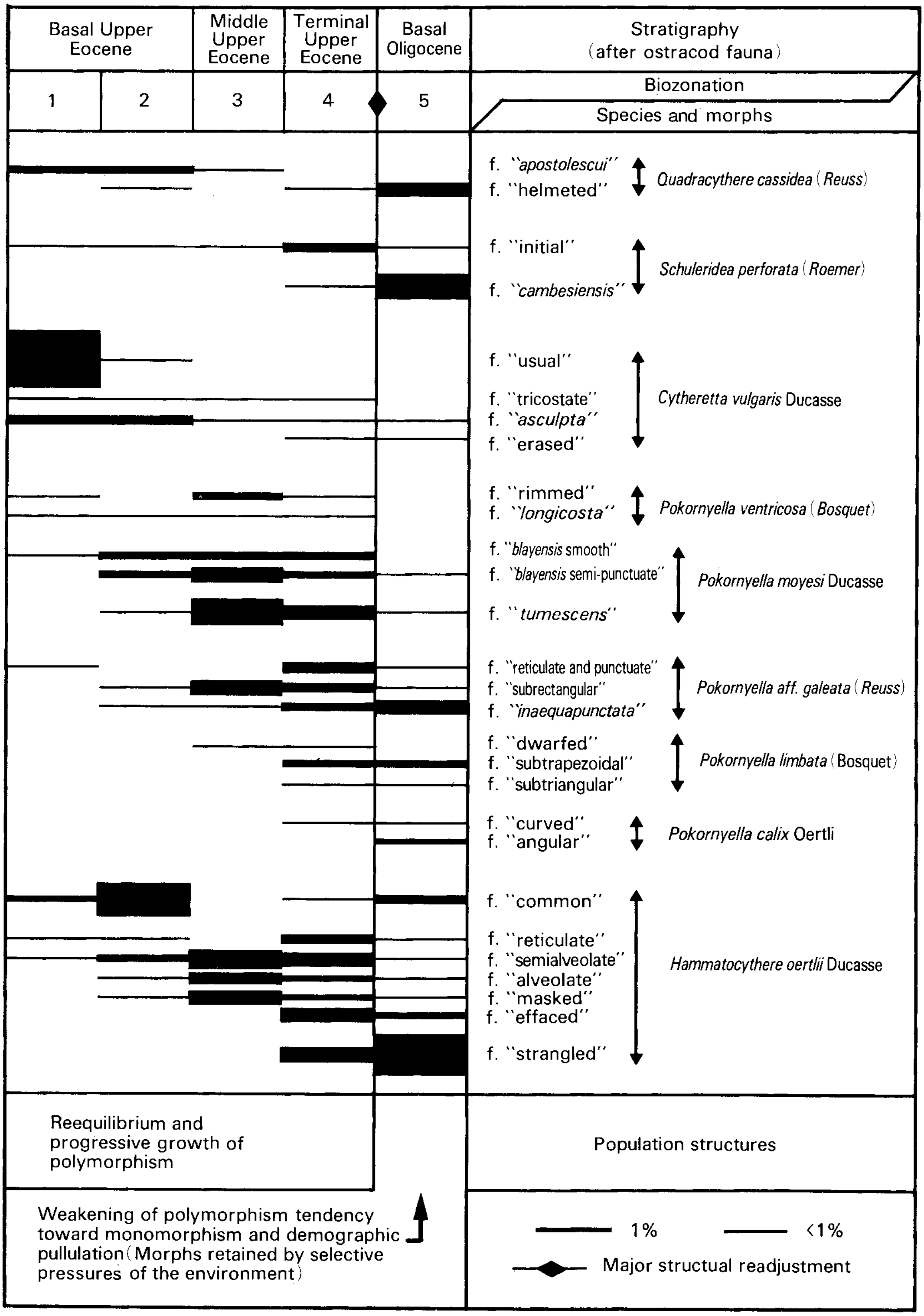
As early as 1963, Reyment drew attention to the importance of polymorphism in ostracods. In his recent works (1982, 1983a and b) he provides information on the setting of *Oertliella chouberti R.* from a *O. tarfayensis R.* morph.

The evolutive transition from *Hammatocythere oertlii* Ducasse to *H. hebertiana trituberculata* (Reuss) s.s. Keen has in this study been reconstructed in the upper Eocene and basal Oligocene levels from northwest Aquitaine (Text-fig. 1). This example is a clear illustration of speciation by conservation and dominance of a morph. It emphasizes the part played by selection.

Ostracods at the Eocene/Oligocene Limit North of the Aquitaine Region (Ducasse *et al.*, 1985)

Information on Medoc ostracod assemblages occurring successively from the upper Eocene to the base of Oligocene enabled us to set five successive stratigraphic horizons corresponding to local biozones. Similar results were obtained as early as 1972 by Marionnaud on the basis of paleontological analyses (macro/microfauna and microflora). These ostracofaunal and terrain data helped us to study co-evolution of ostracods and environments both in time and space in the upper Eocene and lowermost Oligocene.

Between biozone 4, indicating the regression of the end of the Eocene and biozone 5, correspond-



TEXT-FIG. 2—Populational structures of some Medoc ostracod species at the Eocene-Oligocene boundary.

ing to the transgression of the Oligocene base, the number of forms or species diminishes. This decrease is uncommon and must have occurred during a major climatic stress (drop in temperature) characterizing the Eocene/Oligocene limit (Cavelier, 1979; Chateauneuf, 1980; Pomerol, 1985).

In order to better understand the impact of environment upon organisms, we took into account eventual species changes and carried out structural populational analyses. To this end we examined species belonging to five genera (Text-fig. 2). These species show characteristics that are typical of phenotypic polymorphism: their populations consist of various groups or morphs marked by size, contour and/or ornamentation features. We made sure beforehand that sexual dimorphism was not the cause of this phenotypic polymorphism.

Intraspecific evolution of species throughout the upper Eocene varies both qualitatively (number and nature of morphs) and quantitatively (number of individuals within morphs). Nevertheless, the most significant change in species is noted between the late upper Eocene (biozone 4) and basal Oligocene (biozone 5). This change may be reflected in:

—total extinction (*P. ventricosa*);
—partial extinction (*P. moyesi*);
—beginning of development (*P. calix*);
—structural readjustment by morph replacement (*H. oertlii, Q. cassidea, S. perforata*).

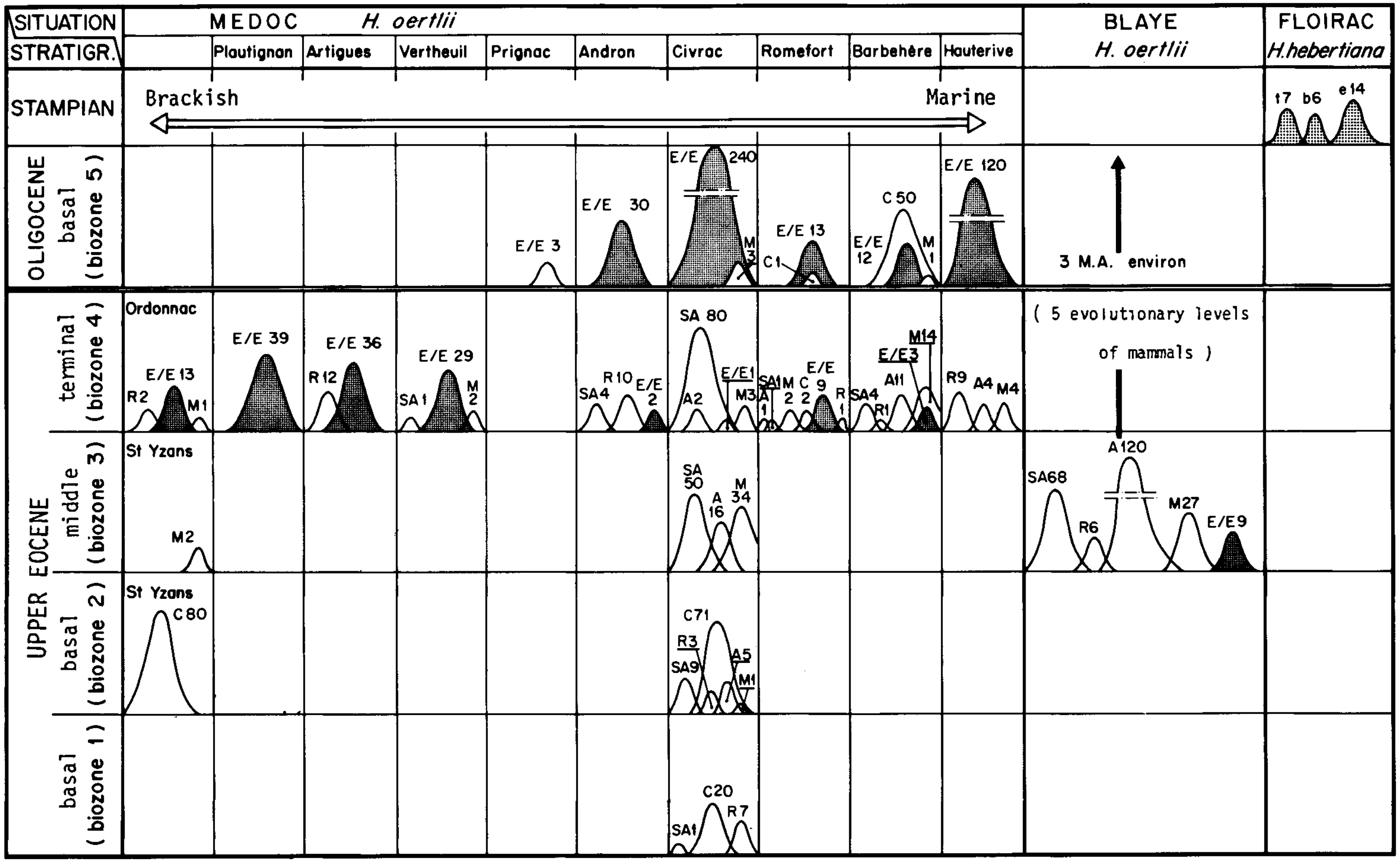
Generally, morphs having undergone recent differentiation persist and multiply rapidly.

FROM *Hammatocythere oertlii* (UPPER EOCENE) TO *H. hebertiana trituberculata* (LOWER OLIGOCENE)

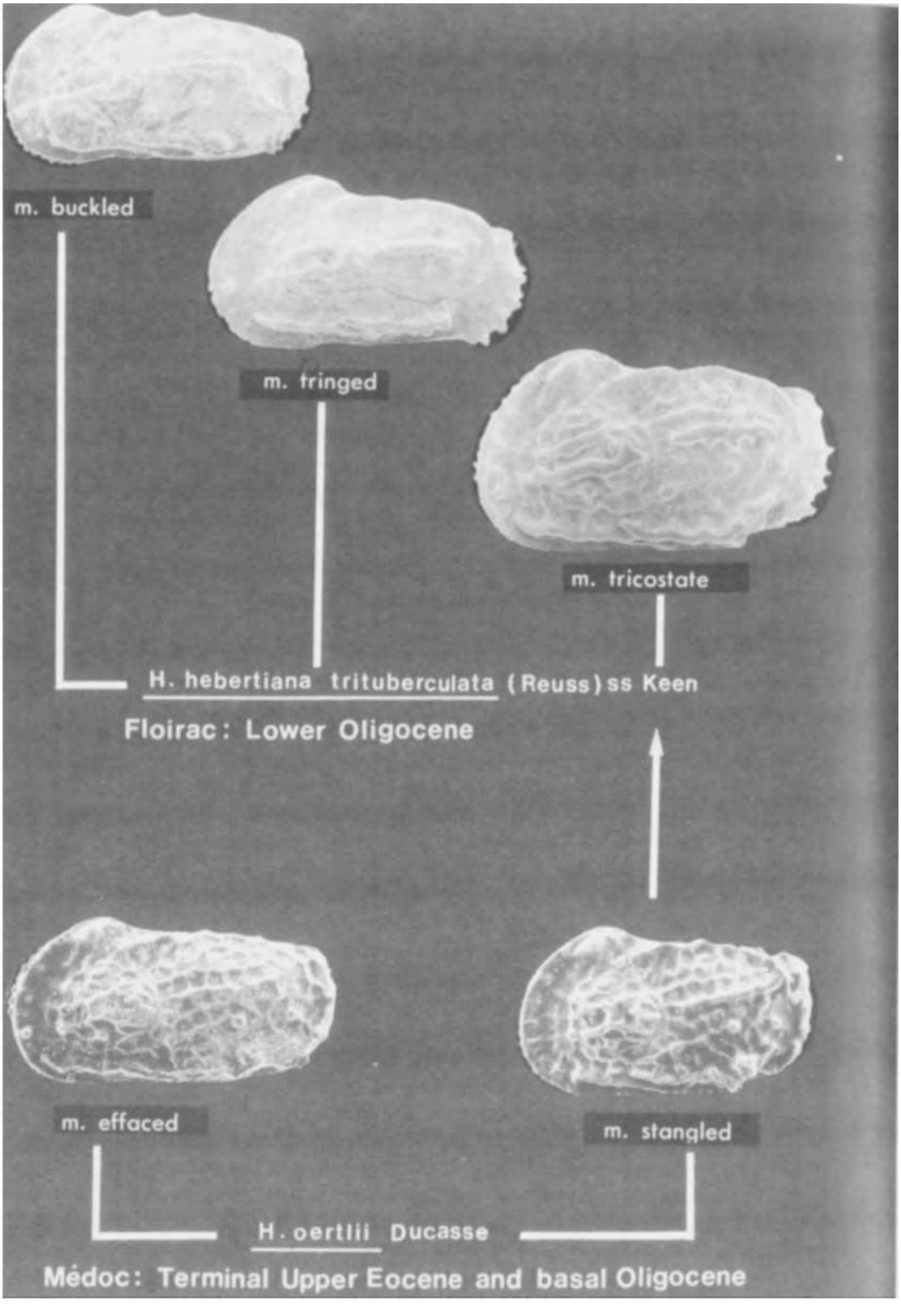
The upper Eocene in Blaye, north of Bordeaux, is characterized by the frequent occurrence of *H. oertlii* populations whose polymorphism has been studied by Keen (1976), and Ducasse and Rousselle (1978, 1979). The polymorphism of these populations implies micro-evolutive fluctuations (differential morph percentages) induced by the instability of a margino-littoral environment. In the trangressive level that marks the top of the sedimentary series, studied populations attain maximum polymorphism with five individualized morphs. A new species, *H. hebertiana trituberculata*, appears in Floirac after a gap corresponding to the late upper Eocene and lowermost Oligocene. This species is so like *H. oertlii*, that as early as 1979 we considered it to be its plausible descendant and foresaw the arrival of a new species from a morph of the mother-species. From then onwards, we only had to trace the evolution of speciation and determine its causative agent.

The continuous sedimentary record obtained in the Medoc region and corresponding to the Eocene/Oligocene limit enabled us to locate *H. oertlii* and fill in the gaps of its historical background. Text-figure 3 shows the spatio-temporal evolution of the species in Blaye and Medoc. Morphs are represented by curves indicating the numerical importance of their representatives. Both the sedimentological and ostracofaunal contexts helped us to determine the ecological polarity of the environment, ordinarily a difficult task because of the instability of the margino-littoral milieu.

The polymorphism of *H. oertlii* appears to be more intense in marine rather than in brackish environments. It was also noted that during the late upper Eocene (biozone 4) "strangled/effaced" morphs are far less represented in marine than in brackish milieus, whereas during the basal Oligocene they persist and thrive in environments vivified by the transgression, the remaining morphs tending to disappear. It must be emphasized that speciation is here due to the persistence and increasing development of "strangled/effaced" morphs (winner in the intraspecific competition



TEXT–FIG. 3—From Upper Eocene *Hammatocythere oertlii* to Oligocene *H. hebertiana trituberculata* in the northern Aquitaine Basin (France). Evolution is envisaged in terms of populational structures. Constitutive morphs of the populations analysed are represented by the Gauss curves the height of which varies in function of the number of individuals. Morphs are abreviated as follows:
Hammatocythere oertlii: A = morph "alveolate"; C = morph "common"; E/E = morph "couple of morphs "strangled/effaced"; M = morph "masked"; R = morph "reticulate"; SA = morph "semi-alveolate".
H. hebertiana trituberculata: e = morph "elongate"; b = morph "buckled"; t = morph "trituberculate".


m. buckled
m. fringed
m. tricostate
H. hebertiana trituberculata (Reuss) ss Keen
Floirac: Lower Oligocene
m. effaced
m. stangled
H. oertlii Ducasse
Médoc: Terminal Upper Eocene and basal Oligocene

between morphs of the *H. oertlii* species). According to mammalogists (Sudre, 1978; Ringeade, 1984) this phenomenon must have lasted some 3 million years.

EVOLUTION BY CONSERVATION OF "STRANGLED/EFFACED" MORPHS WITHIN THE ENVIRONMENT

According to Lete (1984), who proposed the hypothesis of "morphs as ecological markers", the development of "strangled/effaced" forms in the least marine levels of the late–upper Eocene is an indicator of their capacity to adapt in brackish environments. Their persistence in the transgressive marine environment at the base of the Oligocene could be due to an increase in climate humidity and dilution of the coastal marine milieu by continentally-derived fresh water inputs.

The occurrence of "strangled/effaced" morphs along with species displaying none of the recognized brackish characteristics at the base of the Oligocene gives rise to another hypothesis, that of "resistance morphs". It is, in fact, assumed that climatic degradation took place at the end of the Eocene, a phenomenon likely to have occurred in shallow marine environments in the immediate vicinity of the continent. Under such circumstances, "strangled/effaced" morphs should cease to be ecologic markers, but merely resist environmental changes, whether these are diluting, colder or drier (late upper Eocene). With the recurrence of more marine, warm and humid conditions at the base of the Oligocene, one should expect these "strong" morphs to have been favorably affected by selection.

In both hypothetical cases, selection is a determining factor.

POLYMORPHISM AND SELECTION

Because polymorphism is "discontinuous variation within a population with the rarest "morphs" existing at a frequency greater than that which can be maintained by recurrent mutation alone" (Ford, 1940) it gave rise to controversial discussion with regard to the omnipresence of selection. By refusing this important aspect of the synthetic theory, adepts of the neutralist thesis questioned the validity of the concept of adaptness. Detailed analysis of an organism should reveal mosaics of characters, some of which will be "adaptive," *i.e.* related to selection, and others "neutral" in relation to selection.

Morphs may adapt to environmental conditions in a global manner; their variant percentages are the direct result of selective pressures governing the environment. Clark (1976) pointed out that the adequation of morphs to the environment is not expensive (environmentally cued polymorphism). Lamotte and Génermont (1983), in an article dealing with polymorphism and speciation, came to the conclusion that polymorphism is congruent with important spatial heterogeneity as long as each individual can choose the parcel of territory which suits it best.

It is most likely that "strangled/effaced" morphs have persisted because of the impact of selection within the environment, where they occurred in more abundant amounts than the other morphs constituting the same species. This selective stasis is a better explanation than the environmental stasis (Cronin, 1984) of the speciation phenomenon.

PLATE 1—Evolution from *Hammatocythere oertlii* to *H. hebertiana trituberculata* in the northern Aquitaine Basin (France). Morphs are illustrated by left valves ×50.

Monomorphic Speciation

The "founder effect" (Mayr, 1963) originates in the hazardous nature of the genome transported by fragments of species that are isolated and confronted with the selective challenges of the environment, their only support being chance-dependent genetic recombinations or mutations. Speciation resulting from the survival of a small population within a new adaptive zone implies harmony between stochastic phenomena and selective determinism.

In the example given in this study, chance does not intervene in the isolation of the fragment from the mother-species. Morphs are, in fact, independent within the species they represent. Their reactions to environmental changes are different; in this manner their spatio-temporal segregation is explained.

The phenotypic uniformity of morphs could, however, undermine their genetic richness and capacity to generate new specific groups. Smather's (1961) observations show that monomorphic populations deriving from polymorphic species, uphold an important selective value that is reflected in their tendency to multiply. The contrary occurs with inbreeding monomorphic populations whose selective performances remain very poor.

The phenotypic uniformity of morphs covers a large range of non-apparent heterogeneous genetic characteristics whose selective and evolutive value is important.

Conclusions

The study of the environment in relation to evolving organisms is of great interest to the research worker, especially when distinct periods of worldwide climatic changes are involved. Hence the study of ostracods conserved in levels ranging between the upper Eocene and basal Oligocene, (period of important climatic events) that revealed evolutive phenomena governed by selection. This is, in fact, reflected in the elimination, conservation and/or tolerance of morphs. Selective variations are clearly perceptible with polymorphic species whose populations modulate locally the frequency of morphs, depending upon environmental conditions. The selective conservation of "strangled/effaced" morphs of the *H. oertlii* species within different environments (from colder or drier brackish environments to warmer and damper marine environments) indicates their tolerance and subsequently accounts for their persistence and contribution to the genesis of a new species. Speciation by monomorphism is an aspect of the punctualists' "bottle-neck effect" (Stanley, 1975). Selection and adaptation do, however, have a greater impact on speciation than chance. As such this phenomenon is congruent with the Darwinian principle.

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DISCUSSION

Singh: How does pollen analysis help in determining the palaeotemperature of a basin?

Peypouquet: The presence of various types of pollen provides a picture of the vegetation, which reflects the prevailing climate of a basin. Based on pollen diagrams, Chateauneuf was able in 1980 to determine the palaeoclimatology of the Paris basin at the Eocene/Oligocene boundary.

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Evolution

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The Pathways of Morphological Evolution of Bythocytheridae

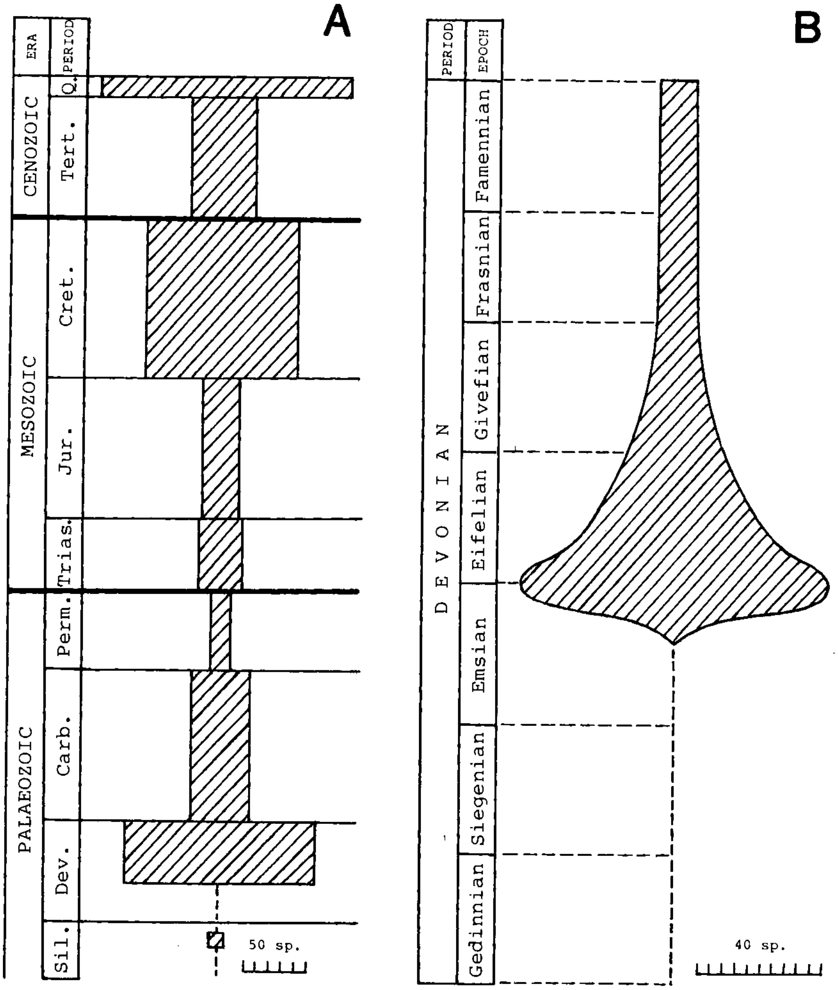
E. I. SCHORNIKOV
Academy of Sciences of the USSR, Vladivostok, USSR

ABSTRACT

Morphologically, bythocytherids are close to Bairdiacea and, very probably, they evolved from a common stock. The evolution of the Bythocytheridae fauna had two flourishing periods—the Devonian and the Cretaceous—and two crises: in the late Palaeozoic and at the boundary between the Cretaceous and the Cenozoic. The morphological evolution of the Bythocytheridae (and probably that of all Ostracoda) is extremely mosaic. The evolution of shell is characterized by numerous transformations and new features. Soft body parts, with the sole exception of the organs connected with reproduction, evolved mainly through reduction. There are many cases of both parallel and successive formation of structures, which are similar in their function and localization, and their subsequent reduction. The progressive development of some structures occurs through transformation under the influence of, as a rule, opposite processes: partial reduction of the appearing structures and further development of remaining parts. New structures generally appear following the complete reduction of preceding analogues.

The Bythocytheridae are the most archaic (basic) group of Cytheracea. A direct ancestral group of Bythocytheridae is unknown. Morphologically, Bythocytheridae are close to Bairdiacea and, very probably, they evolved from a common stock (Hartmann, 1963). The hypothesis that Bythocytheridae originated from Tricorninidae (Gründel and Kozur, 1971, 1973) was constructively criticized by Reynolds (1978). Schallreuter (1968) was the first to unite Berounellidae and Tricorninidae in one taxon, Berounellacea. Recently, Schallreuter (1979) has referred the Tricorninidae to the Bairdocypridacea. The Ordovician genera *Syltere, Sylterella* and *Conodomyra,* assigned to the Cytheracea by Schallreuter (1977, 1978, 1979) differ from the other Cytheracea and cannot belong to this superfamily. Cytheracea are basically distinguished from the other Podocopida by the morphology of the adductor muscles and the presence of a spinneret seta on the antenna. In addition, the primitive characters of the most archaic Cytheracea (Bythocytheridae) are adductor scars consisting of 5 stigmae ranged in a vertical row, the tubelike caudal process and the lateral reticulation of the carapace.

In our estimation, 663 species of Bythocytheridae are known at the present time, including 3 new recent species belonging to new genera which will be discussed in the present paper, and 78 new species that we have found in the material obtained from the Obisafit beds by E. D. Mikhailova (Leningrad Mining Institute). The Obisafit beds are referred to the Lower-Middle Devonian boundary deposits (Kim, Erina, Apekina and Lesovaya, 1984). The samples were collected in the western Zeravshan Ridge (South Tien-Shan) in the territory of the Kitab State Geological Reserve.



TEXT-FIG. 1—Development of species richness of the Bythocytheridae fauna through time. A, from Silurian up to present; B, in Devonian.

The earliest reliably identified Bythocytheridae are known from the Middle Silurian (Ludlovian): *Berounella* (1 species), *Kirkbyellina* (3 species) and, probably, the genus *Scaphium* with two species (Bouček, 1939; Jordan, 1964; Copeland, 1968). No bythocytherid species were found in later deposits until the upper part of the Lower Devonian (the Emsian).

The Emsian contains the richest bythocytherid fauna represented by almost all the Devonian genera. Only two of the described genera *Paraberounella* and *Praebythoceratina*, appear in the late Devonian. A majority of the Devonian bythocytherid fauna is concentrated in the Upper Emsian–Lower Eifelian. Even apart from the Obisafit species complex, they comprise almost half of the Devonian bythocytherid fauna. In its turn, the Devonian bythocytherid fauna is the richest in comparison with the fauna of other Palaeozoic systems. Text-fig. 1 shows the changes in species richness of Bythocytheridae over the course of time. The list of superspecific taxa includes reference to geological periods.

High indices of diversity of bythocytherids obtained for later geological epochs, as compared with the Cretaceous, result primarily from the fact that these ostracods are better preserved and well studied. For example, approximately half of Recent bythocytherids are represented by

Sclerochilini which occur mainly on rocky substrates near the shore and are very seldom preserved in fossil material.

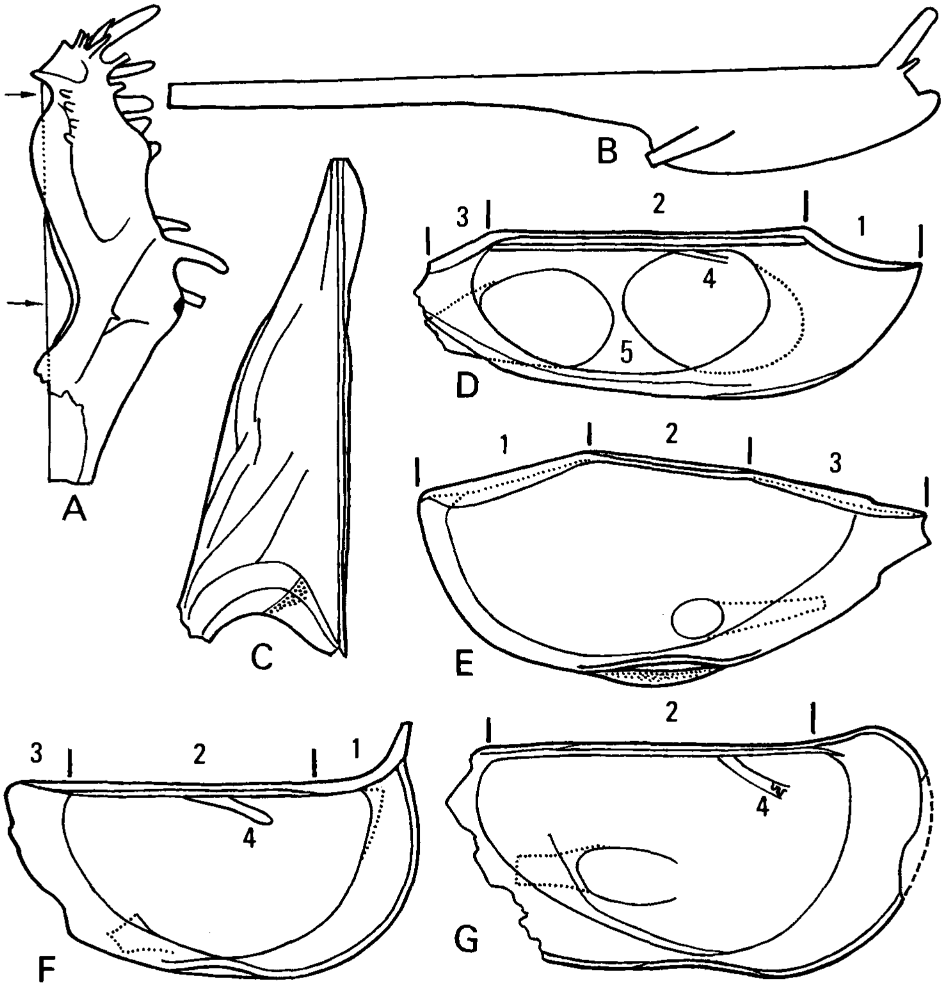
Of course, the picture of the development of the group, based on the examination of lists of taxa established so far is provisional and can, to a greater or less extent, be changed by any new discovery of a rich bythocytherid complex (like the Obisafit one). Nevertheless, it is clear that the evolution of the Bythocytheridae had two partricularly flourishing periods, one in the Devonian and the other in the Cretaceous, with the probable acme of its entire evolution during the Upper Emsian-Lower Eifelian. The evolution of the Bythocytheridae survived two crises: in the late Palaeozoic and at the Cretaceous-Tertiary boundary; the Permian crisis was the most severe. It hardly seems possible that several forms known from the Ludlovian and obscure until the Emsian gave rise to the richest and highly diversified bythocytherid fauna of the late Emsian. Probably, the process of formation of this fauna was more gradual and the Pre-Devonian history of this group lasted longer so that the origin of this fauna should be traced far back, perhaps as early as the Ordovician, when the radiation of the basic stocks of Podocopida took place.

The following system of classification is proposed for the Bythocytheridae. The list includes only those undescribed taxa, which are discussed herein; the specimens depicted are deposited in the Leningrad Mining Institute (LMI), and the Institute of Marine Biology (IMB).

- Bythocytheridae Sars, 1926, Sil.-Quat.
  - Berounellinae Sohn et Berdan, 1960, Sil.-Dev.
    - Berounellini Sohn et Berdan, 1960, Sil.
      - *Berounella* Bouček, 1936, Sil.
    - N. trib., Sil.?–Dev.
      - N. gen. 1, Dev.; n. gen. 2, Dev.; n. gen. 3, Dev.; n. gen. 4, Dev.
      - ? *Scaphium* Jordan, 1964, Sil.
  - N. subfam., Sil.–Carb.
    - *Kirkbyellina* Kummerow, 1939, Sil.–Carb.
    - N. gen., Dev.
    - ? *Ranicella* Gründel et Kozur, 1971, Carb.
  - Bythocytherinae Sars, 1926, Dev.–Quat.
    - Monoceratinini Szczechura, 1964, Dev.–Perm.
      - *Fueloepicythere* Kozur, 1981, Perm.
      - *Monoceratina* Roth, 1928, Dev.–Perm.
      - *Pseudomonoceratina* Gründel et Kozur, 1971, Dev.?–Carb.–Perm.
      - *Triceratina* Upson, 1933, Dev.–Carb.
      - N. gen., Dev.
    - Bythocytherini Sars, 1926, Dev.?–Quat.
      - *Bythoceratina* Hornibrook, 1952, Cret.–Quat.
      - *Bythocythere* Sars, 1966, Quat.
      - *Bythocytheromorpha* Mandelstam, 1958, Cret.
      - *Crassacythere* Gründel et Kozur, 1971, Cret.
      - *Cuneoceratina* Gründel et Kozur, 1971, Jur.?–Cret.
      - *Cytheraeison* Hornibrook, 1952, Paleog.–Quat.
      - *Dentibythere* Schornikov, 1982, Quat.
      - *Hanaiceratina* McKenzie, 1974, Neog.–Quat.
      - *Miracythere* Hornibrook, 1952, Paleog.–Quat.
      - *Nemoceratina* Gründel et Kozur, 1971, Carb.?–Trias.
      - *Neoberounella* Gründel et Kozur, 1972, Perm.?–Trias.
      - *Nodobythere* Schornikov, 1981, Quat.
      - *Orientobythere* Schornikov, 1981, Quat.
      - *"Parabythocythere"* Gou et Huang, 1982, Neog.–Quat. (non Kozur, 1981)
      - *Pariceratina* Gründel et Kozur, 1971, Cret.–Paleog. (= *Cretaceratina* Neale, 1975)
      - *Patelacythere* Gründel et Kozur, 1971, Trias.?–Paleog.–Quat.
      - *Praebythoceratina* Gründel et Kozur, 1971, Trias.–Jur.
      - *Pseudoceratina,* Bold, 1965, Neog.–Quat.

Retibythere Schornikov, 1981, Quat.
Rhombobythere Schornikov, 1982, Quat.
Tuberoceratina Gründel et Kozur, 1972, Trias.–Cret.?
Veeniceratina Gründel et Kozur, 1971, Cret.–Paleog.
Velibythere Schornikov, 1982, Quat.
? *Paraberounella* Blumenstengel, 1965, Dev.–Perm.–Trias.?
Nagiellini Gründel et Kozur, 1971, Trias.
Nagiella Kozur, 1970, Trias.
Protojonesiini Gründel et Kozur, 1971, Jur.–Cret.
Protojonesia Deroo, 1966, Cret.
Saxellacythere Gründel et Kozur, 1971, Jur.
Taxodiella Kuznetsova, 1957, Cret.
Triebacytherini Gründel et Kozur, 1971, Perm.?–Trias.
Triebacythere Gründel et Kozur, 1971, Trias.
?*Valumoceratina* Knüpfer, 1967, Perm.
Vitjasiellini Schornikov, 1981, Paleog.–Quat.
Vitjasiella Schornikov, 1976, Paleog.?–Quat.
Bythocytherinae incertae sedis
Acvocaria Gramm, 1975, Trias.
Covracythere Gramm, 1975, Trias.
Racvetina Gramm, 1975, Trias.
Keijicytherinae Kozur, 1985, Dev.–Quat.
Striatobythoceratinini Kozur, 1985, Dev.–Perm.
Striatobythoceratina Kozur, 1985, Dev.?–Carb.–Perm.
Torista Kozur, 1985, Dev.
N. gen. 1, Dev.–Carb.; n. gen. 2, Dev.
N. trib. Dev.
Hercynocythere Blumenstengel, 1974, Dev.
N. gen., Dev.
Keijicytherini Kozur, 1985, Dev.–Trias.
Keijicythere Kozur, 1985, Perm.–Trias.?
Parabythocythere Kozur, 1981, Perm.
N. gen. 1, Dev.; n. gen. 2, Dev.;
Jonesiini Schornikov, 1981, Jur.–Quat.
Jonesia Brady, 1866, Quat.
Kurilocythere Schornikov, 1981, Quat.
Nealocythere Schornikov, 1982, Quat.
Phlyctobythocythere Bonaduce, Masoli, Pugliese, 1976, Quat.
Plenocythere Swanson, 1979, Quat.
Ruggieriella Colalongo et Pasini, 1980, Quat.
N. gen. 1, Quat; n. gen. 2, Quat.
Pseudocytherinae Schneider, 1960, Trias.?–Quat.
Pseudocytherini Schneider, 1960, Cret.–Quat.
Antarcticythere Neale, 1967, Quat.
Pseudocythere Sars, 1866, Cret.?–Quat.
Pteropseudocythere Schornikov, 1982, Quat.
Rostrocythere Schornikov, 1981, Quat.
?*Triassocythere* Gründel et Kozur, 1972, Carb.?–Trias.
Sclerochilini Schornikov, 1981, Cret.–Quat.
Convexochilus Schornikov, 1982, Quat.
Oviferochilus Schornikov, 1981, Quat.
Sclerochilus Sars, 1866, Cret.?–Quat.
Bythocytheridae? incertae sedis
Bytholoxoconcha Hartmann, 1974, Quat.

Gramm (pers. comm.) proposed that the Editiinae, a highly aberrant group previously referred to the Bythocytheridae (Knüpfar, 1967; Gründel and Kozur, 1971, 1973; Gramm, 1975), should be

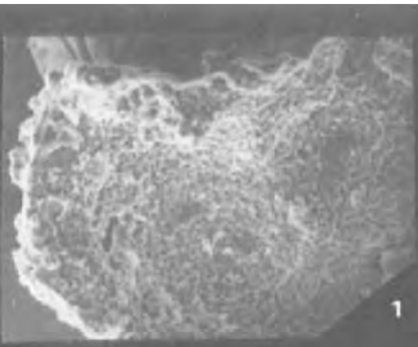


TEXT-FIG. 2—Shell structure of Bythocytheridae, n. subfam. and Berounellinae.
A. *Kirkbyellina*? sp., ventral view of valve; arrows indicate orifices of shell (Obisafit beds). B. *Kirkbyellina spinosa* (Blumenstengel, 1962) (after Blumenstengel, 1977). C, D Berounellinae n. trib., n. gen. 1, sp. C. Dorsal view of valve. D. Inside view of valve (LMI 100/300, Obisafit beds). E. Berounellinae n. trib., n. gen. 2, sp., inside view of valve (LMI 101/300, Obisafit beds). F. Berounellinae n. trib., n. gen. 3, sp., inside view of valve (LMI 103/300, Obisafit beds). G. Berounellinae n. trib., n. gen 4, sp. 1, inside view of valve (LMI 114/300, Obisafit beds). Designations: 1, anterodorsal border; 2, central dorsal (hinge) border; 3, posterodorsal border; 4, internal elevation corresponding to S_1; 5, internal elevation corresponding to S_2.

regarded as a separate family of the Cytheracea (Editiidae) with only two genera: *Editia* and another new one established by Gramm. We agree with Gramm and place the remaining taxa previously referred to the Editiinae in the Bythocytheridae.

As early as the Devonian, Bythocytheridae were represented by four of the five subfamilies recognized. Each one seems to be evolutionarily more advanced from the hypothetical ancestral group. The distribution of the basic morphological characters of these subfamilies is a mosaic and suggests that the origin of these subfamilies was connected with radiation.

Berounellinae: The shells with very elongate anterodorsal margins, S_1 and S_2 are usually conspicuous.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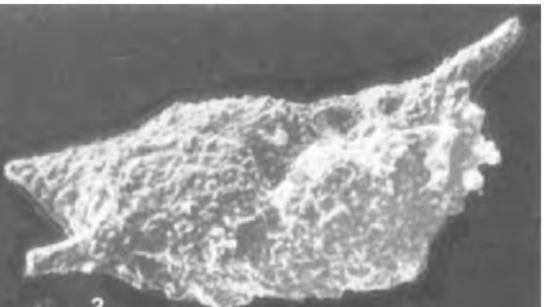
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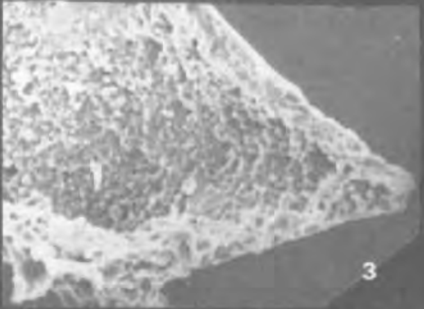
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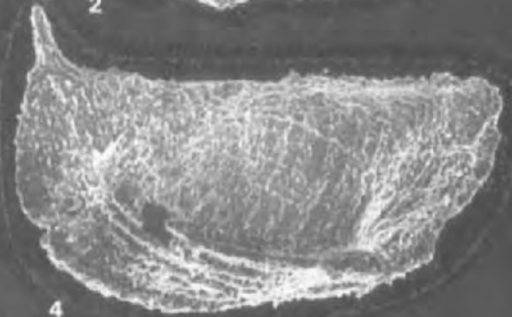
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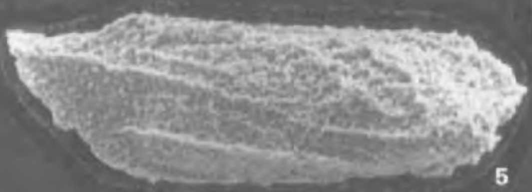
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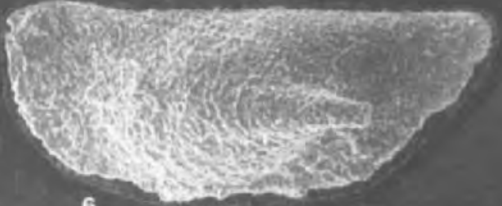
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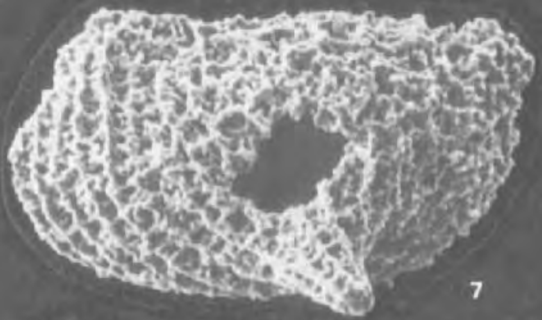
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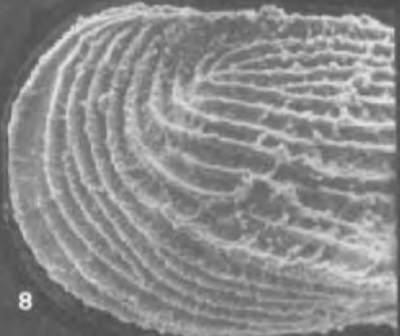
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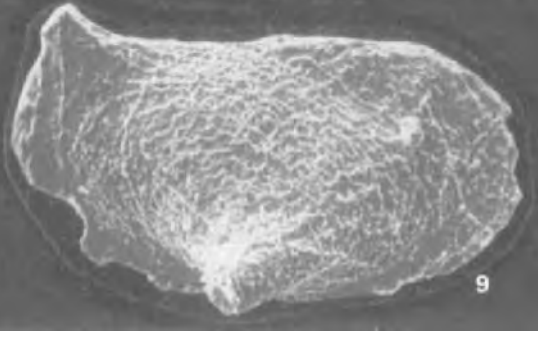
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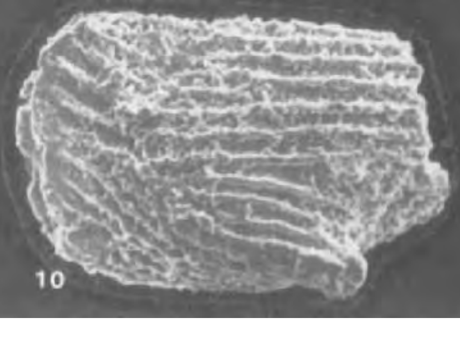
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Berounella and *Kirkbyellina* are not thought to be synonymous, but are regarded as belonging to different subfamilies. Berounellinae n. trib. with 4 new genera from the Obisafit beds is assigned to the subfamily Berounellinae (Text-fig. 2C–G, Plate 1, figs. 4–6). *Scaphium* may also belong to this subfamily. The forms referred to this subfamily have very elongate, more or less horizontal anterodorsal and posterodorsal margins, due to which they become similar to some Bairdiacea, particularly to *Acanthoscapha.* However, this similarity is not evidence for the direct origin of this group from *Acanthoscapha*-like ancestors. *Acanthoscapha* is one of a highly specialized group adapted to life in semi-liquid mud. The elongate anterior and posterior ends of the shell function as stabilizers similar to analogous formations in a number of pelagic Halocyprididae and swimming Cyprididae (Hartmann, 1966). This similarity is obviously convergent.

Bythocytheridae n. subfam. have S_1 and S_2. S_2 is V-shaped, narrow and deep in the region of the adductor muscles and broad and shallow dorsally. This subfamily includes *Kirkbyellina* and a new genus from the Obisafit beds, which is close to them and characterized by a strongly reduced caudal process (Plate 1, figs. 2, 3). In external view *Ranicella* is similar to *Kirkbyellina* and may also belong to the new subfamily. However, the lack of information concerning the internal morphology of the *Ranicella* shell makes this supposition questionable. Schallreuter (1968) and Gründel and Kozur (1971, 1973) only considered the morphology of *Kirkbyellina* when they stated the similarity between Berounellinae and Tricornidae. At the same time, *Kirkbyellina* exhibits a number of peculiar features that characterises it as a highly specialized form: a hypertrophied caudal process and the presence of 3 gaping orifices in the closed shell (in addition to the orifice in the caudal process). The orifices are located anterodorsally, anteroventrally and posteroventrally. Reynolds (1978) observed only anterodorsal and posteroventral orifices. She assumed that they were filtrators and that these orifices served for circulation of water. However, in known Recent ostracods, filtrators do not need these orifices. We believe that, very probably, they inhabited semi-liquid sediments. Their anterodorsal and lateral spines and long caudal process would serve as stabilizers. The domicilial orifices allowed the extension of the antennulae, antennae and thoracopods. This enabled the animals to move with their shells closed. It is possible that these orifices were surrounded by dense setae (similar to the rostral incisure in Myodocopina). They prevented the sediment particles from entering the domicilium. It seems impossible that the remaining bythocytherids could originate from *Kirkbyellina*-like forms. On the inside surface of the sulcus in *Kirkbyellina,* apodemes have been found to which the muscles were attached. The apodeme top, to which the adductor was attached, is oblong vertically and has a small area to which a limited number of muscle bundles (apparently 5) can be joined (Plate 1, fig. 1).

Bythocytherinae originally had only S_2 and usually a well pronounced lateral sculpture. The adventral inflation is frequently present. In contrast to the ventrolateral inflation of the Keijicytherinae and Pseudocytherini, this inflation does not occupy the adductor area but lies below it. In the Palaeozoic specimens the hinge was adont, in the Post-Palaeozoic it was lophodont or more

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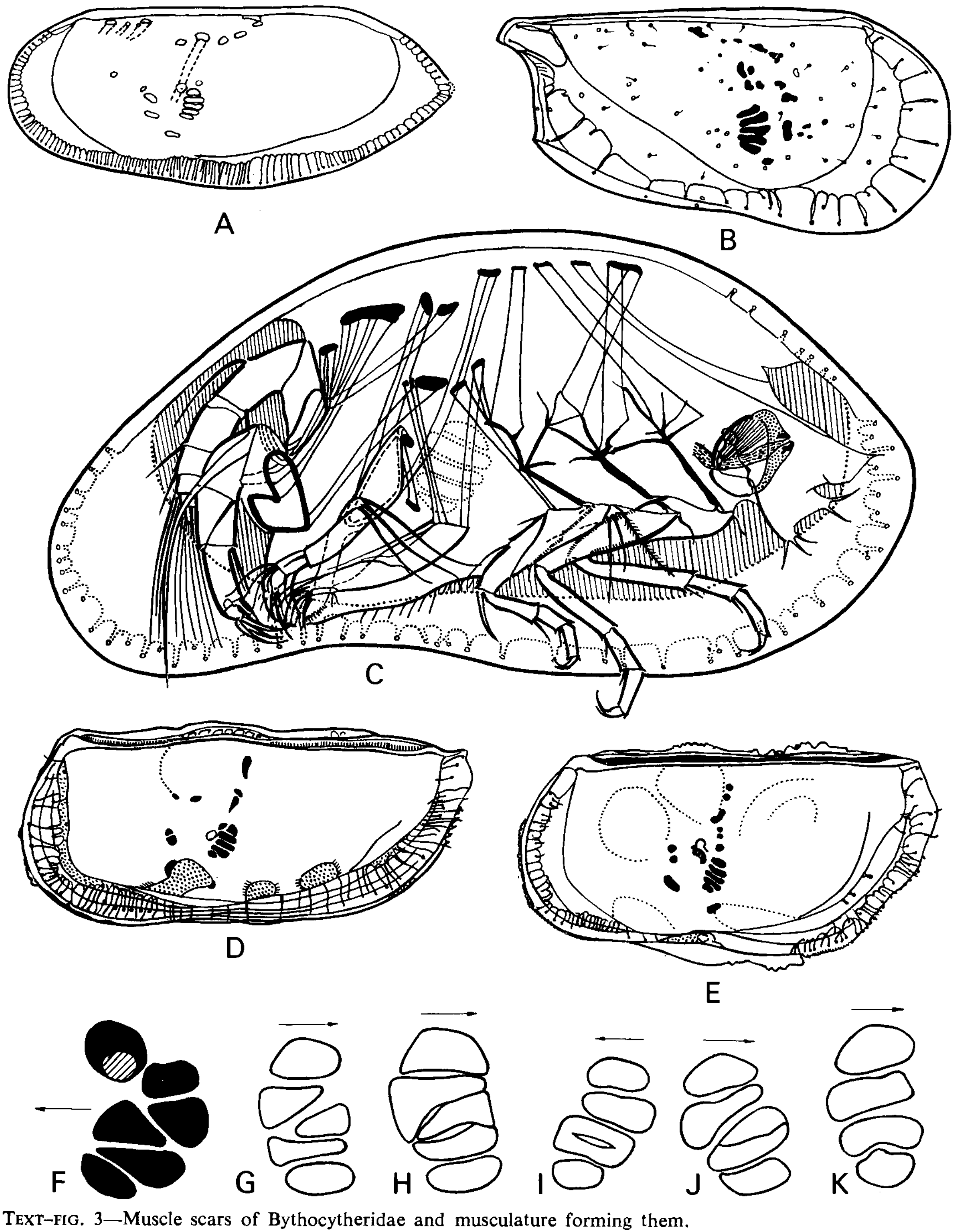
PLATE 1—Fig. 1. *Kirkbyellina* sp. Interior view of the right valve, arrow pointing to adductor apodeme, × 300 (Obisafit beds). Figs. 2, 3. Bythocytheridae n. subfam., n. gen., sp. 2. Exterior view of the right valve × 180. 3. Caudal process, interior view, × 300 (LMI N 222/300, Obisafit beds). Fig. 4. Berounellinae n. trib., n. gen. 3, sp. Exterior view of the left valve, × 175 (LMI N. 103/300, Obisafit beds). Fig. 5. Berounellinae n. trib., n. gen. 1, sp. Exterior view of the left valve, × 210 (LMI N 100/300, Obisafit beds). Fig. 6. Berounellinae n. trib., n. gen. 4, sp. 2. Exterior view of the left valve, × 130 (LMI N 112/300, Obisafit beds). Fig. 7. Striatobythoceratinini n. gen. 1, sp. 1. Exterior view of the left valve, × 225 (LMI N 234/300, Obisafit neds). Fig. 8. Striatobythoceratinini n. gen. 1, sp. 2. Anterior part of the left valve, × 290 (LMI N 134/300, Obisafit beds). Fig. 9. Striatobythoceratinini n. gen 2, sp. Exterior view of the right valve, × 250 (LMI N 139/300, Obisafit beds): surface sculpture is false, formed as a result of diagenesis. Fig. 10. Stsiatobythoceratinini n. gen. 1, sp. 3. Exterior view of the left valve, × 155 (LMI N 235/300, Obisafit beds).



TEXT–FIG. 3—Muscle scars of Bythocytheridae and musculature forming them.
A, *Jonesia simplex* (Norman, 1865); B, *Pseudocythere moneroni* Schornikov, 1981; C, *Sclerochilus* (*Sclerochilus*) *firmulus* Schornikov, 1981; D, *Nodobythere nodosa* Schornikov, 1981; E, *Retibythere bialata* Schnornikov, 1981; F, *Cytheralison* sp. G-K, *Rhombobythere mica* Schornikov, 1981. G, normal adductor scar; H-K, different variations of the adductor muscle scar. (A, after Schornikov, 1980; B-E, after Schornikov, 1981; F, after McKenzie, 1974; G-K, after Schornikov, 1982a).

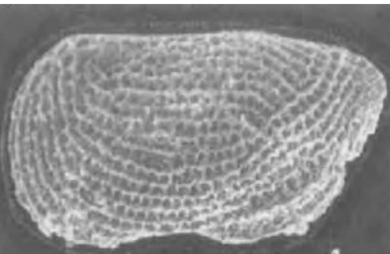
complex. The adont hinge may be formed secondarily as the result of reduction of some elements (*Rhombobythere*). Seven tribes are recognised in this subfamily (see list).

Monoceratinini S_2 is V-shaped, weakly developed, occasionally reduced (*Pseudomonoceratina*). In Keijicytherinae and Pseudocytherinae, there is a "diffuse" dorsal muscle field (Text-figs. 3A–C). Apparently groups with originally V-shaped S_2, including Monoceratinini, had the same muscle field. Representatives of this tribe are reliably established only from the Palaeozoic deposits.

Other tribes of Bythocytherini originally had a furrowed S_2, formed as vertical furrow. Muscle scars in the middle of the dorsal muscle field are arranged in a vertical row (Text-figs. 3D, E). In the case of reduction of the furrowed S_2, the scars of the middle part of the dorsal muscle field ranged into a vertical row indicate that earlier the S_2 was furrowed. This has been established for *Cytheralison, Miracythere, Hanaiceratina, Taxodiella, Vitjasiella* and some other genera.

Keijicytherinae are characterised by the presence of S_1 (occasionally reduced) and the absence of S_2. The dorsal muscle field is "diffuse" and does not form a vertical row of muscle scars (Text-fig. 3A). Here 3 Palaeozoic tribes with adont hinge are included: Striatobythoceratinini (Plate 1, figs. 7–10) having a lateral spine or ventrolateral inflation occupying the adductor, n. trib. (Plate 2, figs. 1–4) lacking the lateral spine and ventrolateral inflation; the genus *Hercynocythere* and a n. gen. are included herein. The representatives of both tribes have a distinctly pronounced flange and usually well expressed lateral sculpture. Keijicytherini (Plate 2, figs. 5–7) is characterised by a trend towards reduction of the flange and lateral sculpture as a consequence of adaptation to life in sediments. The Mezozoic—Cenozoic tribe Jonesiini is distinguished from the Palaeozoic tribes by its lophodont hinge and characterised by a trend towards reduction of the flange, the absence of lateral sculpture or the presence of secondarily formed lateral sculpture, such as longitudinal striae, furrows, carinae and plicae. The shells of the representatives of Jonesiini and Keijicytherini are homeomorphic. Both tribes exhibit a trend towards the formation of internal transverse ribs (see Schornikov, 1981, p. 33). Jonesiini probably originated from the least specialised representatives of Keijicytherini though it is possible that they originated from some other less specialized group such as, for example, n. trib. In spite of considerable differences in their shell morphology, the appendages of the Recent Jonesiini are strikingly similar to those of the Bythocytherini. This led to their unification in one subfamily (Schornikov, 1981). It is now obvious that the Bythocytherinae and Keijicytherinae were separate as early as the Devonian. The evolution of the Keijicytherinae proceeded by the way of adaptation to life in sediments which is reflected in the morphology of the shell. Both Devonian and Recent Bythocytherinae live on the sediment surface. The shells of different groups of Bythocytherinae underwent considerable, differently directed transformations, but in many features remained similar to those of archaic forms. The appendages of the ancient Bythocytheridae and Keijicytherinae were strongly articulated and armed with a greater number of setae. This is evident from a number of ancestral features mosaically distributed in different groups of Bythocytheridae and other Cytheracea (Schornikov, 1981, 1982b). The similarity in the appendages of Bythocytherinae and Keijicytherinae is homeomorphic. In these animals, fusion of some parts of the appendages and reduction of their elements proceeded in parallel. In their morphology it was not possible to find any noticeable feature that could be regarded as new compared to their ancestral state. Special transformations in the structure of appendages involved only small details such as slight changes in the proportion, form and plumage of some elements.

Pseudocytherinae reliably established from the late Cretaceous onwards are characterised by the absence of sulci or the presence of a slight vestige of S_1 (in some Pseudocytherini). The dorsal muscle field is "diffuse" (Text-figs. 3B, C). Organs connected with food intake are subject to strong transformation, together with considerable reduction of ancestral elements. Muscles forming the peripheral scars of the central muscle field are also reduced. Other appendages are also considerably reduced as compared with the ancestral type, but have a number of archaic features as compared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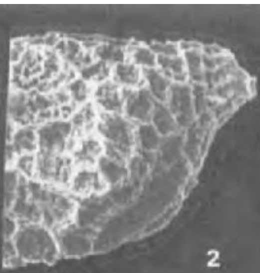
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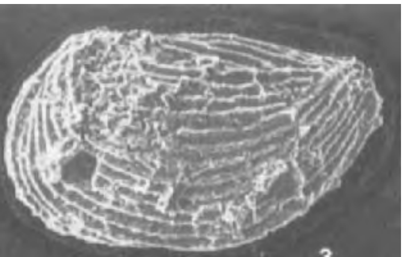
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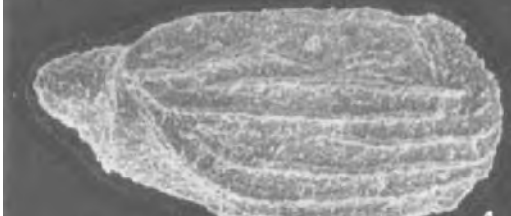
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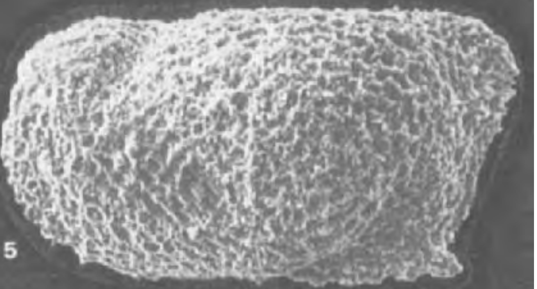
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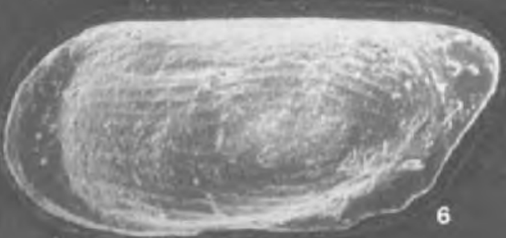
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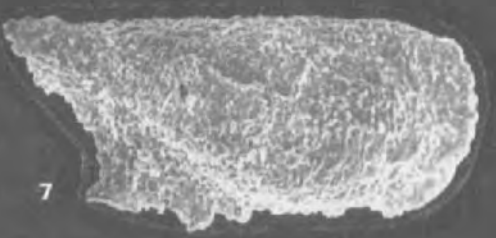
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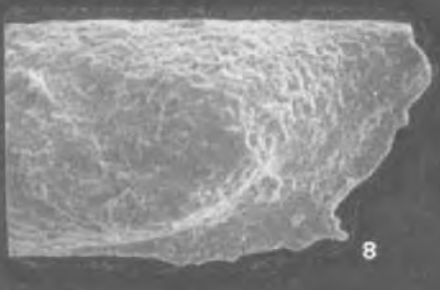
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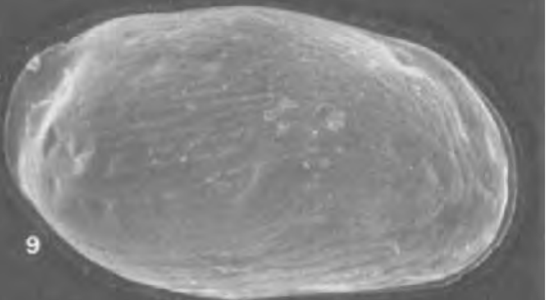
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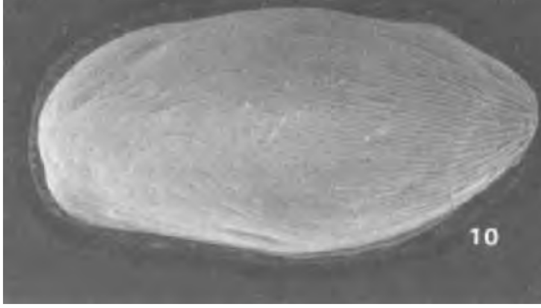
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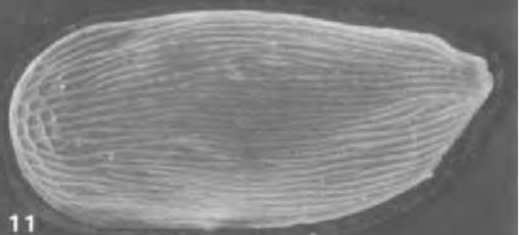
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with the Jonesiini and Bythocytherinae. Pseudocytherini are characterized by destabilization of the hinge structure and interposition of the free border of the right and left valves. In Sclerochilini, the interposition of the valves significantly changed and resulted in formation of a two-listed hinge with the right valve overlapping the free border (Schornikov, 1981). The lateral sculpture is either absent or formed secondarily, such as several costae arming the borders (in some Pseudocytherini). Pseudocytherini still have slight vestiges of the flange, which is absent in Sclerochilini. Very probably, the Pseudocytherinae originated in the Post-Palaeozoic from the Keijicytherinae group specialised for living in sediments. Their ancestors had reduced lateral sculpture and a strongly reduced flange. The transformation of the mandible and maxillula and masticatory apparatus apparently occurred with the development of symbiotic relationships with sessile benthonic organisms (commensalism and probably, parasitism). In the Pseudocytherini and Sclerochilini, parallel reduction of the anterior endites of the maxillulae occurred and the terminal setae of the first endite and the palp transformed into hooks that serve for fixing the animal on food objects.

For the sake of brevity only some most interesting items of the morphological evolution of Bythocytheridae are considered below.

Adductor Muscle Scar: In the present state of knowledge we can only guess at the early history of formation of the adductor muscle scar in the Cytheracea. This scar originated, presumably, from the archaic rounded and multi-element scar as a result of reduction of peripheral muscle bundles through rudimentation, as was the case with the formation of the oblong vertical scar in the Platycopa (Gramm, 1985). It is very probable that some scars fused, since in Recent Cytheracea each stigma of the adductor is formed by several muscle bundles. There is some correlation between the degree of vertical extension of the scar and the parallelity of the lateral sides of the shell where the adductor is attached (Schornikov, 1982a). One of the prerequisities of the formation of the vertically extended few-element adductor in Cytheracea is the presence of flattened-parallel areas in the region of the adductor attachment. They may result from the lateral compression of the shell, as in Cytherellidae, the formation of a deep S_2, the formation of a transverse "internal elevation" as the result of considerable thickening of the shell wall in the middle part as in Berounellinae n. trib., n. gen. 1 (Text-fig. 3D), or the formation of apodemes with flattened-parallel tops as in *Kirkbyellina* (Plate 1, fig. 1) and *Vitjasiella beliaevi* Schornikov, 1976 (Schornikov, 1976, 1981).

It is still not clear which of the pathways or probably, several pathways, were realized in the course of evolution. In any case, our studies have shown that as early as the Devonian, the adductor muscle scar of the Bythocytheridae was vertically extended and consisted of few elements (presumably 5). This construction of the adductor muscle scar is one of its most stable states, which has been maintained in the Bythocytheridae right up to the present day, in spite of considerable transformations of the shell during the evolution of this group. Only the form and inclination of the row has changed in connection with the spatial arrangement of the planes of the opposite sides of the shell to which the adductor was attached. However, further evolution of the adductor muscle scar in the Cytheracea resulted in one more stable state consisting of 4 elements, and further

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PLATE 2—Fig. 1. *Hercynocythere* sp. 1. Exterior view of the left valve, ×160 (LMI N 145/300, Obisafit beds). Fig. 2. *Hercynocythere* sp. 3. Posterior part of the left valve, ×165 (LMI N 164/300, Obisafit beds). Fig. 3. *Hercynocythere* sp. 2. Exterior view of the left valve, ×150 (LMI N 236/300, Obisafit beds). Fig. 4. Keijicytherinae n. trib., n. gen., sp. Exterior view of the right valve, ×215 (LMI N 144/300, Obisafit beds). Fig. 5. Keijicytherini n. gen. 1, sp. Exterior view of the left valve, ×110 (Obisafit beds). Fig. 6. *"Monoceratina" sublimis* Polenova, 1952. Male shell, view from the left, ×150 (Holotype). Fig. 7. Keijicytherini n. gen. 2, sp. Exterior view of the right valve, ×105 (Obisafit beds). Fig. 8. Monoceratinini n. gen., sp. Posterior part of the left valve, ×320 (Obisafit beds). Fig. 9. Jonesiini n. gen. 1, sp. Exterior view of the right valve, ×85 (IBM N 1796, Australian waters of the Indian Ocean, Recent). Fig. 10. Jonesiini n. gen. 2, sp. Left valve of the A-1 Instar stage, ×100 (IBM N 1777, Australian waters of the Indian Ocean, Recent). Fig. 11. *"Pseudocythere"* cf. *P. fueguensis* Brady, 1880. External view of male left valve ×105 (IBM N 1776, Australian waters of the Indian Ocean, Recent).

reducing to merely 2. The 4-element adductor muscle scar was formed iteratively. The study of the Recent bythocytherids (Schornikov, 1982a) indicated that a decrease in the number of elements in the adductor scar may be associated with the formation of a more or less spherical shell (*i.e.* the most robust, other conditions being equal). In *Cytheralison* and *Rhombobythere* (Text-figs. 3F, G) and in the Terrestricytheracea, which possess strongly convex shells, the middle adductor scars are triangular in shape and shifted horizontally with respect to each other. At the same strength of musculature, vertical shortening of the adductor attachment zone thus became possible, which sets fewer limitations for the formation of the convex shell. With strongly convex walls such an adductor also appears insufficient for optimal function. A contradiction arises here between the value of strengthening of the shell through optimisation of its form and the limitation for vertical extension of the area where each of the five adductor elements could be separately attached. It is not, therefore, by chance that *Rhombobythere mica* Schornikov, 1982, which possesses an almost round shell in cross-section, exhibits strong variation in the form of the adductor scars (Text-figs. 3G–K). Sometimes, this species forms a 4-element scar because of the fusion of the two lower of the middle stigmae. In this case, the strength of the adductor increases. In the case examined, the area of the 4-element scar (Text-fig. 3K) proved to be 18% more than that of the 5-element scar common to the genus (Text-fig. 3G).

Lateral sculpture: The problem of the primary sculpture in this group is similar to the familiar problem of the "hen or egg". Reticular structures are mostly widespread in nature. This is primarily associated with "granulation" of natural objects. Undoubtedly, throughout the evolutionary history of the Bythocytheridae ancestors, retiform relief of integuments appeared repeatedly. This relief was transformed, reduced and re-appeared. A majority of the ancient Bythocytheridae have a relatively uniform lateral reticulation of the shell. This is assumed to be the original primary sculpture in this group.

Bythocytheridae exhibit various transformations of the archaic lateral reticulation: reduction, hypertrophy and more frequently, simultaneous reduction of some elements and hypertrophy of the remainder. Hypertrophied elements are subjected to various transformations. Sometimes stable states are observed when the sculpture produced conforms perfectly to the established relationships between the environment and organism. Some characteristics of such sculpture can extend to a great number of the descendent taxa of the group. However, a possibility (and hence a tendency) always persists toward changing these relationships and then the former characteristics, once stable, prove to be no longer optimal. As a consequence, the structures which have achieved a morphofunctional peak for this group are again subjected to reduction.

A new, secondary sculpture usually appears on the shells with completely reduced lateral sculpture. This new sculpture may be similar to, or different from, the previous one. Later on it undergoes transformations analogous to those suffered by the primary sculpture.

Sets of these parallel and successive transformations, complete to a greater or less extent, are frequently observed in each subfamily or frequently even within smaller taxa. They are most completely represented in the Keijicytherinae.

Striatobythoceratinini n. gen. 1 (Plate 1, figs. 7, 8, 10): Most species of the genus have a pronounced, relatively uniform reticulation. Sometimes, it undergoes reduction so that it appears almost indistinguishable. Completely smooth forms were not found in the group, but in a species of the genus closest to it the shell surface is smooth (Plate 1, fig. 9). The latter species apparently inhabited semi-liquid mud and possesses, beside the lateral spine, a large posterodorsal spine. The caudal process is completely reduced. Thus, it exhibits a convergent similarity with a Recent inhabitant of Tanhanika Lake, *Kavalacythereis braconensis* Wouters 1979. N. sp. 1 (Plate 1, fig. 7) has a somewhat hypertrophied lateral sculpture. This hypertrophy is irregular. Mesh walls oriented along the border of the valve are most conspicuous. Analogous hypertrophy of some elements and reduction of others resulted in the formation of the sculpture found in n. sp. 2 (Plate 1, fig. 8). In basic transformations, only longitudinal walls are hypertrophied and all the transverse walls reduced as, for example, in n. sp. 3 (Plate 1, fig. 10). These modifications of the sculpture of longitudinal costulation and costation are characteristic of many Palaeozoic representatives of this subfamily adapted to live in sediments. Later on, it can be further reduced as in *"Monoceratina" spinosa* Polenova, 1952, on the almost smooth surface of which only few fine striae remain weakly discernible (Polenova, 1952). Some other transformations of reticulation can also be observed within the *Torista*. For example, in *Torista hercynica* (Blumenstengel, 1974) and *Torista* cf. *T. hercynica* (Blumenstengel, 1974), only a few of the transverse costae are hypertrophied. These strong costae form a solid framework strengthening the shell (Blumenstengel, 1974). This sculpture is characteristic of ostracods inhabiting the marine turbulent zone.

Keijicytherinae n. trib. (Plate 2, figs. 1–3): Analogous transformations of the lateral sculpture can be observed in the genus *Hercynocythere* (compare Plate 1, figs. 7, 8, 10 and Plate 2, figs. 1, 3, 4). The sculpture of n. trib., n. gen., sp. (Plate 2, fig. 4) is an example of further hypertrophy of some longitudinal costae and reduction of the remaining ones, as compared with the species shown in Plate 1, fig. 10. *Hercynocythere* sp. 3 (Plate 2, fig. 2) represents the initial stage of the formation of the shell framework built of transverse costae which strengthen the shell and in *Hercynocythere multicostata* Blumenstengel, 1974, the analogous costae are considerably larger. Relatively uniform hypertrophy of the reticulation mesh walls is exhibited in *Hercynocythere reticulata* Blumenstengel, 1974 and *Hercynocythere concentricostata* Blumenstengel, 1974. The meshes of *H. reticulata* are small, but very deep. and the spongiose sculpture of H. *concentricostata* is similar to that of *Cytheralison* (Blumenstengel, 1974).

Keijicytherini (Plate 2, figs. 5–7): The members of this tribe are adapted to live in sediments. Reduction of the lateral sculpture is frequently observed in this tribe. In some species reticulation is fairly well represented (Plate 2, fig. 5), while in a majority of forms it is reduced to either fine longitudinal costulae or absent (Plate 2, figs. 6, 7). Although many members of the tribe were already smooth-shelled in the Devonian, the remains of primary lateral sculpture are still present in some Permian forms. For example, *Parabythocythere permica* Kozur, 1981 possesses a very slight reticulation (Kozur, 1981).

In the Palaeozoic forms with reticulate and costulate sculpture investigated by the writer, the number of longitudinal costulae was limited and did not exceed 20, usually being 18–20. This, apparently, corresponds to the number of rows of epidermal cells forming the archaic reticulate sculpture. The arrangement of a few strongly hypertrophied costae is irregular and connected with distribution of mechanical loads over the shell rather than with the arrangement and number of epidermal cells.

The last known Keijicytherinae form with vestiges of the archaic sculpture is probably *Monoceratina*? s. 4135 *sensu* Kristan-Tollmann, 1983 (non Michelsen, 1975) from the Middle Triassic of South China (Kristan-Tollmann, 1983) which has about 10 large longitudinal ribs on its valve. The Jurassic Jonesiini: *Monoceratina*? *multistriata* Michelsen, 1975, *Monoceratina striata* Triebel et Bartenstein, 1938, *Monoceratina*? s. 4135 Michelsen, 1975 and some others, have undoubtedly a secondarily formed lateral sculpture consisting of numerous longitudinal striae.

A majority of Recent Jonesiini lack lateral sculpture, or the elements of sculpture are usually longitudinally oriented, as if it were a recollection of the longitudinally-directed sculptural elements of their ancestors. Apparently, a long-continued history of the existence of longitudinal costulate sculpture may have some influence on tissues responsible for the formation of new sculpture in the descendants after the old one has disappeared. Interestingly, the lateral sculpture present in some Paradoxostomatidae is represented by longitudinal striae or costulae. Jonesiini, Pseudocytherinae and Paradoxostomatidae probably originated from ancient Keijicytherinae adapted to live in sediments while other groups of Cytheracea with lateral reticulation originated from Bythocytherinae inhabiting the sediment surface. Longitudinally directed elements of the sculpture of Recent Jonesiini and the ribs of their ancestors cannot be regarded as homologous, however. Evidently, these sculptural elements formed anew in each group separately.

The cuticular sculpture formed as longitudinal striae in *Nealocythere* is indiscernible in subfossil specimens with destroyed epicuticle. It is frequently represented by very numerous fine costulae with a fairly diversified structure of details in various groups (Plate 2, figs. 10, 11). Sometimes, these costulae are arranged obliquely rather than longitudinally. In some forms, a part of the originally fine costulae are reduced and the remaining ones are hypertrophied. This is, for example, the case with *Pseudocythere* sp. 1 from the Miocene of southwestern Australia (Whatley and Downing, 1983). It resembles *"Pseudocythere"* cf. *P. fueguensis* Brady, 1880 (Plate 2, fig. 11), but differs from it in having 10 thick longitudinal costae in the middle part of the shell, instead of 40 fine costulae. Interestingly, in both cases secondary reticulation was formed at the anterior border because of the appearance of vertical anastomoses between the neighboring longitudinal ribs. Some forms, for example *Phlyctobythocythere anomala* Bonaduce, Masoli, Pugleiese, 1986, have fragments of slight longitudinal costulae which are probably vestiges of longitudinal costae once hypertrophied and then subjected to strong reduction. Besides this, there are peculiar pits on the valves in this species.

A fairly interesting sculpture is observed in Jonesiini n. gen. 1, sp. (Plate 2, fig. 9), which has longitudinal grooves instead of costulae. Reticulation formed by anastomosing grooves is observed in the anterior part of the shell. This reticulation seems to correspond to the pattern of arrangement of the epidermal cells. It is similar to the sculpture of *Xestoleberis chilensis austrocontinentalis* Hartmann, 1978, which formed instead of the reduced original reticulation of the Xestoleberididae. The longitudinal sculpture of *Ruggieriella* is represented by plicae changing the inside surface of the valves. Presumably, it originally formed as plication from the sculpture similar to that of Jonesiini n. gen. 1, sp. Sometimes, a rib fringing the border of a valve is newly formed, as for example, in *Ruggierella* sp. (Cronin, 1983). Analogous ribs, which acquired the function of strengthening the valve margin instead of the lost flanges appeared in *Rostrocythere* and some *Pseudocythere* (Schornikov, 1981, 1982a).

Appendages. In contrast to the eventful history of the shell morphology, the evolution of the appendages seems to be very sluggish and tends mainly towards reduction of their morphological elements. The few considerable evolutionary shifts in the appendage morphology of ostracods are essentially not new features, but rather transformations of earlier established elements. Among them is the formation of a filtering apparatus in *Vitjasiella* which resulted from hypertrophy of a bundle of setae at the frontal corner of the hypostome found in all Bythocytherini and Jonesiini (Schornikov, 1976, 1981); and transformation of mandibles and maxillulae in the Pseudocytherinae, accompanied by the reduction of some elements and the hypertrophy of others. Among relatively significant new features only the increased number of teeth of the mandibular gnathobasis (in Sclerochilini) as compared to other Podocopida can be mentioned here. The structure of the organs connected with reproduction shows significant diversity even in close groups of Bythocytheridae. This is seen in the sexual dimorphism of the appendages shown in the varying structure of apical claws on the male antennae of different groups and the hypertrophy of the II thoracopod in male Jonesiini. The structure of the penis and the genital tubercle in females is also diversified at the species level (see Schornikov, 1981).

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The Evolution and Distribution of Cytherettine Ostracods

MICHAEL C. KEEN
University of Glasgow, Scotland

ABSTRACT

The morphology of living cytherettines is discussed and, taken in consideration with undoubted Tertiary cytherettines, a diagnosis of the subfamily is given. True cytherettines are basically considered to be restricted to Europe, the eastern seaboard of the U.S.A., the Gulf and the Caribbean. Ostracods from S. America, S. Africa, and Southeast Asia referred to the cytherettines are regarded as unrelated homeomorphs. Tethys, far from being an aid in their distribution, was actually an important barrier and restricted the true cytherettines to areas north of Tethys until the late Palaeogene. The cytherettines range from the late Cretaceous (Santonian) to the present day.

INTRODUCTION

The cytherettines form one of the commonest and most diverse groups of shallow marine ostracods in the Tertiary of Europe and of the eastern and southern U.S.A. Something like 200 species have been described, with many more awaiting description. However, at present, the group is represented by just two genera, *Cytheretta* Müller, 1894 and *Protocytheretta* Puri, 1958, which contain some 13 species. Such a small number of living species leads to difficulties in separating generic characters from those of only specific value, not just within the carapace but with the soft parts as well. Cytherettine ostracods have also been described from all the other continents except Antarctica, but as argued further on, the case for placing most of these in the subfamily is rejected or at the very best considered to be not proven. The thesis is developed that the cytherettines originated in the shallow seas of Europe in the late Cretaceous and spread both eastwards and westwards in the early Tertiary, but that Tethys was always an important barrier to their migration. Their centres of development were on the north side of Tethys. The extensive and well described Tertiary faunas from the southern shores of Tethys, from West Africa, North Africa, the Middle East, Pakistan, India, and Southeast Asia have not yielded a single true cytherettine to date.

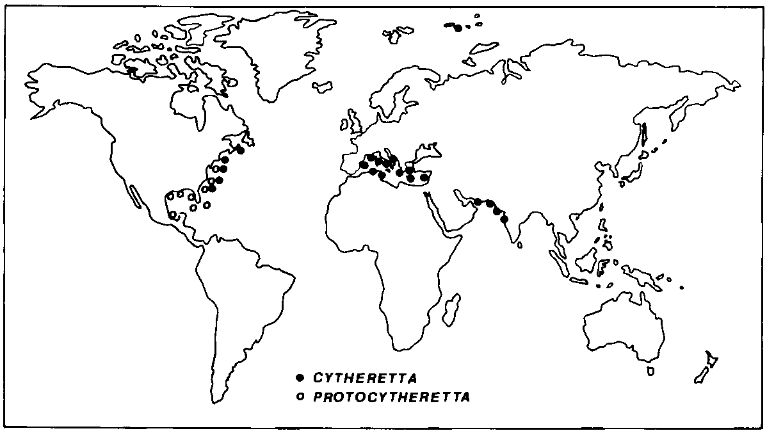
The earliest members are found in the Upper Cretaceous of Europe where they form a fairly inconspicuous part of the fauna. They are present but not abundant in the Palaeocene of Europe and the Caribbean, becoming common from the Eocene onwards. Several evolutionary lineages can be recognised, and it is possible to study evolutionary changes of some of these in great detail. On the whole they show strong provinciality, so while they are valuable for local correlation, they are not so useful over greater distances.

In this study the cytherettines are regarded very much in the manner of Triebel's original concept, so that many genera included by other authors are excluded here. The approach adopted is that of classical phylogeny: firstly the recognition of a readily distinguished group of ostracods based on morphology; and secondly a consideration of their geological history, geographical distribution and migration in order to understand intragroup and intergroup relationships. The first half of the paper considers the morphology of species and genera which are incontrovertibly cytherettines, and from which a diagnosis of the subfamily is formed. The second half examines other genera included by some authors in the light of this diagnosis, finally leading to a discussion of their geological history and distribution.

LIVING CYTHERETTINES

Cytheretta Müller, 1894

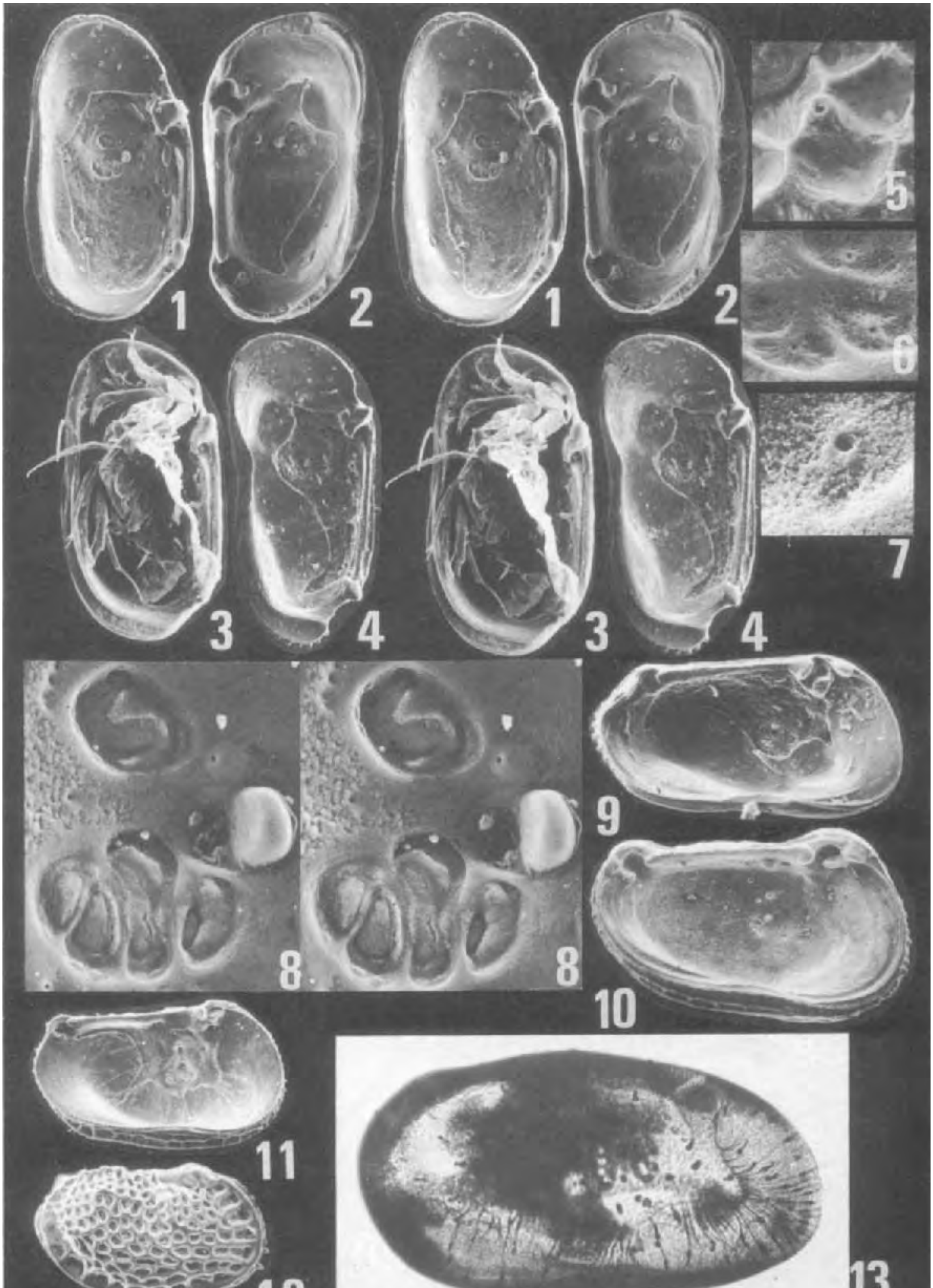
The type species, *Ilyobates*? *judaea* Brady, 1868 (subjective senior synonym of *Cytheretta rubra* Müller, 1894) has been described and illustrated by Müller (1894) and more recently by Keen (1972a) and Athersuch (1977a) so that a great deal is known about the carapace and soft parts. The type species lives today throughout the coastal waters of the Mediterranean (Text-fig. 1) and is also recorded from Quaternary sediments. A second living species, *Cytheretta adriatica* Ruggieri, 1952, has a similar distribution (Text-fig. 1); unlike *C. judaea*, the type specimens are of Quaternary age, but there is no doubt that the living specimens belong to the same species. Athersuch (1977b) has described Recent and Quaternary carapaces as well as the soft parts. A third species, rather



TEXT-FIG. 1—Distribution of Recent species of cytherettines.

PLATE 1—To illustrate the internal features of the cytherettines:

Figs. 1, 8. *Cytheretta maddocksae* Jain. fig. 1 ×65, fig. 8 ×500. Right valve female, stereo-pairs. Specimens donated by A. J. Keij from Holocene of Bandar Abbas, Iran (entrance to Persian Gulf). Fig. 2. *Cytheretta alexanderi* Howe and Chambers, ×60, female left valve, Cocoa Sand (U. Eocene), Choctaw Co. Alabama. Fig. 3. *Cytheretta edwarsi* (Cushman, 1906), ×55, female right valve, Recent off Cape Hatteras. Figs. 5, 10. *Paracytheretta reticosa* Triebel. fig. 5. normal pore canal ×500. fig. 10. left valve ×65. Thanet Beds (Palaeocene), Herne Bay, Kent, England. Note that the sinuous inner margin of fig. 10 is not preserved. Figs. 4, 9. *Protocytheretta daniana* Brady, ×55. fig. 4. female right valve. fig. 9. female left valve. Specimens donated by J. E. Hazel, from Recent off Cape Hatteras, U.S.A. Figs. 6, 7. *Protocytheretta karlana* to show normal pore canals. fig. 6 ×300, fig. 7 ×500. Specimens from Miocene Chipola Marl, Florida. Figs. 11, 12. *Neocytheretta snelli* (Kingma). fig. 11 ×65, female left valve. fig. 12 ×65, female right valve. Specimens donated by A. J. Keij, South China Seas, Recent (N3°34′34″, E110°13′). Fig. 13. *Cytheretta judaea* (Brady), ×90, female left valve to show radial pore canals.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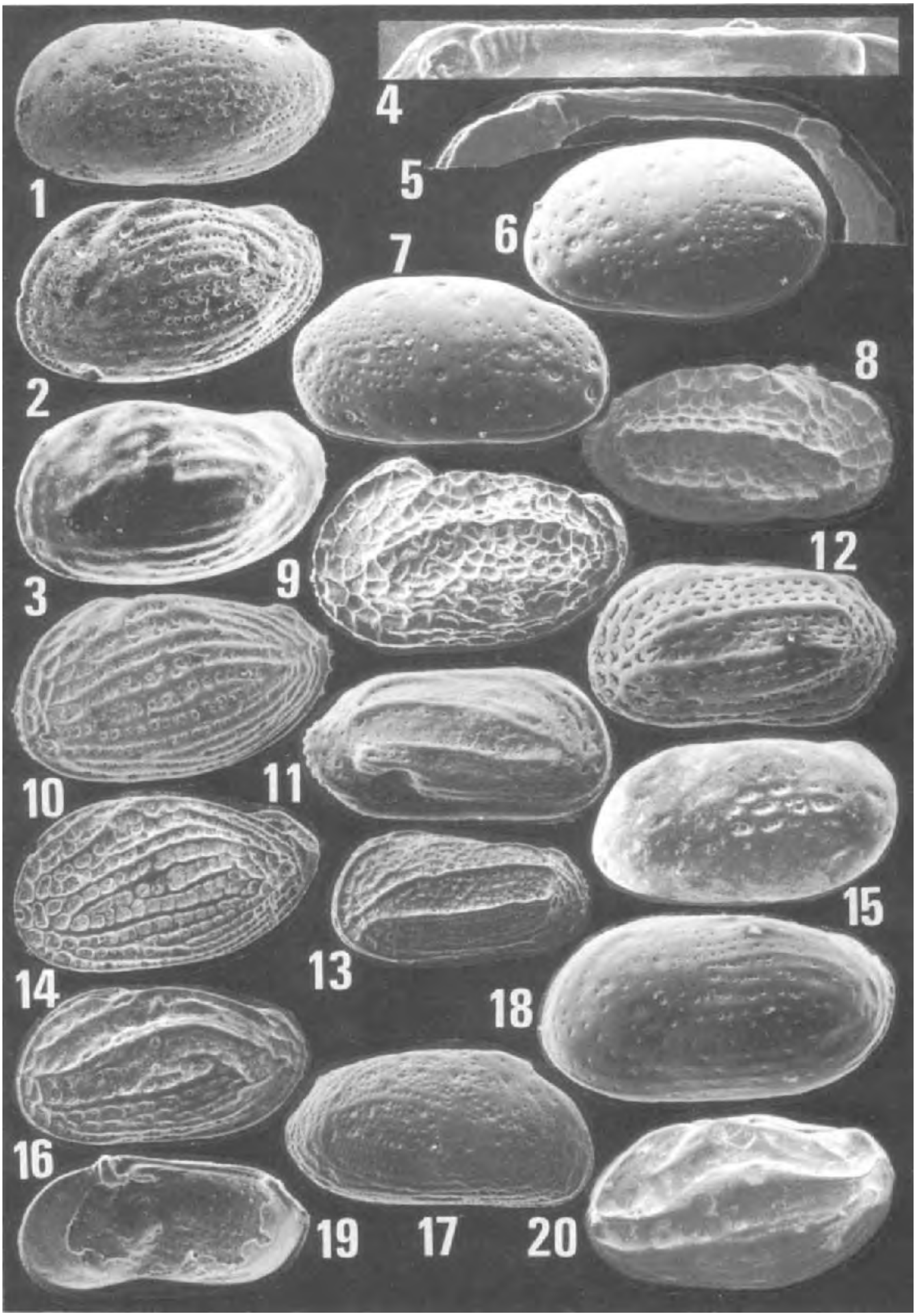
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similar to *C. judaea,* is *C. maddocksae* Jain, 1977, recorded from the northern shores of the Arabian Sea (Text-fig. 1); its soft parts have not been described however.

North American cytherettines have been placed into two distinct taxa: *Pseudocytheretta* Cushman, 1906 and *Protocytheretta* Puri, 1958. Only the latter will be discussed here, and Cushman's genus is regarded as a synonym of *Cytheretta.* Two living species are recorded from the eastern seaboard of the U.S.A. (Text-fig. 1), *C. edwardsi* Cushman, 1906 (type species of *Pseudocytheretta*) and *C. tracyi* Blake, 1929. The former is also known from Pleistocene sediments in the region. The differences between these two species are slight and it is possible that they are synonymous, but as no specimens of *C. tracyi* have been studied, this possibility is left open.

The final living species of *Cytheretta* is *C. teshekpukensis* Swain, 1963, originally described from the late Pleistocene of Arctic Alaska and more recently described as a living species off Franz Josef Land by Neale (1975) (Text-fig. 1). Swain (1963) also recorded *C. edwardsi* from the Pleistocene Gubik Formation of Alaska; however, as pointed out by Hazel (1967) there are sufficient differences to suggest that the Alaskan specimens belong to a different species of *Cytheretta.*

All of these species are elongate-ovate in shape, the two valves are unequal in size, the left valve being larger with a greater height; both valves have a slight, but noticeable posterior hinge-ear; the dorsal margin of the right valve is slightly convex with two concavities, one at the anterior giving the impression of a slight anterior hinge-ear, the other and more prominent at the posterior suggesting a small posterior process. The male is more elongate than the female in lateral view. The left valve over-reaches the right in most places, but this is particularly prominent in the postero-dorsal and antero-dorsal angles. The carapace may initially appear to be unornamented, but all species are punctate. The strength of the puncta varies within all species so is an intraspecific character; some specimens of *C. judaea* appear almost smooth, others have quite distinct longitudinal rows of small puncta (see illustrations in Athersuch, 1977a). *C. maddocksae* has, in addition to the rows of small puncta, some large pit-like depressions developed on the carapace (Pl. 2, figs. 6, 7). *C. adriatica* has thin longitudinal ridges developed, but again these are of variable strength so that some specimens appear to have only longitudinal rows of puncta, while in others the ridges are the dominant feature of the carpace (see illustrations in Athersuch, 1977b); this is also true of *C. teshekpukensis.* This intraspecific variation in ornamentation is a recurrent theme in the cytherrettines. None of these species have marginal spines, and none have eye spots or any ocular struc-

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Plate 2—Note sexual dimorphism, fig. 1 (male) and fig. 2 (female); inequivalve, fig. 6 (left) and fig. 7 (right), fig. 8 (right) and fig. 9 (left); stronger tricostate ornament of right valve (cf. figs. 8 and 9); homeomorphy (cf. figs. 2 and 10). Figs. 1–3. *Cytheretta alexanderi* Howe and Chambers, ×60. fig. 1, male left, Oligocene. N. Carolina; fig. 2, female left, Cocoa Sand (U. Eocene), Choctaw Co. Alabama; fig. 3, female left, Moody's Branch (U. Eocene), Alabama. Note the change in ornament from oldest (fig. 3) to youngest (fig. 1). Figs. 4, 5. *Argenticytheretta (Argenticytheretta) patagoniensis* Rose, ×87, photographs donated by J. Rose, specimens from M. Eocene, Magallanes Province, Chile. fig. 4, hinge of left valve; fig. 5, hinge of right valve to show socket for "snap-knob". Figs. 6, 7. *Cytheretta maddocksae* Jain, ×65, specimens from Bandar Abbas, Iran. Figs. 8, 9. *Paracytheretta reticosa* Triebel, ×65. fig. 8, right valve; fig. 9, left valve, Thanet Beds (Palaeocene), Herne Bay, Kent, England. Fig. 10. *Cytheretta grandipora cratis* Keen, ×75, female left valve, Marnes a *P. ludensis* (U. Eocene). Figs. 11–13. *Protocytheretta daniana* Brady, ×55. fig. 11, female right valve; fig. 12, female left valve; fig. 13, juvenile left valve, Recent, on Cape Hatteras; note stronger tricostate ornamentation of the juvenile. Fig. 14. *Cytheretta haimeana* (Bosquet), ×70, female left valve, Sables de Moiselles (M. Eocene), Paris Basin. Fig. 15. *Cytheretta burnsi* (Ulrich and Bassler), ×50, from Calvert Cliff, Maryland (Miocene); this is the punctate form, other variants may be totally smooth. Fig. 16. *Cytheretta* aff. *C. decipiens* Keij, ×70, female left valve from Marnes a *P. ludensis* (U. Eocene), Chavencon, Paris Basin. This specimen is intermediate between the genera *Cytheretta* and *Flexus.* Compare it with fig. 14; it can be seen that the tricostate ornamentation has arisen by suppression of some longitudinal ridges and stronger development of others. Fig. 17. *Cytheretta teshekpukensis* Swain, ×40, photograph donated by J. W. Neale; female right valve from Pleistocene Gubik Formation, Alaska. Fig. 18. *Cytheretta adriatica* Ruggieri, ×40; female left valve, Recent, Rimini, Italy. Fig. 19. "Unknown genus", ×90; specimens donated by R. Whatley, Recent of San Antonio, Argentina. Internal right-valve, note socket for "snap-knob". Fig. 20. Undescribed species of the *C. laticosta* group, ×67; M. Eocene, Whitecliffe Bay, Isle of Wight, England.

tures as they are all blind. The normal pore canals are simple, with two types of setae, simple hairs or "bristle-like" hairs. Larval forms are rather similar to the adults, although more triangular in lateral outline with greatest height towards the anterior, and ornamentation is usually weaker. *C. judaea* develops opaque areas in the carapace which seem to have a constant position in all specimens.

Internally the most conspicuous feature is the broad undulating inner margin, often preserved as a white opaque area in fossil specimens. This has generally been taken to be the most important diagnostic feature of the cytherettines and is the first structure described in Müller's original generic description. The inner margin has three principle indentations, one at the anterior, one in the anterior part of the ventral border, the third at the posterior (Pl. 1). There is only one major ventral indentation, although a second minor one may be present as in the type species. There are no vestibules. The selvage is more prominent in the right valve. The selvage is much stronger at the posterior of the right valve in *C. adriatica, C. edwardsi,* and to a certain extent *C. teshekpukensis,* and is a considerable way from the posterior margin so that a flange groove is formed. The selvage is very close to the anterior margin in all species. The anterior and ventral radial pore canals are long, slightly sinuous, simple, sometimes cross one another, and are usually bulbous near the outer margin. They sometimes appear to be paired, one being a true radial pore canal, the other being false (Pl. 1, fig. 13). In life they bear prominent simple setae. The posterior radial pore canals fall into two groups, a larger dorsal group of closely spaced straight canals and a ventral group similar to, but shorter than, the anterior and ventral radial pore canals. The part of the inner lamella in which the straight posterior radial pore canals are situated is not fused to the outer lamella, but this is not a true vestibule due to the presence of the radial pore canals.

The central group of muscle scars has a vertical row of four adductors; the lower two touch, the upper scar partially embracing the lower; the third scar is elongate and is the largest; the dorsal-most scar is circular. The frontal scar is large and irregular; it approaches a 'U' shape, with a shorter anterior arm; in the type species the upper part of the anterior arm forms a separate small detached scar. There is a very prominent knob-like fulcrum (fulcral point) situated between the adductor muscle scars and the frontal scar; in the type species it lies just to the anterior of the gap between the upper two adductor muscle scars; in *C. adriatica* it is more dorsally situated, in front of the dorsal-most adductor muscle scar, and in *C. edwardsi, C. maddocksae,* and *C. teshekpukensis* it is in front of, but above, the dorsal-most adductor muscle scar. A single mandibular scar is present just to the anterior of the ventral indentation but is not always visible. There are several prominent dorsal scars; one large and one small scar are present vertically above the fulcrum, another just below the posterior part of the anterior socket, and two more can be seen below the anterior half of the hinge; a depressed scar is present near the junction of the inner margin with the anterior hinge element. The various muscle scars described here are illustrated on Pl. 1.

The hinge is modified holamphidont. In the left valve an outgrowth of the selvage forms an antero-dorsal lobe in front of the anterior socket; this rests on an antero-dorsal platform in the right valve. The anterior socket is partially open ventrally, bordered by an antero-ventral lobe which fits into a modified part of the anterior tooth of the right valve. The postero-median bar is crenulate, although not always conspicuously so, and is swollen at both ends, forming a small antero-median tooth at the anterior and a swelling at the posterior which may be almost as prominent, as in the type species. The posterior socket is open ventrally. In the right valve the anterior tooth has a steep anterior face with a gentler posterior slope which curves round the anterior slocket partially closing it ventrally. The posterior tooth is almost as prominent and is elongate in shape.

The soft parts have been completely described for *C. judaea* (Müller, 1894; Athersuch, 1977a), *C. adriatica* (Athersuch, 1977b), and *C. edwardsi* (Cushman, 1906), and partially described for *C. teshekpukensis* (Neale, 1975). All have a three-jointed exopodite of the second antennae; and the posterior border of the protopodite of the first thoracic legs have no seta. The male has an asymmetric pair of first thoracic legs in the first three species listed, but it is not known whether this is also the case in *C. teshekpukensis*. The joints of the right leg are shorter and broader than those of the left, a character much more marked in *C. adriatica* and *C. edwardsi* than in the type species. *C. adriatica* also shows a similar asymmetry in the second thoracic legs of the male. All are blind. In life, *C. judaea* appears reddish-brown; *C. edwardsi* is chestnut-brown in the central areas and a "delicate pink" elsewhere.

Protocytheretta Puri, 1958

The type species, *Cythere daniana* Brady, 1869, was originally described as a living species from Veracruz, Mexico; it is known from the Gulf coast of the U.S.A., Florida, the Bahamas and as far north as the coast of New Jersey. The centre of distribution for the genus is in the Caribbean and the Gulf of Mexico. In this study, all of the living cytherettines from the Gulf and Caribbean region are placed in *Protocytheretta* rather than *Cytheretta*, the genus to which most were originally referred. The following species are known to be living at present: *P. daniana*, *P. montezuma* (Brady, 1866) (Bahamas), *P. pumicosa* (Brady, 1866) which might by a synonym of *P. daniana* (Benson and Coleman, 1963, p. 26) (Bahamas, Cuba, and said to be widespread in the Gulf of Mexico by Garbett and Maddocks, 1980), *P. louisianensis* (Kontrovitz, 1976) (Texas and Louisiana), *P. ambifera* (Krutak, 1971) (Veracruz, Mexico), *C. littorea* (Garbett and Maddocks, 1980) (Texan coast), *P. sahni* (Puri, 1952) (eastern Gulf of Mexico and eastern seaboard) and *P.* aff *sahni* (eastern seaboard). *Paracytheretta multicarinata* Swain, 1955 is a species of *Reticulocythereis* Puri, 1960 and unrelated to the cytherettines.

There are no published descriptions of the soft parts of *Protocytheretta* so it is only possible to describe the morphology of the carapace. The description of the shell structure of *P. daniana* is based on specimens provided by Dr. J. E. Hazel from off Cape Hatteras, N. Carolina (Pl. 1, figs. 4, 9; Pl. 2, figs. 11–13). The carapace is quadratic in lateral view, both valves have a marked postero-dorsal angle with a posterior process and spines; the left valve is larger than the right. The dorsal margin is almost straight. Males are more elongate. There are some eight posterior denticles on each valve. It is normally stated that the ornament consists of three longitudinal ridges with reticulation between. In general appearance there do seem to be three ridges, but closer inspection reveals several other subsidiary ridges in the ventral region; a second shorter ridge associated with the adorso-lateral ridge, and two ridges along the dorsal margin, one at the posterior, the other at the anterior. The right valve appears more tricostate than the left. There are no swellings of the valve associated with these ridges. Larval forms appear much more tricostate and have stronger anterior marginal rims than the adults. Internally, the hinge is similar to that of *Cytheretta*, but with a more obviously crenulate hinge bar, and in the left valve more prominent antero-dorsal and antero-ventral lobes. The inner margin has three deep indentations, along the anterior, posterior, and ventral border; the posterior segment of the inner margin is very broad and almost reaches as far as the dorsal margin. The central muscle scars are similar to *Cytheretta*, but with a more circular frontal scar; the fulcrum is prominent and slightly to the dorsal of the topmost adductor; there is a single mandibular scar situated near the junction of the ventral indentation and the anterior segment of the inner margin. The radial pore canals are similar to *Cytheretta*, but lack the closely packed straight posterior radial pore canals, and show more common pairing of false and true canals. Normal pore canals are simple.

Other species are essentially similar. Some have more prominent anterior or posterior hinge ears in the left valve (*e.g. P. louisianensis, P. littorea*), some are more prominently tricostate (*e.g. P. sahni*, but especially the Miocene species *P. inaequivalvis* (Ulrch and Bassler, 1904). The species differ in lateral outline, details of ornament including the strength of the longitudinal ridges and type of intercostal ornament (puncta, pits, reticulation), outline of inner margin, and size.

TERTIARY CYTHERETTINES

Europe

The Tertiary cytherettines of Europe form such a large and variable group of ostracods that it is not possible at present to give a coherent picture of their distribution, evolution, and relationships. In this interim report, ten distinct groups are listed, all of which probably warrant generic status. Their stratigraphical and geographical ranges are also given. All are inequivalve, show sexual dimorphism, lack ocular structures, and have internal features similar to *Cytheretta.*

Paracytheretta Triebel, 1941: Santonian-Palaeocene; southern England, Denmark, Germany, Poland, Kazakstan (U.S.S.R.). Left valve with a prominent anterior hinge ear and less prominent posterior hinge ear; anterior and posterior marginal spines may be present; ornamentation of three longitudinal ridges associated with a swelling of the carapace (in some Cretaceous species, *e.g. P. ptygmata* Triebel and Malz, 1969, 3 swollen ridges may be very prominent), intercostate areas smooth or reticulate.

Flesus Neviani, 1928: Oligocene-Pleistocene; W. Europe, central Europe, S. Ukraine, Turkmenia, Mediterranean. Left valve with anterior and posterior hinge-ears, sub-triangular in outline; ornamentation of three prominent longitudinal ridges, intercostal ornament varies from fine puncta to reticulation; in dorsal view posterior end narrows abruptly forming a tail-like end; anterior denticles may be present, posterior spines always present (see Weiss (1983) for illustrations of the type species *F. plicatus* (V. Munster)).

C. haimeana (Bosquet, 1852) group: M. Palaeocene–U. Eocene; N.W. Europe, Northern Aquitaine, Southern Ukraine (?). Left valve with a prominent posterior hinge ear and less prominent anterior hinge ear; posterior spines and anterior denticles may be developed; ornamentation of some 10–12 longitudinal ridges, intercostate ornament varies from puncta to reticulation; tendency for weak, tricostate appearance, also for anterior areas to become unornamented; ornamentation varies intraspecifically. Selvage prominent with posterior flange groove.

C. eocaenica Keij, 1957 group: M. Eocene–Miocene; W. Europe, Germany, S. Ukraine, Turkmenia, Kazakstan in the U.S.S.R. Left valve with prominent posterior hinge ear; no marginal spines. Ornamentation may be lacking, but is usually several longitudinal rows of pits; ornamentation varies intraspecifically.

C. laticosta (Reuss, 1850) group: M–U. Eocene; England, Belgium, Paris Basin only. Massive carapace. Left valve with a posterior hinge ear and convex dorsal margin in front of this; ornamentation of three prominent longitudinal ridges, dorsal ridge convolute, median ridge swollen centrally, ventral ridge more prominent in right valve because left valve has several other subsidiary ventral ridges; ornamentation of puncta related to normal pore canals; anterior and posterior denticles present. Selvage prominent with flange groove.

C. tenuipunctata (Bosquet, 1852) group: Oligocene–Pliocene; W. Europe, central Europe, Turkish Thrace, eastern Europe, S. Ukraine, Turkmenia, Mediterranean. Slight posterior hinge-ear in left valve, dorsal and ventral margins sub-parallel; posterior marginal spines not developed, small anterior denticles may be present; ornamentation of up to 13 longitudinal ridges, intercostal ornamentation varying from puncta to reticulation; intraspecific variation in ornamentation; wide flange groove at posterior.

C. sagri Deltel, 1964 group: U. Eocene–Oligocene; Aquitaine, Italy. Posterior hinge-ear in left valve, anterior hinge-ear may be developed; prominent posterior spines, occasional anterior denticles; ornamentation of some 13 longitudinal ridges often weakly developed, if at all, in the anterior half of valve, intercostal ornamentation of puncta or reticulation.

C. rhenana Triebel, 1952 group: U. Eocene-Miocene; western and central Europe. Left valve may have a posterior hinge-ear, anterior obliquely rounded; no marginal spines; smooth or with horizontal rows of pits; selvage of right valve marginal.

C. semipunctata (Bornemann, 1855) group: Oligocene-Pliocene; western, central Europe, Mediterranean. No marginal spines; ornamentation of coarse pits, dorsal area often smooth.

There are also several species from Aquitaine which do not readily fit into any of these groups, and rich cytherettine faunas in the Upper Eocene and Oligocene of the U.S.S.R. which probably fall into yet further groups (*e.g.* Nikolaeva, 1978). There are also two rare cytherettine genera described from Europe:

Lixouria Uliczny, 1969, type species *Cythereis unicostulata* Kuiper, 1918. This genus was based on Pliocene material from Greece which unfortunately was not similar to the designated type species (see Sissingh, 1973). The type species is rare and is the only published species of the genus, being found in the Middle Oligocene of Holland and the Upper Oligocene of the Hamburg area (Uffenorde, 1981). Wouters (unpublished Ph.D. thesis, 1978) records further rare species from the Miocene of Belgium. The internal characters are similar to *Cytheretta,* with a sinuous inner margin and prominent fulcrum; externally the carapace resembles *Cytheretta* but has a very prominent keel-like straight ventral ridge on both valves; the surface may be smooth or punctate. There is no eye spot or other ocular structure, despite Sissingh (1973) listing one.

Puricytheretta Russo and Bossio, 1974, type species *P. melitensis* Russo and Bossio, 1974, is only recorded from deep water Miocene sediments of Malta. Although placed in the Cytherettinae by the authors, it was regarded as being intermediate between *Ruggieria* Keij, 1957 and *Cytheretta,* and thus connecting the two subfamilies Cytherettinae and Pterygocytherinae. Its shape is similar to *Cytheretta;* the left valve is smooth but the right valve has a straight ventral ridge and a few rows of pits. Internally it is very similar to *Cytheretta* except that the inner margin, while broad, is not sinuous. There are no eye spots or other ocular structures. The central muscle scars have a fulcrum; the radial pore canals are similar to *Cytheretta,* with true and false canals.

Beatamoosina Uffenorde, 1981, type species *B. cuxhavenensis* Uffenorde, 1981, from the Upper Oligocene and Miocene of Germany, was placed in "unterfamilie Incertae sedis" by Uffenorde. It may be a cytherettine. (See Uffenorde, 1981 for discussion).

North and Central America

There are three major groups of cytherettines, two of which, *Cytheretta* and *Protocytheretta,* have already been described. These both appeared in the Miocene and continue through to the present day. The third group characterises the Middle and Upper Eocene of the Gulf states of the U.S.A. and the southeastern seaboard. It is typified by *Cytheretta alexanderi* Howe and Chambers, 1955 (which could be a junior synonym of *C. jacksoni* Meyer, 1885, Hazel pers. comm.). *Cytheretta arrugia* van den Bold, 1957 from the Palaeocene of Trinidad and Venezuela may belong to this group, but it may not be a cytherettine at all; otherwise it is only found in the Middle Eocene–Oligocene sediments of the Gulf states, Florida, Alabama, and N. and S. Carolina, and in the Oligocene of Trinidad (Van den Bold, 1960) and Florida. Cursory examination of specimens from various localities and horizons suggests that the species could easily be subdivided. The three specimens illustrated on Pl. 2 (figs. 1–3) show the differences in ornamentation with intercostal pitting becoming more dominant in younger specimens. The carapace is strongly inequivalve, the larger left valve has a prominent posterior hinge-ear and a less marked anterior hinge-ear, the right valve has a small posterior process; sexual dimorphism is prominent, with more elongate males; small marginal anterior and posterior denticles are present; ornamentation consists of about 12 longitudinal ridges which fade towards the anterior; intercostal areas are smooth or pitted. There are no eye spots or other ocular structures. Internally the features are as for *Cytheretta* (Pl. 1, fig.

2); the hinge of the left valve has prominent antero-dorsal and antero-ventral lobes, the hinge-bar is weakly crenulate; the frontal scar is 'U' shaped, the fulcrum is prominent; the radial pore canals are as for *Cytheretta*, including some closely packed straight posterior radial pore canals.

Szczechura (1971) has figured tricostate cytherettines from the Palaeocene of West Greenland.

A DIAGNOSIS OF THE SUBFAMILY CYTHERETTINAE

Second antennae with three-jointed exopodite; first pair of thoracic legs of males asymmetric, joints of right leg being shorter and broader than left. No eyes or ocular structures. Sexual dimorphism of carapace distinct, with more elongate males. Carapace ovate, valves distinctly asymmetric with larger left valve. Carapace ornament of puncta, pits, reticulation or ribs all arranged longitudinally. Intraspecific variation in ornament common. Normal pore canals simple; simple and bristle-like setae present. Inner margin broad, undulating, with three prominent indentations at anterior, ventre, and posterior; no vestibules; radial pore canals simple, mostly long, curving and bulbous toward outer margin, often in pairs, one of each pair being false; at posterior a group of short straight radial pore canals may be present in postero-dorsal position. Selvage may be prominent, flange groove may be present. Hinge modified holamphidont; in left valve an antero-dorsal lobe present in front of anterior socket, antero-ventral lobe on antero-ventral side of socket, all sockets open ventrally, postero-median bar of left valve crenulate with antero-median tooth and a posterior swelling; teeth of right valve large and prominent. Central muscle scars with four adductors, dorsal most small and ovate, second scar down largest and elongate, lowest two scars intimate; frontal scar complex 'U' shaped, upper part of anterior arm with a tendency to become detached; prominent fulcrum between adductors and frontal scar. A single mandibular scar is present near ventral indentation of inner margin.

The most important features of the carapace are considered to be: prominent inequivalve, lateral outline, longitudinally arranged ornamentation, lack of a sub-central tubercle, lack of any ocular structures, the characteristic hinge, the sinuous inner margin, lack of vestibules, type of normal and radial pore canals, central muscle scars with fulcrum, and the single mandibular scar.

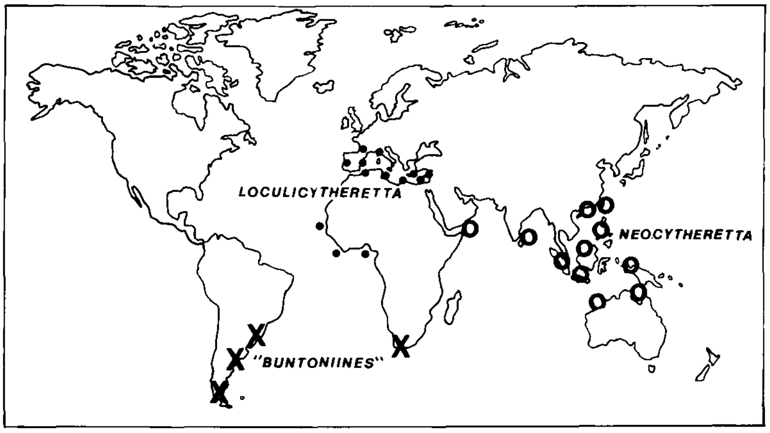
These characters make the cytherettines a well defined group which is regarded as a subfamily of the Trachyleberididae in agreement with the arguments of Hazel (1967).

Importance has been attached to the lack of ocular structures and the sinuous inner margin. It should be pointed out that the overlap of the left valve associated with either the anterior hinge-ear or the antero-dorsal lobe of the hinge can give the appearance of an eye tubercle and has often been mistaken as such. Secondly, some species, especially of the *C. tenuipunctata* group can have an inner margin which is approaching being non-sinous; and preservation often destroys the duplicature, thus giving the appearance of a non-sinuous inner margin

Homeomorphy is common amongst the cytherettines; this has been discussed by Keen (1982); (also compare Pls. 1, 2, figs. 3, 10). The tendency in some groups for development of tricostate ornamentation is quite common; care must be taken in interpreting this feature. It has obviously arisen independently several times within the cytherettines. *Flexus* probably evolved from the *"D. haimeana"* Group (Keen, 1972a); a form intermediate between *Flexus* and this group is figured on Pl. 2 (cf. figs. 10, 14).

OTHER CAINOZOIC GENERA WHICH HAVE BEEN PLACED IN THE CYTHERETTINAE

There is a whole list of genera which have placed in the subfamily and which are rejected or



TEXT-FIG. 2—Distribution of Recent and fossil "pseudocytherettines".

considered dubious members. In the latter case this is often due to lack of information and the decision was taken to exclude them until further information is available.

Loculicytheretta Ruggieri, 1954 has been regarded as a cytherettine by many authors, notable exceptions being Morkhoven (1963), Triebel and Malz (1969) and Keen (1972a). Hartmann and Puri (1974) proposed a new tribe, the Loculicytherettini, as a subdivision of the Cytherettinae. The genus has attracted a lot of attention because of the postero-ventral loculi developed on the exterior of the female. These have been regarded as brood pouches, flotation devices, or as aids in copulation. Carbonel and Colin (1982) have demonstrated that the loculi form by migration and enlargement of fossae present on the ventral ridge of instars and adult males. Two distinct groups of species are present (Bismuth *et al.*, 1978), the Eocene *Heptaloculites* Ruggieri, 1963, and the Miocene–Recent *Loculicytheretta.* Carbonel and Colin (1982) have argued that these are totally unrelated, but other authors (*e.g.* Bismuth *et al.*, 1978) have regarded the two as synonyms. The type species of *Loculicytheretta, Cythere pavonia* Brady, 1866, is found living today in the Mediterranean and off West Africa (Text-fig. 2), and has been well illustrated by Morkhoven (1963), Doruk (1973) and Athersuch and Bonaduce (1976). The outline and ornamentation do bear a resemblance to cytherettines such as *Flexus* and to larval forms referred to *Falunia* (see below), but there are considerable differences which suggest it is not a cytherettine. The hinge is very different, the anterior sockets of both valves have well developed ridges closing them ventrally, the anterior socket of the left valve is very small, there are no antero-dorsal or antero-ventral lobes in the left valve, and the anterior tooth of the right valve is of a different shape; there is a clear ocular sinus (Doruk, 1973, Pl. 1:43:240: figs. 1–2); the central muscle scars are situated in a depression, have different shaped adductor scars and no fulcrum; the inner margin is not sinuous; the radial pore canals are straight and apparently without bulbous ends. Against this, Athersuch and Bonaduce (1976) thought that some anatomical details of the soft parts suggested affinities with the cytherettines. It is still considered that the weight of this evidence excludes *Loculicytheretta* from the cytherettines.

Neocytheretta Morkhoven, 1963: This genus is widely distributed in the late Tertiary and Recent of Southeast Asia, and has been place in the cytherettines by several authors (*e.g.* Morkhoven, 1963; Hazel, 1967; Hartmann and Puri, 1974). This classification is based solely on the presence of a sinuous inner margin. The hinge is very different from the cytherettines, lacking the subsidiary features, having ventrally closed sockets, and a more complex anterior tooth in the right valve; there is an ocular sinus and a very prominent eye tubercle; the frontal scar is simple and there is no fulcrum; the broad inner margin leaves only the central areas non-calcified; the radial pore canals are branching and non-bulbous; externally, the ornamentation is totally unlike that of the cytherettines, with ridges, reticulation, and the presence of dorsal spines or tubercles. The lateral outline differs with its characteristic upwardly curved postero-ventral margin. Thus *Neocytheretta* is excluded from the subfamily, following the opinion of Triebel and Malz (1969), Keen (1972*a*), and Malz (1980). In the last paper, Malz described several Plio/Pleistocene species from Java, N. Borneo, and Taiwan and suggested a relationship with *Alocopocythere* Siddiqui, 1971, illustrating species (*A. kendengensis* (Kingma, 1948) and *A. hui* Malz, 1980) with sinuous inner margins. Gramann (1975) and Hu (1977) had previously equivocated these two genera, although Hartmann and Puri (1974) placed *Neocytheretta* with the Cytherettinae, and *Alocopocythere* in the Echinocythereidini. This emphasises the problems arising when too much importance is attached to a single morphological feature, *i.e.* the sinuous inner margin, without regard to the total morphology.

Several species of *Cytheretta* have been recorded or described from California and the Pacific coast of Nicaragua (see Swain and Gilby, 1974). Swain and Gilby described two new species, *Cytheretta minutipunctata* and *C. rothwelli* (= *C.* aff. *C. daniana* of Swain, 1969). They figured several appendages of the first of these species but their description is not complete enough to know whether or not they are cytherettines. The second antennae do appear to have a three-jointed exopodite, but there is no mention of any asymmetry in the first pair of male thoracic legs. The external appearance of the species is cytherettine, but there are differences. *C. minutipunctata* has large normal pore canals, a small ocular sinus, two frontal scars and no fulcrum, small anterior and posterior vestibules, and a hinge where the anterior socket of the right valve is closed ventrally. *C. rothwelli* has an eye spot and an ocular sinus, lacks a fulcrum, has an anterior vestibule, and a much weaker hinge in the right valve. The inner margin of both species is broad, but not sinuous. These seem to be sufficient grounds for doubting whether these are true cytherettines. *Pseudocythereis* Skogsberg, 1928 from South Georgia, S. Atlantic, has been placed in the family by several authors, including Skogsberg (1982), Puri (1958), Hazel (1967) and Hartmann and Puri (1974). The only description available for the soft parts is the original one by Skogsberg who was undoubtedly comparing it with *Cytheretta judaea.* Species described by Swain (1963) from the late Pleistocene of Alaska do not belong to the genus.

Other genera sometimes placed in the family are: *Buntonia* Howe 1935, *Ambocythere* Van den Bold, 1957, and *Netrocytheridea* Howe and Laurencich, 1958. None are regarded as cytherettines (Keen, 1972a). Several authors (*e.g.* Hazel, 1967) have commented on the close relationship between the buntoniids and cytherettines although only Morkhoven (1963) and Grundel (1974) place *Buntonia* within the cytherettines. Morkhoven did this on the basis of the similarity between the second right thoracic leg of the male and similarity in the anterior radial pore canals. However there are sufficient differences in the hinge, marginal zone, shape, ornamentation and lack of fulcrum to exclude them from the cytherettines. Malz (1982) has demonstrated that the buntoniids are probably homeomorphic with, and fairly unrelated to, *Ambocythere.*

South American "cytherettines"

Rossi de Gracia described three new cytherettine genera from the Miocene of Argentina in 1969. These are *Argenticytheretta, Bensonia,* and *Grekoffiana.* Although it has not been possible to examine material from Argentina, it has been possible to come to some conclusions concerning these genera. Rose (1975) has described several species of *Argenticytheretta* from the Eocene–Miocene of southern Chile, published in the Stereoatlas. He recognised three new subgenera, *Argenticytheretta* (*Argenticytheretta*), *A.* (*Magallanella*) and *A.* (*Chilea*). From his descriptions it is clear *Argenticytheretta* is not a cytherettine: ventrally inflated right valve unlike any cytherettine, presence of an eye tubercle and ocular sinus, broad but not sinuous inner margin, no fulcrum in central muscle scars, non-bulbous radial pore canals, small anterior vestibule, and hinge with a "snap-knob" (Rose, 1975) which consists of a socket in the right valve and knob in the left developed at the postero-cardinal and angle (Pl. 2, fig. 5). *Bensonia* was described as being similar to *Cytheretta* but with a regular inner margin. *Cytheretta knysnaensis* Benson and Maddocks, 1963 was placed in the new genus by Rossi de Garcia and paratypes of this species have been examined with the help of Dr. Benson. Species of the genus certainly look like cytherettines, but there are several characters seen in *C. knysnaensis* which suggest it is not a cytherettine: presence of a weak eye tubercle and a pronounced ocular socket, a hinge similar to *Cytheretta* but with much weaker terminal teeth in the right valve and anterior sockets closed ventrally, straight non-bulbous radial pore canals which often occur in pairs, broad but non-sinuous inner margin, and presence of a small anterior vestibule. Bertels (1975) has described and figured two species of *Bensonia* from the Upper Oligocene–Miocene of Argentina which have an eye tubercle and ocular sinus, and also a smooth hinge-bar; the genus is placed in the subfamily Buntoniinae. *Grekoffiana* was described as being similar to *Protocytheretta* but with a regular inner margin, and Rossi de Garcia places *Cythere daniana* Brady the type species of *Protocytheretta* Puri, in the new genus. There is therefore the possibility of *Grekoffiana* being a junior synonym of *Protocytheretta.* Unfortunately, Rossi de Garcia's description of the type species and genus is inadequate to arrive at any firm conclusion, but the suspicion remains that the alleged similarity to *Protocytheretta* is a red herring and that *Grekoffiana* is not a cytherettine. Bertels (1968) described a new genus *Huantraiconella* from the Palaeocene of Argentina, with a type species *H. prima* Bertels, 1968 showing a remarkable homeomorphy with *Cytheretta;* Bertels (1973) compares this species with *Cytheretta nerva montensis* Marliere, 1958 from the Montian of Belgium. However, Bertels is in no doubt that internally this is a buntoniine, and (1973) describes forms transitional between *Buntonia* and *Huantraiconella. Huantraiconella* possesses both an eye tubercle and an ocular sinus. Another genus described by Bertels (1975) is *Harringtonia* from the Palaeocene of Argentina, another buntoniine with cytherettine appearance which also has the "snap-knob" of *Argenticytheretta.*

In conclusion, it seems that there is a group of ostracods in South America, probably belonging to the subfamily Buntoninae, which are homeomorphic, with, but unrelated to, the cytherettines. Other genera which may belong to this group include *Togoina* Apostolescu, 1961, *Protobuntonia* Apostolescu, 1961, and *Soudanella* Apostolescu, 1961. These are best known from the Lower Tertiary of West and North Africa, but *Togoina* and *Soudanella* are known from the Palaeocene of Argentina (Bertels, 1975). Thus it is possible to conceive of a South Atlantic group of pseudocytherettines. Yajima (1982) has placed all these South American genera in the tribe Buntoniini of the subfamily Buntoninae.

As a postscript, Dr. R. Whatley has presented the author with some Recent "cytherettine" ostracods from San Antonio, Oeste Prov. de Rio Negros, Argentina (Pl. 2, fig. 19). They certainly appear cytherettine, even have a sinuous inner margin and lack any ocular structures. However, the sinuous inner margin has 4 ventral indentations and is unlike that of *Cytheretta;* the anterior sockets are closed ventrally, the posterior tooth of the right valve is small, the median hinge bar is much more coarsely crenulate in its posterior half (as seen in *Argenticytheretta* Pl. 3, fig. 4), there is a "snap-knob" developed and the central muscle scars lack a fulcrum. It is also very small (0.55–0.60 mm) and the lateral outline is more suggestive of *Buntonia.*

West Africa

Reyment (1981) has recorded a single specimen of *Cytheretta*? sp. from the Maastrichtian of Ghana. The specimen is a carapace so no details are known of the internal structure. It looks like a cytherettine, but it is not so dissimilar from "*Leguminocythereis*" species recorded from West Africa, so it is regarded here as a homeomorphic species unrelated to *Cytheretta.* There are no other records of cytherettines from the extensive late Cretaceous and Tertiary faunas of West Africa.

Australia

Whatley and Downing (1983) recorded a *Cytheretta* species from the Miocene of Victoria, represented by one adult and 2 juvenile valves. The features they describe are mostly cytherettine; the only non-cytherettine characters are the bifurcating radial pore canals, very large normal pore canals, and lack of a fulcrum. The case for this being an Australian cytherettine is regarded as unproven, and it could be a species of *Australimoorella* Hartmann.

MESOZOIC CYTHERETTINES

Paracytheretta is the only Mesozoic genus clearly accpeted as a cytherettine. Deroo (1966) described two new genera from the Maastrichtian of Holland, *Acuticytheretta* and *Semicytheretta.* Unlike *Paracytheretta,* these do not exhibit all of the cytherettine characters, and Triebel and Malz (1969) only accepted *Semicytheretta* into the subfamily, although Keen (1972a) accepted both. *Acuticytheretta* approaches the cytherettines in lateral outline, although it is more like *Protobuntonia,* and it has a larger left valve. The hinge is cytherettine and has ventrally closed anterior sockets, but does have the antero-dorsal lobe of the left valve. The central muscle scars are cytherettine, but appear to lack the fulcrum. The duplicature is broad, especially at the anterior and posterior, but the inner margin is non-sinuous. There do not appear to be any ocular structures. The two species of *Semicytheretta* described by Deroo seem very different; both are inflated ventrally, which is not a cytherettine character, but whereas the type species *Cypridina furcifera* Bosquet, 1847 has an almost smooth surface, *C. elegans* Bosquet, 1847 is more like *Paracytheretta* with three prominent longitudinal ridges. The hinge and inner margin are described as being similar to *Cytheretta,* as are the muscle scars although it is not clear whether there is a fulcrum. The problem here is that of dealing with possible early members of a group and deciding whether they should possess all the characters that eventually evolved to define the taxon. If the cladistic approach is adopted, *Acuticytheretta* would probably be excluded, but the phylogenetic approach still leaves open the possibility of its inclusion.

Going further back into the Mesozic, the recognition of cytherettines becomes very difficult. Gründel has published a series of papers (*e.g.* 1976, 1977) in which he interpreted the cytherettines in a totally different manner from that of Triebel. He has divided the family Cytherettidae into 3 subfamilies and 10 tribes, and includes the buntonines as well as Jurassic genera such as *Pleurocythere* Triebel, 1951. A further problem arises from the fact that Grundel places individual genera into different tribes and even subfamilies in different publications. It is not possible to discuss Grundel's classification in detail because of space, but essentially it is rejected and Triebel's original concept adhered to. Certainly some Cretaceous species of genera such as *Costaveenia* Grundel, 1966, *Mosaeleberis* Deroo, 1966 and *Anticythereis* Van den Bold, 1946 show some resemblance to cytherettines, and even Jurassic genera such as *Pleurocythere* could be viewed in this light. However, homeomorphy is rampant in the Mesozoic cytheracean ostracods, with the parallel development of features. Until relationships are better understood, the morphological similarities with cytherettines are best regarded with suspicion. Thus we can trace the group back into the Upper Cretaceous, but at the moment no further. It is to be expected that the immediate ancestors of the group will not have all the characteristics of the cytherettines. In particular, one could expect the fulcrum to be absent as in all other trachyleberids; ocular structures could be present; the inner margin would not be sinuous; the terminal hinge elements would be less pronounced and possibly denticulate. Ancestral groups would probably continue alongside the newly evolved cytherettines for some time. It is not clear whether all the various cytherettine groups can be traced back to a common ancestor, although this is the assumption followed here. New views on the way evolution proceeds suggest that a new group such as the cytherettines could evolve very rapidly and not even resemble their immediate ancestors very closely.

THE GENERA INCLUDED IN THE CYTHERETTINAE

The previous discussion has argued the case for inclusion or exclusion of genera which have been referred to the Cytherettinae. There are some problems remaining. *Pseudocytheretta, Cylindrus* Neviani, 1928, and *Prionocytheretta* Mehes, 1941 are usually regarded as synonyms of *Cytheretta.* For a discussion on *Pseudocytheretta* see Hazel 1967; it is clear that the neontologists Müller and Blake both regarded the differences between the soft parts of *Cytheretta* and *Pseudocytheretta* as not being of generic significance. Yet there are differences, and *C. edwardsi* in some respects is closer to *C. adriatica* than to *C. judaea* (degree of asymmetry of male first thoracic legs, presence of a flange groove, size) and it is still open to discussion whether *Pseudocytheretta* should be accepted as a valid genus. The type species of *Cylindrus* is *Cythere jurinei* Munster, 1830, a member of the "*C. eocaenica* group" described earlier; this species would thus become the genotype, and although *Cylindrus* is preoccupied and thus not available as a name, Neviani's genus could still be valid. The same argument could apply to *Prionocyteretta* which might belong to the "*C. tenuipunctata* group".

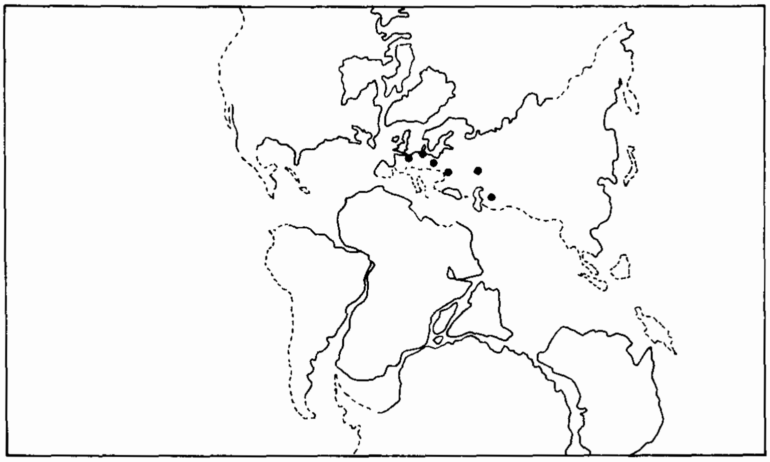
The so-called "*Falunia* problem" is inescapable in any essay on the cytherettines. The type species is *Falunia girondica* Grekoff and Moyes, 1955; in 1958 Moyes made this species a subjective junior synonym of *Cythere sphaerulolineata* Jones, 1857. Most subsequent authors have accepted this opinion and several other species have been assigned to the genus from Miocene and Pliocene sediments. A further problem arises from the fact that the material of *F. girondica* used in diagnosing the genus did not include any adult specimens. Thus two problems present themselves: is *F. girondica* a junior synonym of *C. sphaerulolineata;* and what is the adult like? Liebau (1975), Ruggieri (1976) and Wouters (unpublished Ph.D. thesis, 1970) have all considered *F. girondica* to be a juvenile *Cytheretta;* Ruggieri (1976) has proposed the name *Olimfalunia* for those species placed in *Falunia* and which are not cytherettids; members of this taxon are probably closely related to the genera *Celtia* Neale, 1973 and *Hiltermannicythere* Bassiouni, 1970. Wouters goes one step further and suggests splitting *Cytheretta* into two, based on whether the larval form resembles the adult or not. The author's own observations support the idea that some cytherettines have larval stages with ornamentation unlike the adult, and certainly lateral outline can be quite different, but it is not at all apparent that this is a consistent feature which can be used in generic diagnoses. The evidence is certainly strong enough to warrant making *Falunia* synonymous with *Cytheretta,* but further discussion must await the publication of Wouters' ideas.

The valid genera of the Cytherettinae are:

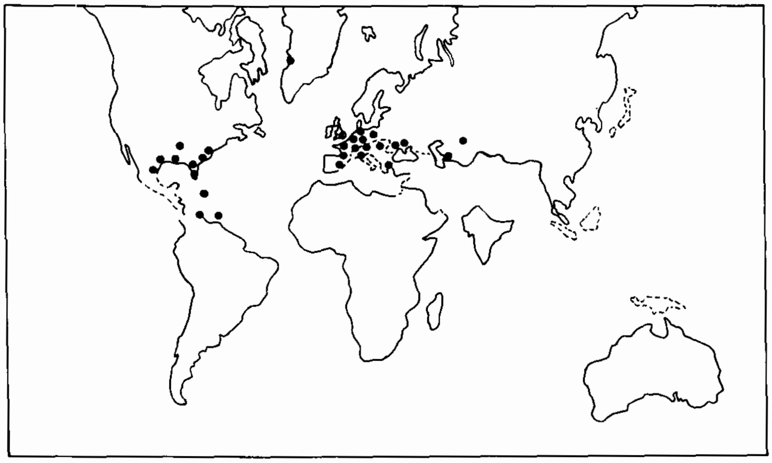
Cytheretta Müller, 1984
Acuticytheretta Deroo, 1966
Flexus Neviani, 1928 (obj. syn. *Eucytheretta* Puri, 1958)
Lixouria Uliczny, 1969
Paracytheretta Triebel, 1941 (sub. syn. *Golcocythere* Grundel, 1968)
Protocytheretta Puri, 1958
Puricytheretta Russo and Bossio, 1974
Semicytheretta Deroo, 1966

THE EVOLUTION AND DISTRIBUTION OF THE CYTHERETTINAE

The cytherettines emerged as a recognisable taxon in the late Cretaceous of northern, central, and eastern Europe (Text-fig. 3). The principal genus was *Paracytheretta* and the early cytherettines showed a "boreal" distribution, not being recorded in Tethyan deposits. It should be remembered that the Cretaceous "boreal" is a geographical term, and the climate was warm. No cytherettines have been recorded in the oldest Palaeocene, but they are present in Europe from the Mid-Palaeocene onwards. *Paracytheretta reticosa* Triebel, 1941 from the Mid-Late Palaeocene of northern Europe provides a definite link with late Cretaceous members of the genus. *Cytheretta nerva,* the oldest member of the *C. haimeana* group, appears in the Montian and members of this group become abundant in northern Europe and are also found in the Palaeocene of southern Aquitaine. The evolution of this group has been studied in a series of papers by Keen (1972a,b,



TEXT-FIG. 3—Distribution of Cretaceous cytherettines.



TEXT-FIG. 4—Distribution of Palaeogene cytherettines.

1978, 1981); some species, such as *C. costellata* (Roemer, 1838) have been shown to be polymorphic and successive population changes have been recorded. In North America there are no records of Cretaceous or Palaeocene cytherettines; the oldest species, *C. arrugia* Van den Bold, 1957, is found in the Palaeocene of the Caribbean (Trinidad, Venezuela). There are no records at all from the Lower Eocene. The Middle Eocene saw a great radiation of many groups of cytherettines in Europe, including the *C. eocaenica* group, which is found from Aquitaine in the west to the Aral Sea in the east. This group may be ancestral to all Neogene and Holocene species commonly referred to *Cytheretta,* but its own ancestry is not clear. The Middle Eocene also saw the first cytherettine on the North American continent, *C. alexanderi* in N. and S. Carolina, and this group is the characteristic Eocene cytherettine. This multicostate group is almost certainly related to the Eocene multicostate cytherettines of Europe and probably migrated from Europe during the early to mid Eocene.

Oligocene cytherettines are rare in N. America, but in Europe they are very diverse and abundant. The typical Oligocene cytherettines are those of the *C. tenuipunctata* group, recorded from England to the Ukraine. Their taxonomy is very complex, intraspecific variation is rife (Keen, 1972a,b, 1982). Geographical variation between populations can be recognised. In southern Europe, in Aquitaine and northern Italy, the *C. sagri* group is common.

The Miocene was probably the time when the cytherettines reached their peak of development. They are common throughout Europe, from the Atlantic to the Urals, frequently dominating shallow water sediments, and for the first time are present in the Mediterranean basin and the N. African coast. They are, however, noticeably absent from the Middle East, Pakistan, and India, apart from the genus *Flexus. Cytheretta* and *Protocytheretta* are abundant in North America, but have rather different distributions. *Cytheretta* species are found from Florida northwards to Maryland but are dominant in the north; *Protocytheretta* species range from Louisianna to Maryland, but are dominant in the south. This distribution pattern is continued to the present, with *Protocytheretta* being the only cytherettine of the Gulf and Caribbean, although ranging northwards to New Jersey, and *Cytheretta* being restricted to the eastern seaboard from Florida to Nova Scotia. *Cytheretta* species of North America are clearly related to European cytherettines, and probably migrated from Europe during the Oligocene. *Protocytheretta,* on the other hand, has no obvious European relatives, and may be a native American genus, perhaps derived from an unknown multicostate group during the Oligocene. The taxonomy of the North American and European Neogene cytherettines is confused, and their true diversity probably hidden. There must be in the region of 50 species in Europe and perhaps 25 in N. America.

The cytherettines were still widely distributed in the Pliocene of Europe, being recorded from eastern England, Belgium and Germany as well as southern Europe and the Mediterranean. However, the end of the Pliocene witnessed a rapid contraction to the present day distribution shown on Text-fig. 1. Although they have a limited European distribution today, for the first time cytherettines are present to the south and east of Arabia, where *C. maddocksae* presents a problem. It has no obvious Neogene ancestors so it is fairly certain that the ancestors of the species migrated from the Mediterranean. The problem is, how? The eastern Mediterranean has been cut off from the Arabian Sea and Indian Ocean since the early Miocene. Another problem is raised by *C. teshekpukensis*; its ancestors presumably lived amongst the late Pliocene cytherettines of northern Europe or N. America; it is also the only cold water cytherettine.

In conclusion, through most of its history the main centre of cytherettine evolution has lain in Europe. At least three migrations to N. America can be recognised. The cytherettines did not colonise the northern shores of Tethys in any abundance until the Oligocene, having their main centres of distribution in the shallow "boreal" seas of Europe north of Tethys. Tethys was never a channel of migration, and by the time the cytherettines had become abundant in these southern seas, Tethys had virtually ceased to exist and we are really dealing with the Mediterranean. The climatic changes of the Pleistocene had a dramatic effect on the cytherettines of Europe; they are now reduced to a very minor role in Mediterranean coastal waters. The main centre of cytherettine distribution at present is the Gulf coast and eastern seaboard of N. America.

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DISCUSSION

Hartmann: I agree with your systematic opinion. I also think that Buntoniinae do not belong to Cytherettidae, but you should not use the term "boreal" for the waters of northern Europe in Cretaceous and Tertiary time. See Vesper's paper at the Delaware symposium.

Keen: I agree that "boreal" is a misleading term, but I merely follow standard stratigraphical practice and use the word as it is commonly used for Mesozoic and Tertiary realms—a northern realm, but clearly not a cold one.

Hazel: As I understand your talk, you consider *Pseudocytheretta* and *Cytheretta* to be synonymous. Are not the soft parts of the type species somewhat different?

What is the age of the oldest cytherettine?

Keen: The soft parts of three cytherettine species are known in detail, *C. judaea, C. adriatica,* and *C. edwardsi.* They all differ, and in some respects the Mediterrancean *C. adriatica* and the North American *C. edwardsi* might be more closely related, especially when the carapace is also considered. However, it is difficult to know how important these differences are; are there three genera? two? or one? I have chosen the more conservative viewpoint and consider them to belong to a single genus, but admit that I have a fairly open mind on the question.

As will be clear in the text, I have followed Triebel's concept of the cytherettines, so the oldest member is a *Paracytheretta* of Santonian age from northern Europe.

Hazel: *Cytheretta alexanderi* is a junior synonym of *C. jacksonensis* Meyer: Meyer's material is preserved in the U. S. National Museum of Natural History, and comes from the type area of the Jackson Group.

Keen: Very interesting.

McKenzie: Since you place South American taxa, as does Reyment, with "Buntoniinae", how do you regard the relationship of Buntoniinae to Cytherettinae? Are both groups cytherettids?

Keen: I regard the Cytherettinae and Buntoniinae as subfamilies of the Trachyleberididae, and so regard them as being quite distinct. However, as you know, many authors have commented on the possible relationship of these two subfamilies and it is likely that they are closer relatives to each other than to other trachyleberidid subfamilies.

McKenzie: What do you consider to be the relationship of *Alocopocythere* to Cytherettinae?

Keen: I follow Malz's opinion on *Alocopocythere,* namely that it is closely related to *Neocytheretta* and that these genera are clearly not cytherettines. This is discussed more fully in the text.

Reyment: Your histogram of shifts in morphs through time seems to be a genuine case of evolutionarily significant polymorphism such as recorded by Reyment (*Paleobiology,* 1985, vol. 11 (2)).

Evolutionarily Significant Polymorphism in Marine Ostracods

RICHARD A. REYMENT
Uppsala Universitet, Sweden

ABSTRACT

As is the case for very many arthropods, ostracods may be highly polymorphic for characteristics of the carapace, a condition that can also manifest itself in the extremities. Two classes of ornamental variations occur. There can be ecophenotypic variation under the control of environmental factors such as temperature, salinity, depth and substrate, which may be quasi-continuous (in relation to some underlying thereshold). The second kind is more directly linked to the genotype and is usually indicated by discontinuous polymorphism. Polymorphism in the ostracod carapace was first documented by Reyment (1963) for Late Cretaceous and Paleogene species, but it was not until 1978 that the phenomenon began to achieve broad recognition.

Ecophenotypic variability is seldom of higher evolutionary dignity, whereas genetic polymorphism is often associated with speciation. Ostracod carapaces may display polymorphism for shape, ornament of the lateral, dorsal and ventral surfaces, the antero-marginal strip, and spinosity. All, or some of these properties can be incorporated in evolutionarily significant changes, either in connection with rapid shifts, almost saltational in nature, or by a gradual, stochastic process of morphological displacement. The principles are illustrated by reference to species of *Echinocythereis, Brachycythere, Buntonia, Oertliella, Veenia (Nigeria), Cytherella, Limburgina, Anticythereis, Leguminocythereis, Protobuntonia* and *Aurila.*

INTRODUCTION

Arthropods are often highly polymorphic. This is visibly obvious for insects and a significant portion of modern genetic theory has been developed around the study of morphs of the fruit-fly. Crustacean polymorphism has been given much less attention than that of insects. Ornamental polymorphism in marine ostracods was first reported by Reyment (1963) and further studied by Reyment (1966) and Reyment and Van Valen (1966). The subject was not taken up by others until Keen (1972) described polymorphism in cytherettids. Further contributions have been made more recently by Ducasse and Rousselle (1978), Ducasse (1979) and Ducasse and Cirac (1981), all for Tertiary ostracods.

The polymorphism described by Reyment (1963, 1966) features mainly alternative ornamental states, but also polymorphism in the outline of the shell, including pleiochroism in shape and ornament. Keen (1982, p. 387) has provided a succinct account of the kinds of ornamental variations that may occur in marine ostracods.

The recognition of ornamental polymorphism in living ostracods by zoologists is only of very recent date (Hartmann, 1982). This is, perhaps, hardly to be wondered at owing to the relatively few people actively engaged in the study of living ostracods, coupled with traditionally differently stressed realms of descriptive interest. Doubtless, future work will yield information of substantive evolutionary value.

In the present connection, we shall be concerned with examining evolution in size, shape and ornamental features of the carapace. Perhaps the greatest stumbling block lying athwart the path of a general evolutionary model is the fact that size, shape and ornament appear to be under the control of fundamentally different evolutionary processes (see, for example, Leman and Freeman, 1984) for an account of the problems in relation to three families of bats). It is, therefore, essential that evolution in each of the above three categories be considered separately. Failure to do so must of necessity lead to a confused picture.

The evidence yielded by the present study tends to support the conclusions voiced by Leman and Freeman (1984), to wit, that shape and size are fundamentally different evolutionary roads. However, it will be shown that this opinion cannot be generalized too avidly for shape and ornament in that a pleiochroic relationship may exist between the two.

THE NATURE OF POLYMORPHISM

Polymorphism is discontinuous variation within a population with the rarest morph existing at a frequency greater than that which can be maintained by current mutation alone (Clark, 1976, p. 255).

Let us enter into the subject by way of recent work on waterstriders (Gerridae, Hemiptera) by Zera (1984). Some species of waterstriders are wing-polymorphic, whereby spatial or temporal variation in morph-ratios occur, both among populations of the same species and among species. It is reasonably well understood that there are species which always are fully winged, others that are almost exclusively wingless, and a third category in which intermediary phases of wing-polymorphism occur; thus, there are varying proportions of fully winged, short-winged and, or, wingless morphs. A significant point arising out of the waterstrider work is the fact that observable polymorphic differences are linked to a set of coordinated traits of another kind. As an example, it may be noted that short-winged morphs usually have a fast developmental rate, an early age of first reproduction, and high fecundity.

Waterstriders have been proven to display environmental morphological effects of a quasi-continuous nature. Results for non-gerrids also provide data of interest for crustacean analogies. Zera (1984, p. 1023) reports that there are differences in fitness among morphs and such a difference in a fitness trait is often consistently associated with some particular morph, even in phylogenetically distinct species.

Environmentally cued polymorphism

Clark (1976, p. 256) has lucidly expounded the semantic history of polymorphism and has arrived at the useful conclusion that any feature which gains expression in the phenotype must perforce have a genetic basis, thus making such terms as "polyphasy" and "polyphenism" superfluous. However, in genetically determined polymoprhism, the environment may play little part in the determination of morphs. The alternative, termed "environmentally cued polymorphism" by Clark (1976, p. 256) results where environmental stimuli interact with the genome to bring forth a particular morph. Thus, environmentally cued polymorphism embraces the production of seasonal forms in insects, such as butterflies. Genetically determined polymorphism includes expressions of the genotype such as human blood-groups, and non-environmentally controlled sex determination. Clark (*op. cit.*) pointed out that there are intermediate states of polymorphism in which the characteristics of both kinds are manifested. Thus, genotypes differ in their capacity to develop into a particular morph under various environmental conditions.

With respect to the gerrid waterstriders, it has been ascertained that a particular genotype produces the fully winged morph in summer and the wingless morph in the autumn. A second genotype develops only the unwinged morph during both of these seasons. The question of seasonal adaptation can be met by the strategy of environmentally cued polymorphism in which the morph developed at a particular point in time is largely decided by current, or immediately prior, ecological conditions. Clark (*op. cit.*) observes that speciation may result under conditions in which only one morph is environmentally cued, this leading to the permanent loss of the alternative morph; there are several examples known for New Zealand aphids.

Non-Mendelian sex-ratios

Owing to the greater abundance of females in the majority of marine ostracod demes, evolution in ostracods is dominated by selection on females. Curtsinger (1984) has taken up the question of the significance of meoitic drive and the production of non-Mendelian ratios of gamete-types by heterozygotes. Clark (1978) has examined the environmental determination of sex by environmentally cued polymorphism in a paper which may be relevant for conditions prevailing in marine ostracods. His work is based on detailed studies of sex-determination in nematodes.

VARIATION IN SIZE

Size variation in fossil ostracods can have several causes, for example, seasonal size-classes (*cf.* Hartmann, 1982; Abe, 1983) and fluctuating salinity. The *Echinocythereis* study, referred to below, provides evidence for both sources.

Reyment (1980) treated the question of size in relation to environmental control and a means of isolating this factor was developed. Thus, if all the species of a fossil population display synchronous variation in size, we can expect that these variations reflect a general reaction to environmental fluctuations.

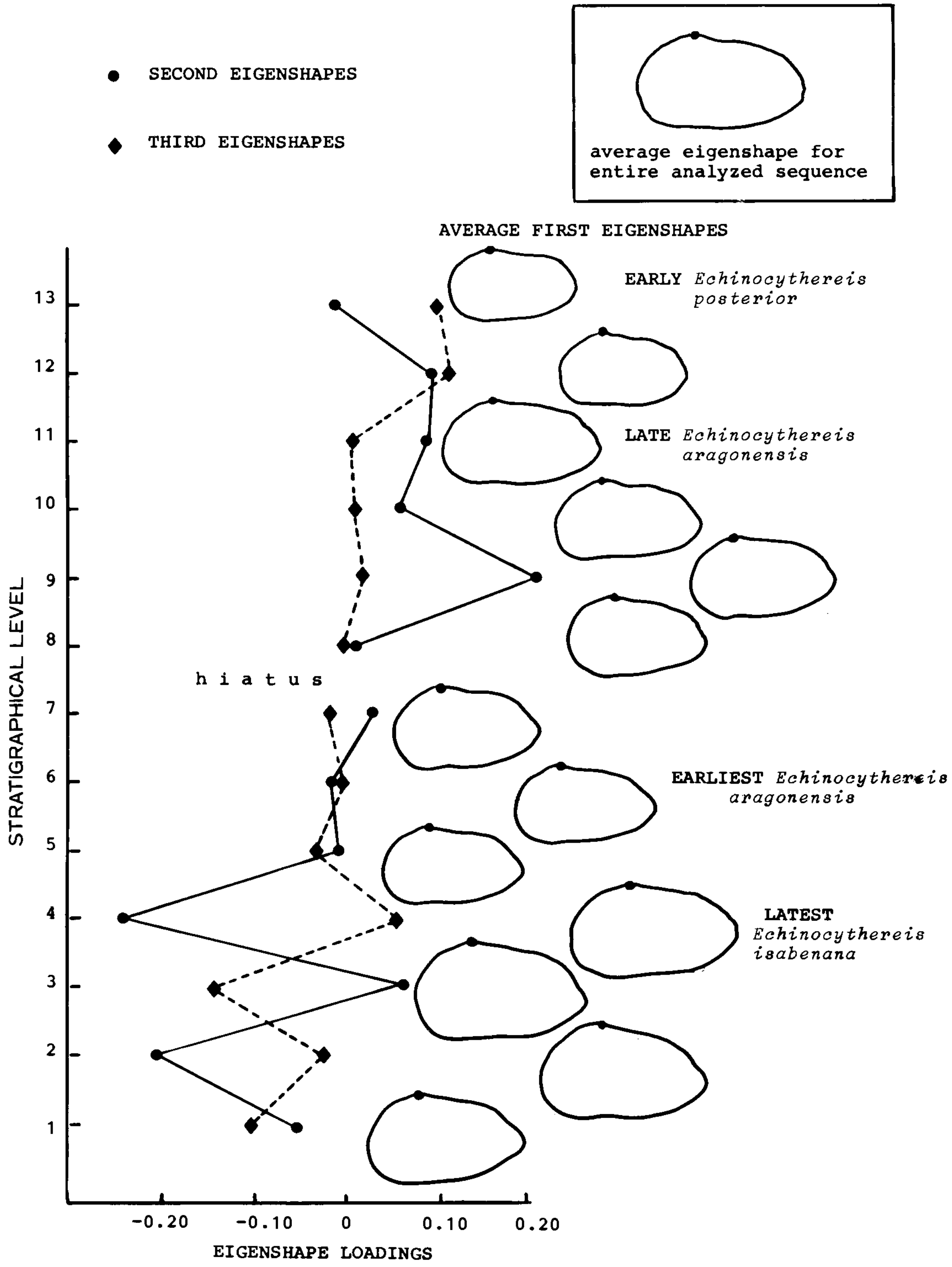
Variation in size in the lineage of *Echinocythereis* reported on by Reyment (1985) possesses the hallmark of environmental influences, as could be demonstrated by the recognition of parallel variability in a species of *Leguminocythereis*. The factor controlling the ecophenotypic variation was probably connected with shallowing of the late Lutetian sea, a suggestion that is supported by geochemical work.

SHAPE POLYMORPHISM

Reyment (1985) identified several shape-morphs in Eocene *Echinocythereis* from northern Spain, the most commonly occurring of which are (1) asymmetrical rounding of the anterior margin; (2) concave posterodorsal margin; (3) underslung venter; (4) concave dorsal margin.

It is not easy to isolate evolutionarily significant shape polymorphisms, but in the present case morphs (3) and (4) could be related to evolution in the lineage. There are several shape-morphs that occur throughout the entire sequence, for example, morphs (1) and (2), which are not involved in speciation events.

A variety of Q-mode principal component analysis has recently been developed by Lohmann (1983) for analyzing changes in the shape of an organism. The observations consist of coordinate pairs determined at regular intervals around the circumference of the shell. This method of shape-



TEXT-FIG. 1—Plots of the second and third eigenshapes against stratigraphical level for three species of *Echinocythereis* from the Rio Isabena section (Eocene, northern Spain). The data were selected for crucial ranges in the speciation events. The figure also displays the computed first eigenshapes for each sample, as well as the computed average first eigenshape for the entire series (inset).

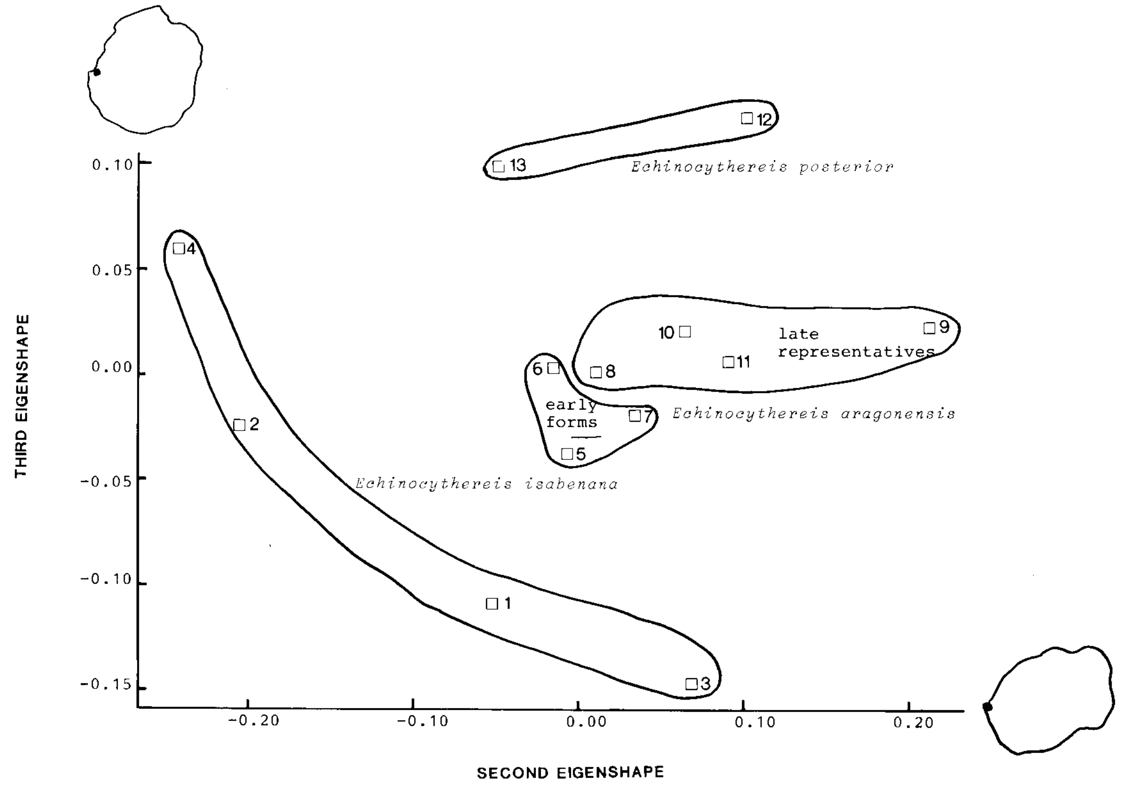
analysis was applied to the critical sections of the *Echinocythereis* lineage, namely, the transition from *E. isabenana* to *E. aragonensis* and the zone of passage from *E. aragonensis* to *E. posterior.*

Multivariate Shape-analysis of Species Changes in *Echinocythereis*

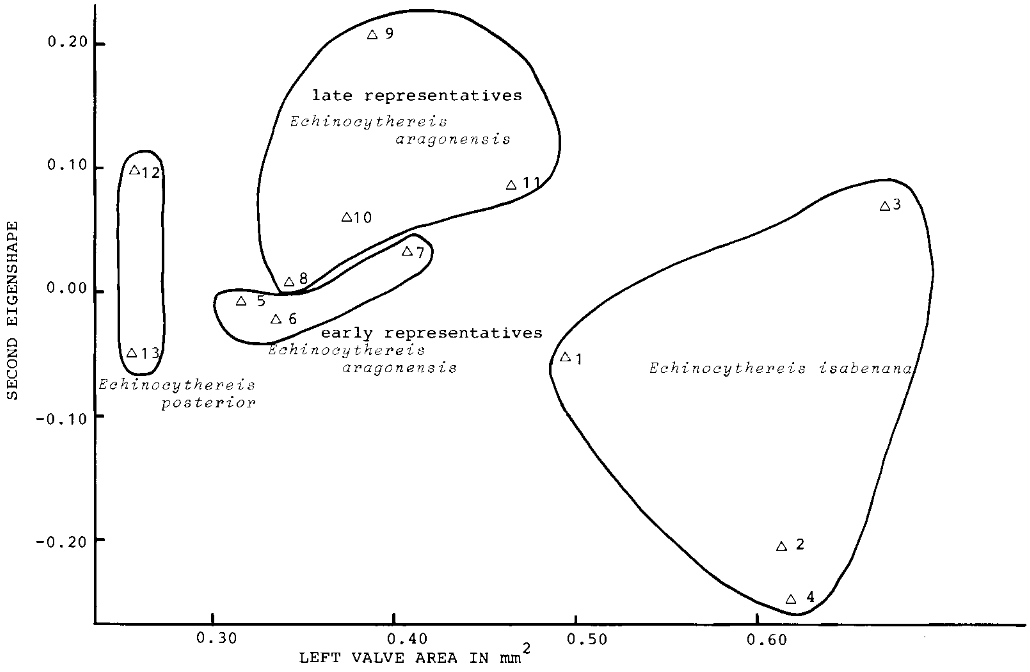
Reyment (1985) has analyzed evolutionary changes in a lineage of ostracods belonging to the genus *Echinocythereis* from the Eocene of northern Spain. The variation in lateral area has already been considered in the above-mentioned publication. The present study is concerned with changes in shape over two transitions between species represented in this lineage. The first of these transitions involves the passage from *Echinocythereis isabenana* Oertli to *E. aragonensis* Oertli. This took place relatively rapidly and was accompanied by a substantial reduction in average size. The second transition was gradual, being marked by a stochastically conditioned replacement of one set of major ornamental features for another set. The samples were selected from the critical zone in which essential features of the descendant, *Echinocythereis posterior,* gained the upper hand, bit by bit.

The present study indicates that there are significant shifts in shape of the shell, but these are very slight. In Text-fig. 1, the computed first eigenshapes are shown in relation to average second and third eigenshapes plotted against the stratigraphical level of the sample. The "average first eigenshape" for the entire sequence is shown in the inset; it is closely approximated by the shape for sample 3 (*E. isabenana*).

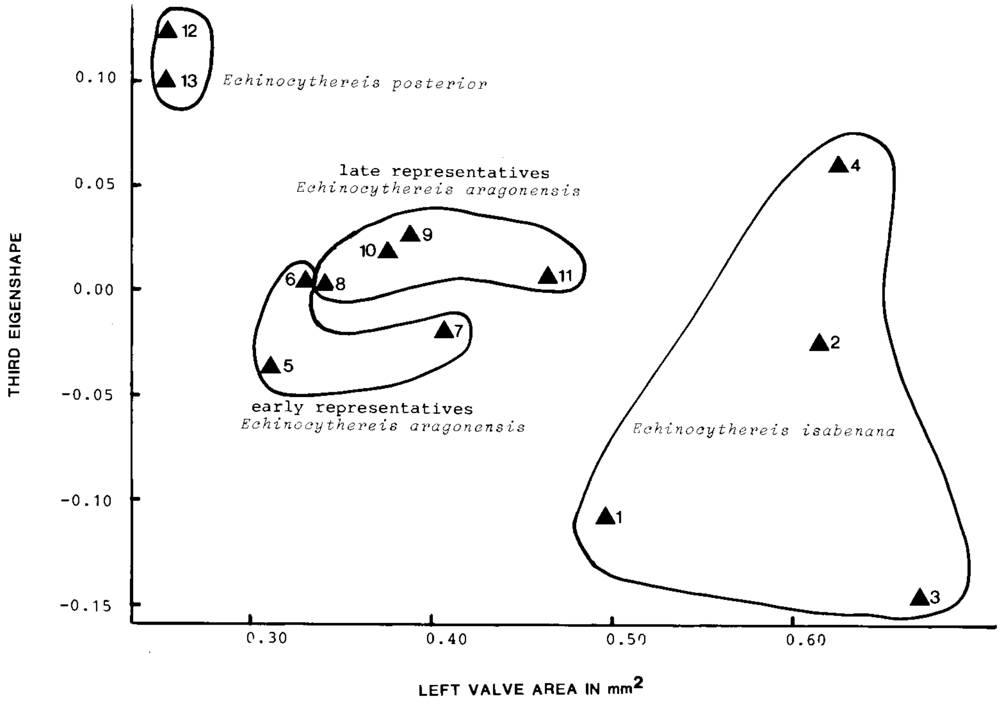
The points for the second eigenshapes show, however, a trend with mainly negative values for the older samples and positive values dominating for the younger samples.



TEXT-FIG. 2—Plots of the second and third eigenshapes for the species of *Echinocythereis*. The computed average eigenshapes corresponding to the respective axes are shown.



TEXT-FIG. 3—Graph of the lateral area of left valves plotted against the average computed eigenshapes for all samples of *Echinocythereis*.



TEXT-FIG. 4—Graph of the lateral area of left valves plotted against the average computed third eigenshapes for all samples of *Echinocythereis*.

The relationships are clearly expressed in Text-fig. 2 in which second and third eigenshapes are plotted against each other. There is clear separation into groupings corresponding to each of the species. A significant feature of this plot concerns the segregation of the samples of *E. aragonensis* into what is essentially a structured constellation, with the older individuals concentrated together. It may, therefore, be concluded that there is shape discrimination in the material. Moreover, this differentiation is disjunct at the species level. This result is somewhat unexpected in relation to the results yielded by the multivariate analysis of standard dimensions of the carapace.

The graph of the lateral area of the left shell plotted against second eigenshapes (Text-fig. 3) shows that this shape category on its own does not differentiate species. In this figure, the differentiation is almost entirely due to differences in area. The corresponding graph for the third eigenshapes (Text-fig. 4) also indicates that this shape-descriptor, on its own, does not distinguish between the species very well.

Summarizing the results of the shape analysis, together with those given in Reyment (1985), it can be shown that the speciation events were accompanied by a reduction in size and significant, though slight, shifts in shape.

ORNAMENTAL POLYMORPHISM

Although, as noted in the introduction, the subject of ornamental polymorphism in ostracods has begun to attract interest, the study by Reyment and Van Valen (1969) on the variation genetics of ostracods, fossil and recent, still stands alone.

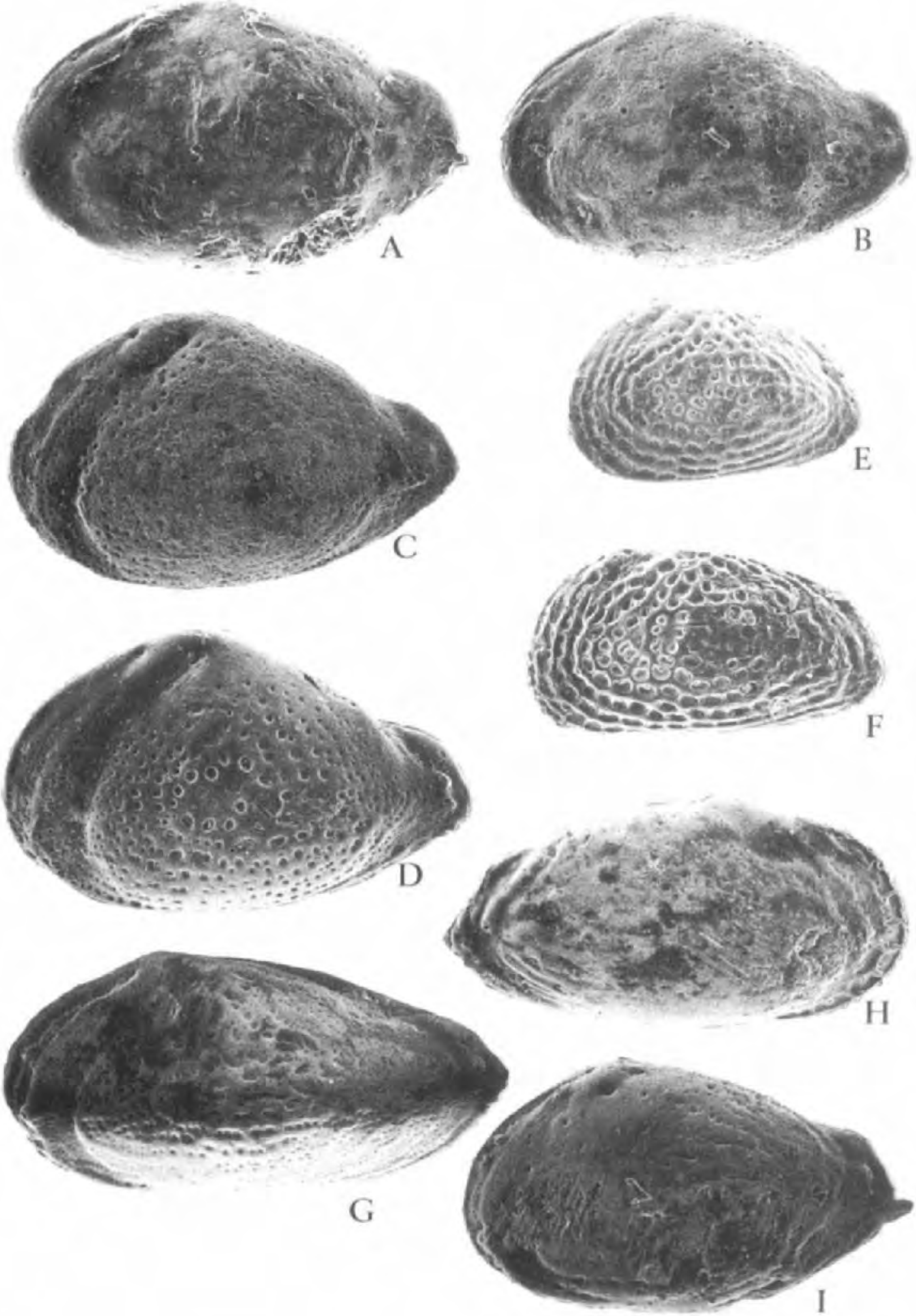
Reyment (1963) reported on several kinds of intrapopulational polymorphism in Nigerian late Cretaceous and Paleogene forms. The most commonly occurring polymorphic condition found involves the presence or absence of a posterior spine. This variety is of wide occurrence in species of *Buntonia s. l.* (Pl. 1, figs. A–D, I). A second type is concerned with the development of regularly walled reticulations as opposed to the same ornamental pattern with "broken" or breached walls. Such ornament was reported for *Brachycythere armata* and *Leguminocythereis lagaghiroboensis* (Pl. 1, figs. E, F; Pl. 2, fig. I). In the latter case, however, there is also polymorphism for a pleiotropic character; thus individuals with irregular lateral ornament have the posterior end of the carapace bluntly rounded, whereas those individuals in the same sample that are regularly reticulated usually, but not invariably, possess a mucronate posterior. The polymorphism is regularly distributed over both sexes (Reyment, 1966; Reyment and Van Valen, 1969). The polymorphic condition in *L. lagaghiroboensis* is recognizable in the last three instars.

In *Buntonia pulvinata* (Pl. 1, figs A–D, I), the opposing states are coarse and irregular pits; a smooth morph also occurs. In *Ruggieria*? *tattami*, a smooth surface contrasts with a reticulate one. In *Cytherella sylvesterbradleyi*, a smooth surface is accompanied by an alternate morph which displays a finely pitted surface. This kind of variation has also been documented by Keen (1982, p. 387) for *Cytherella londinensis*. Ducasse (1981) recorded coexisting shape-morphs in *Cytherella consueta* and *C. transversa* (Paleogene). Examples of ornamental polymorphisms are given in Plates 1 and 2.

In *Anticythereis bopaensis*, the presence or absence of a vestibule could be polymorphic in nature; if this is so, the ability to calcify the anterior strip of the inner lamella may possibly be correlated with the carbonate equilibrium of the seawater.

In a recently published account of Spanish Turonian ostracods (Reyment, 1984), many species were found to show polymorphism in the ornament. Among the cases recorded, the following are of interest in the present connection:

(1) Regular reticulations vs. breached reticulations: (*Spinoleberis petrocorica*?).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(2) Regular reticulations vs. smooth fields superimposed on the reticular pattern: *Limburgina galvensis.*

(3) Reticular walls, thick vs. thin, coupled with discretely manifested differences in the secondary reticular pattern: *Oertliella guadalajarensis.*

(4) Shape-polymorphism in the areas of the hinge-ear and the posterior process. *Oertliella guadalajarensis.*

The polymorphic pairs occur in the same sample in all cases.

Variation in spinosity

An ornamental category, marginal spinosity, tends to display a different underlying pattern from the kinds of ornamental variation hitherto discussed. Reyment and Van Valen (1969), reporting on the ornamental variation in quasicontinuously varying characters displayed by a Recent species of *Buntonia* from the Niger Delta (offshore), found that the variability is more complicated than what has been recorded for fossil species. Several features are involved, namely, size of the carapace in relation to the presence or absence of a ventrolateral spine, the number of spines along the anterior margin, and the number of spines along the posterior margin.

Both anterior and posterior spines increase in number with successive instars. There is a sexual dimorphic relationship also, in that anterior spines are more numerous in males than in females (presumably concordant with the greater size of males, on the average), but the posterior spines are fewer, on the average, in males than in females.

The proportion of individuals lacking the ventrolateral spine is not detectably different in the immature instars, but is much greater in adult males, but not if all males are considered together.

The frequencies of anterior and posterior spines are only feebly associated with each other. However, individuals bearing a ventrolateral spine have, on the average, more anterior and posterior spines than those lacking this spine. An analogous situation occurs in the Maastrichtian-Paleocene species *Brachycythere oguni* Reyment (Pl. 2, figs. E–H).

Reyment and Van Valen concluded that the threshold for spine-making shifts downwards with each increase in age-sex groups (*cf.* Grüneberg, 1951; Rendel, 1967).

Hartmann (1982) has also taken up the question of ornament in relation to ontogeny, though in qualitative terms only. In, Australian *Mutilus pumilis* there may be strongly expressed differences between larval stages and adults, or, at geographically separated locations, larval ornament is retained into the adult stage. This is a rather commonly observed situation in Late Cretaceous and Paleogene ostracods of West Africa; for example, the Cretaceous-Tertiary species *Anticythereis bopaensis* from Nigeria and Benin may produce strongly spinate larvae or almost unspined instars, the latter category carrying over into adults. Hartmann (*op. cit.*) points out the role of temperature and water-chemistry with respect to the calcification of the exoskeleton in *M. pumilis.*

In the same article, he also takes up *Xestoleberis chilensis austrocontinentalis,* in which he found two size classes to occur (size polymorphism), as well as ornamental variation. The two morphs observed are intrapopulational and hence presumed not to be of ecological origin.

Polymorphism in lateral ornament

We shall begin this section by referring again to the lineage of Spanish Eocene *Echinocythereis* Reyment (1985). The three species of this series are all highly polymorphic in their lateral ornament.

PLATE 1—Figs. A–D, I. *Buntonia pulvinata* Apostolescu. A. Smooth lateral surface, posterior spine. B. Smooth lateral surface, no posterior spine. C. Peripherallyp itted lateral surface, no posterior spine. D. Coarsely pitted surface, incipient spinosity. All specimens from borehole Ilaro I (53 m). ×110. I. Incipient pitting; posterior spine. Borehole Araromi I (340 m). Figs. E, F. *Leguminocythereis lagaghiroboensis* Apostolescu. E. Irregular lateral ornament, blunt posterior. F. Regular lateral ornament, blunt posterior, Borehole Gbekebo 1 (722m). ×65. Figs. G, H. *Protobuntonia ioruba* Reyment. G. Pitted surface. H. Smooth, with residual costation in peripheral zone. Borehole Araromi 1 (451 m). × 110.

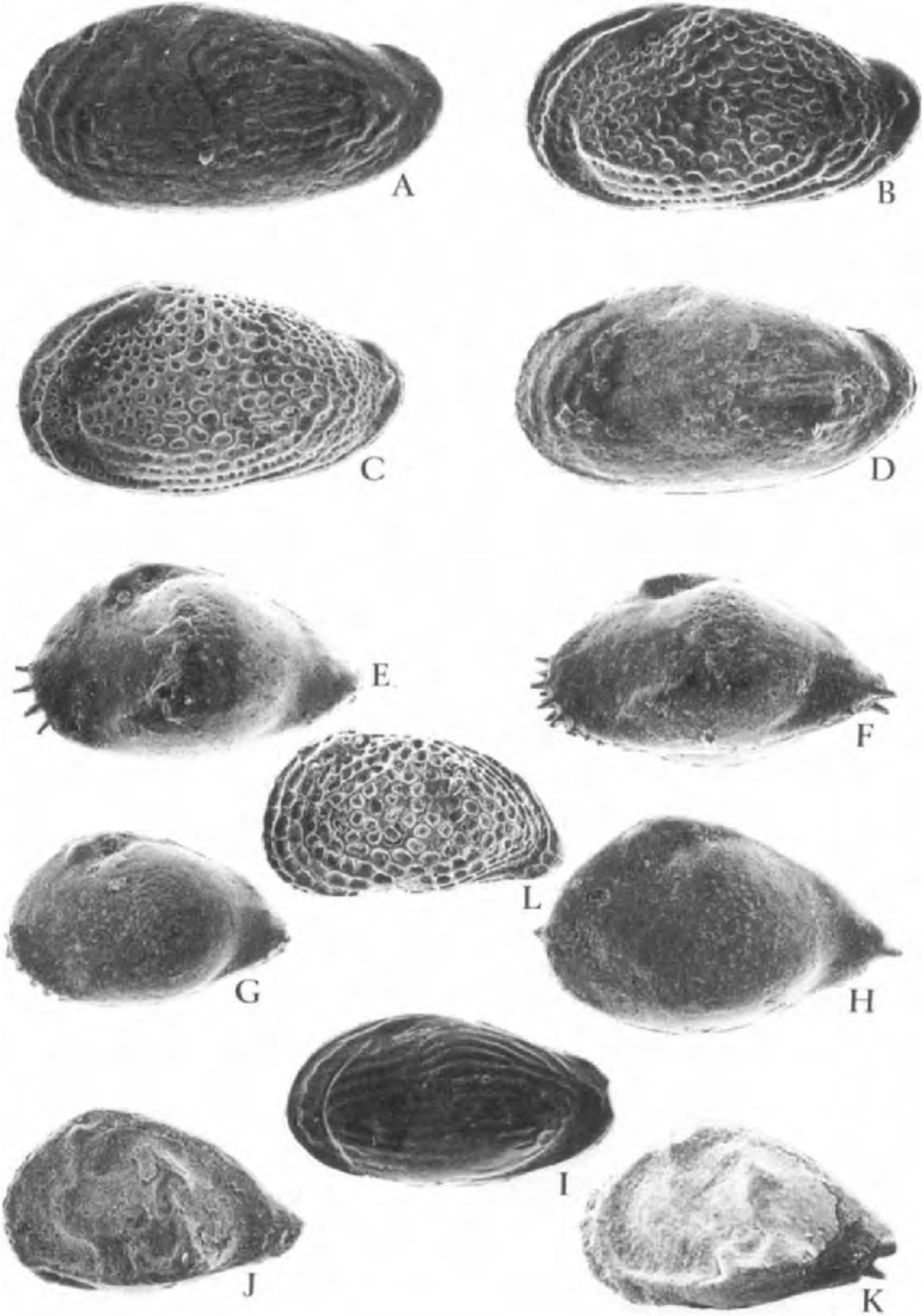
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TABLE 1—SOME ORNAMENTAL MORPHS OCCURRING IN THE SPANISH *Echinocythereis* LINEAGE.

Nature of morph	Vertical distribution	Evolutionary significance
Smooth fields	entire sequence	none
Posterior spinosity	entire sequence	none
Anterior tuberculation (2–3 rows); alternative state smooth	entire sequence	probably none
Papillae joined by filaments leading to reticulation	part of sequence	significant

The most commonly occurring morphs are listed in Table 1. Most of the ornamental variants lack evolutionary significance, meaning they can occur throughout the entire sequence without leading to permanent changes.

An example of a permanent ornamental change concerns the reduction of the relatively coarse tubercles of *E. isabenana* to the noticeably smaller papillae of *E. aragonensis* (*cf.* Oertli, 1960), where they ultimately become more and more frequently united by filaments; this latter state is eventually replaced by a fully developed reticular pattern (with occasional subdued papillae at mural intersections.

At least some of the ornamental variations could be an expression of environmentally cued polymorphism. As noted by Keen (1982, p. 388), the development of smooth areas in the lateral ornament is quite common, both in marine, and more so, brackish water ostracods. However, such smooth areas can have more than one origin. In many cases there is doubtless environmental control; in others, smooth-field polymorphism is evolutionarily significant and heralds a speciation event. Reyment (1982a,b) analyzed two such speciations, with the aid of the methodology of quantitative genetics, for *Oertliella*? *tarfayaensis* (Turonian) and *Veenia rotunda* (Cenomanian-Turonian). The ornamental shifts incurred in this kind of transition, from sculptured to largely smooth, have been described by Liebau (1977). Lively (1986) has further developed this theme.

Owing to the intrapopulational occurrence of the morphs, the ornamental variability recorded for the Spanish Eocene *Echinocythereis* cannot be interpreted in terms of water-chemistry (*cf.* Keen, p. 387, referring to conclusions drawn for *Agrenocythere*), nor bathymetric differentiation. The same remark must of necessity apply to the architectural model for shape and size of the carapace of Benson (1981) and Liebau (1977), in connection with which it is assumed that the role of reaction of the exoskeleten to environmental stresses is of overriding importance.

The transition from *E. aragonensis* to *E. posterior* in the Spanish lineage is accompanied by two fundamental ornamental changes: (1) strengthening of the reticular pattern and (2) the passage from a papillate anterior to reticulated anterior rows (with or without pore-conuli at reticular intersections). The first of these changes seems to be no more than a reinforcement of the ability of the organism to secrete a network between papillae upon a pre-existing framework (Liebau, 1977; Okada, 1981). The transitional mechanism is not one of straightforward displacement of characters but stochastic over short intervals; it is not a random walk, however, when considered over its whole length.

PLATE 2—Figs. A–D. *Protobuntonia punctata* Reyment. A. Subcostate morph. B, C. Coarsely punctate to subreticulate. D. Smooth, Borehold Gbekebo 1 (711 m). ×110. Figs. E–H. *Brachycythere oguni* Reyment. E. Anterior spines. F. Anterior and posterior spines. G. Incipient spinosity; subpunctate. H, Posterior and anterior spines, subpunctate, Borehole Gbekebo 1 (900 m). ×65. Fig. I. *Protobuntonia ioruba* Reyment. Costate morph. Borehole Ilaro 1 (53 m). ×65. Figs. J, K. *Brachycythere armata* Reyment. J. Non-spinate morph. K. Spinate morph, Borehole Gbekebo 1 (988 m). ×65. Fig. L. *Leguminocythereis lagaghiroboensis* Apostolescu. Regularly ornamented and mucronate posterior, Borehole Araromi 1 (305 m). × 65.

Although adequate quantitative data are lacking, it seems as though the evolutionary situation for three Oligocene species of *Cytheretta,* described by Keen (1982, p. 389) is, in part, analogous to that observed for the lineage of *Echinocythereis* reviewed above.

Among the several other examples recorded recently, we note the following: Ducasse and Cirac (1981) have looked at ornamental variability related to environmental factors in Miocene *Mutilus.* These authors believe that depth of water was the controlling factor.

Ducasse and Rousselle (1979) studied species of *Hammatocythere* in the Paleogene of the Aquitaine Basin and concluded that there is a correlation between populations exhibiting well expressed ornamental variability and marine incursions, with polymorphism said to become reduced during periods of regression.

Ducasse and Coustillas (1981) proposed a phylogenetic scheme for *Pokornyella* in which the evolutionary significance of a particular form receives pride of place (a reticulate punctate type is shown as giving rise to a punctate variety).

Ducasse (1983) showed that *Protoargilloecia* from the same environment as previously studied *Cytherella,* is also polymorphic.

In summary, it is clear that ornamental polymorphism is common among some ostracods and that there is a rather obvious correlation between time (latest Cretaceous) and the appearance of pronounced size, shape and ornamental polymorphisms. The evolutionary significance of this observation is unknown. It seems to me that the majority of the recorded cases do not represent stable polymorphism at the regional level. Thus, the Miocene *Mutilus* spp., referred to above, certainly display ornamental and shape variability, but there is a lack of geographical conformity; likewise for Recent *Mutilus* from Australia.

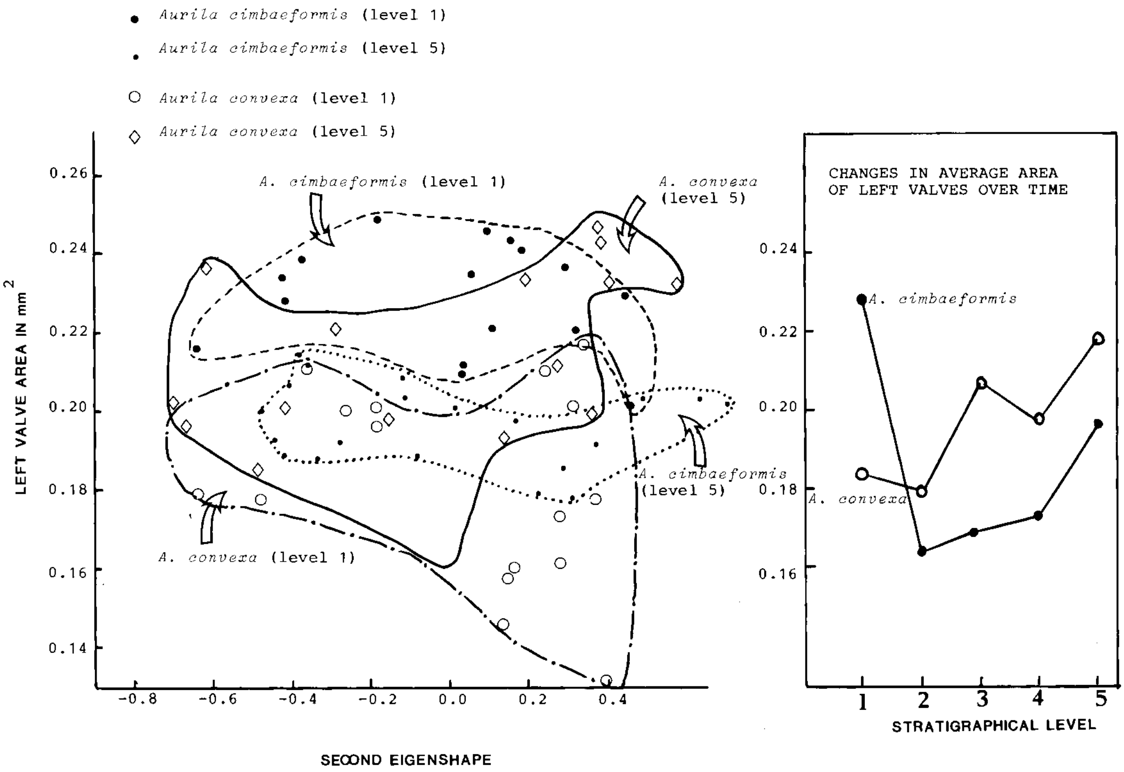
STASIS

A good deal has been written of late on the reality of stasis in evolution as a concept. It is imperative, however, that one be quite sure about what is being looked at and my experience has been that some characters may be in an invariate state whereas others are undergoing substantial evolutionary changes. Hence, the question of stasis depends largely on the character(s) chosen for analysis. The *Echinocythereis* example is a good illustration of this point. It shows that some ornamental variations can be elicited at random in the history of a lineage, whereas others are not static. Moreover, size is in a condition of stasis for part of the history of that lineage, but not all of it.

THE CASE OF THE SPANISH *Aurila*

Aurila convexa and *A. cimbaeformis* occur in great numbers in the Lower Pliocene of southernmost Spain. Although there are clear differences in shape (outline of the carapace) in lateral aspect between the two, a multivariate statistical analysis of 11 characters (including intersecting shape-sensitive variables) carried out by Reyment and Aranki (in prep.) discloses close agreement between them; moreover, there is overlap in at least one of the morphs common to both species.

The linear and quadratic discriminant function analyses leave one with the distinct impression that *A. cimbaeformis* could lie within the limits of polymorphic variability of *A. convexa.* The canonical variate analysis indicates, however, that notwithstanding that there is overlap in the two forms as regards the pooled samples, they are distinct at the level of the sample. Hence, the morphological variation in the two species is different in detail, although its general expression may be different.



TEXT-FIG. 5—Plot of the second eigenshapes against the lateral area of left valves for the *Aurila* data. The inset displays the chronological variation in the average area of the left valves.

It was also ascertained that there is no significant trend in size in either of the species over the 40 m of carbonate sediment sampled.

As far as variability in shape is concerned, an eigenshape analysis strengthens the indications yielded by the standard methods of multivariate analysis. Some aspects of this study are shown in Text-fig. 5. The lowermost and uppermost levels for both species were used for preparing the plot of "eigenshapes" against area of the left valve. The two oldest samples plot in a mutually exclusive fashion. The two youngest samples are more alike with respect to the shape measure; nonetheless, their distributions have different spreads.

The figure also shows the shifts in time of the average left-valve area. The general pattern for both species is similar. There is a drop from the first to the second sample and then a gradual increase over the remaining three samples.

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DISCUSSION

Keen: The changes recorded by Oertli, and now in more detail by yourself, in *Echinocythereis isabenana* and *E. aragonensis* from the Middle Eocene, are also seen in lower Eocene (Ypresian) species from S. England, Belgium, and northern France. The change from papillose populations to reticulate populations in these Ypresian species seems to be synchronous. The description of the papillose species is in press; the reticulate species is *E. reticulatissima* and these form two ostracod zones in the region and seem to be very useful in correlation. The material studied in conjunction with Mr. King shows many of the features you have shown, such as the filaments linking the papillae.

Reyment: Seemingly, the type of ornamental change in question is an inherent property of *Echinocythereis* and one which can be incited to occur under certain conditions. Note, however, that *Echinocythereis scabra,* a long-ranging species, does not seem to have given rise to such changes. Many insect species display variability of the kind concerned here, for example, the development of wing-polymorphism in waterstriders (as discussed in the printed version of my talk). Some morphological responses are identically manifested in different species, others are not.

Henning Uffenorde: There are obviously similar developments in the ornamentation of the genus *Echinocythereis* at different times. For instance, there is also a development from papillate to reticulate morphotypes in the Late Oligocene and Early Miocene of Northern Germany.

Reyment: This is indeed so, and also for other Paleocene ostracod genera I have studied, such as *Buntonia* and *Protobuntonia.* As I indicated in my reply to Dr. Keen, some evolutionary sequences of *Echinocythereis* seem to pass a threshold beyond which evolutionarily registerable changes in ornament may occur, noting that *E. scabra* seems to be remarkably resilient to such changes, although I have observed the rare, random occurrence of y-linked papillae in this species in material from the Pliocene of Southern Spain. A possible explanation may lie with opportunistically available threshold polymorphisms such as embodied in Rendel's (Canalisation and Gene Control, Academic Press, 1967) concept of Make, which provides a useful vehicle for interpreting ecologically triggered polymorphic states in foraminifers (Reyment, 1982, *Palaeogeog., Palaeoclim., Palaeoecology,* v. 38, nos. 1/2, Elsevier, Amsterdam).

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Environmentally Cued Polymorphism of Ostracods

A Theoretical and Practical Approach. A Contribution to Geology and to the Understanding of Ostracod Evolution

J. P. PEYPOUQUET, P. CARBONEL, O. DUCASSE, M. TÖLDERER-FARMER, AND C. LÉTÉ
Départment de Géologie et Océanographie, Unité Associée au C.N.R.S., Institut de Géologje du Bassin d'Aquitaine, Université de Bordeaux I, Talence, France

ABSTRACT

Intraspecific architectural variations in the ostracod tests remains a major problem to which solutions need to be found. Several suggestions are put forward in this study. It is suggested that:

a) the "agradation" and "degradation" concept of tests (Peypouquet *et al.*, 1981) is a phenotypic expression of ostracod polymorphism which is in part environmentally controlled;

b) the "carbonate equilibrium" in the water is a primary factor in the direction of an "agrading" and "degrading" polymorphism;

c) a theoretical biogeochemical model may accredit the previous suggestion;

d) hypothetical climatic and physiogeographical models determine the conditions and places where the preceding model is assumed to take effect;

e) an assessment of the palaeoenvironment and economic interest in the use of "agraded" and "degraded" morphs from geological, marine and continental series may be very instructive;

f) "environmentally cued polymorphism" is a highly reliable means in the study of the ostracod evolution related to the physico-chemical environmental conditions.

INTRODUCTION: PROBLEMS OF ARCHITECTURAL VARIATIONS IN SHELLS

Despite the extensive studies carried out by researchers, both zoologists and micropaleontologists, variability in the ornamentation of ostracod valves still seems to be a source of misunderstanding and confusion. Palaeontologists are confronted with the problem of the concept of species. It is essential that workers provide this contradictory debate with the necessary arguments to answer all the obscure questions raised.

Architectural variations are regarded either as genotypic or phenotypic; in the fossil series a distinction between the two is very difficult to achieve. The mode of variation is a much discussed topic, producing abundant literature references, namely Benson (1974, 1975, 1976, 1981, 1982), Liebau (1971, 1977), Ducasse and Rousselle (1978, 1979a,b), Rousselle *et al.* (1984), Peypouquet (1977, 1979), Peypouquet *et al.* (1980, 1981, 1982), Carbonel (1980), Hartmann (1982), Keen (1976), Reyment (1966, 1978, 1984). Authors have tried to find answers to the questions of mechanisms and factors inducing modifications. Most of the time they have attempted to distinguish between environmental and genome causes. It is a difficult task the success of which can never be guaranteed.

The synoptic work by Keen (1982) for instance, shows the extent to which it is difficult to appreciate the intraspecific variation in Tertiary ostracoda. He regards both size and ornamentation of the shells as two parameters completely independent from one another. In this study particular interest is shown in the second parameter.

The ostracod can by its chromosomic, often polymorphic nature (Tetart, 1975, 1978, 1982) be an organism capable of modifying its morphology in accordance with the physico-chemical parameters of the hydrological environment. Work by Reyment (1984), Keen (1982), Ducasse and Rousselle (1978, 1979) and Peypouquet *et al.* (1980, 1981) support this statement.

Ostracod polymorphism seems to have been triggered by environmental stresses, and the factors relating this biological phenomenon to its extrinsic "initiator" are worthy of consideration, namely the nature and intensity factors. Indeed, the purpose of this study is to propose a theoretical model with regard to ornamentation and environmental variations, the latter having probably instigated the former.

WHY ARE OSTRACODS POLYMORPHIC? IS THERE A BIOLOGICAL EXPLANATION? WHAT IS THE RELATIONSHIP BETWEEN POLYMORPHISM AND ENVIRONMENTAL CHANGE? IS THERE A 'DIRECTION' IN THE POLYMORPHIC VARIATION OF THE OSTRACOD SHELL?

These four questions are the essence of the problem of architectural variations in ostracod shells. Polymorphism, according to Mayr (1963) is applicable to all forms of discontinuous variation affecting the development of a population. It must be noted that the use of the term 'polymorphism' does not have a precise meaning, but is applied to well-defined morphological variations without alluding to the causes responsible for this phenomenon. Polymorphism is, in fact, by definition a genetic phenomenon and in this study we shall comply with the geneticists' concept emphasizing that the phenotype of an organism is the result of interaction between the genotype and the environment. It follows, therefore, that any phenotype feature must have a genetic basis. It must, however, be pointed out that in the Anglo-Saxon literature (Clark, 1976, in particular) there are two opposing terms representing the two extreme cases of one and the same biological phenomenon:

a) *"genetically determined polymorphism"* where the genotype is "essential" or the "principal inductor" in the determination of the morph and where the environment plays little part, if any, in this determination.

b) *"environmentally cued polymorphism"* where the environment interacts with the genotype to elicit a particular morph. For a micropalaeontologist or geologist, the first classification is of course of no great interest; polymorphism will therefore be placed within the context of environmental stimuli interacting with the genotype.

Why have we opted for the second type of polymorphism, as the prominent or major element in the architectural variability? ("agradation or degradation"; Peypouquet *et al.*, 1980).

Environmentally Cued Polymorphism

"Environmentally cued polymorphism" may be considered as a specialized part of the processes which form part of the normal development and maintenance of a population. Normally, it may be assumed that somatic cells in an organism contain the same genotype. Despite this handicap, several zoologists presume that in response to environmental stimuli, different parts of the spectrum of potentials contained in the genome are selectively activated or suppressed, thereby inducing differential specialisation of cells and finally, polymorphism. Organisms may, however, prove to be more "lucky". White (1973) for instance, showed that certain organisms had, with respect to

the somatic cells, dissimilar genetic material. The more recent work by Tetart (1975) pointed out that this was also the case for ostracods. He has, in fact, brought to light the existence of chromosomic polymorphism of somatic cells in *Eucypris virens* and the existence of a primitive and evolved karyotype within the same population. This is a most fundamental point allowing ostracods to express more easily their ornamental polymorphism in relation to the environment.

A Second Essential Point: Test Construction by the Ostracod

a) Ostracods undergo a series of moulting stages (8–9) during their ontogenic development. The loss of the previous carapace as well as the building of a new one is a difficult "ordeal" for the animal. It requires a lot of energy and occurs within only a few days (2 to 3). The basic construction elements are epidermic and epithelial cells. As has been rightly indicated by Okada (1981, 1982a,b), reticulation is form ed above the epidermic cell pattern in such a way that the carapace reticulum looks very much like that of the tissues formed by the underlying epithelial cells. One may, therefore, assume that "smoothing" or "over-reticulation" of ostracods is a more or less important physiological phenomenon directed and brought about by the genome and also likely to be environmentally controlled.

b) The major "obstacle" in the development of ostracods is their incapacity to store calcareous material before the moulting stage in the hemolymph or hepatopancreas. Martin (1977) has already shown that superior Crustacea lack Mg^{++} and look for it in the environment. Turpen and Angel (1971) stated that during moulting the ostracod needs to obtain the whole alkaline reserve directly from the environment, *i.e.* Ca^{++} and Mg^{++}. Although Co^{3-} is sufficiently abundant in the environment, Ca^{++} and Mg^{++} amounts vary greatly according to the state of carbonate equilibrium.

From points a) and b), it is therefore apparent that within a hydrological environment (at the water/sediment interface) where carbonates tend to dissolve, bioprecipitation of ostracod tests is very difficult to realise. In contrast, in a hydrological environment where carbonates tend to precipitate and to be deposited, bioprecipitation of ostracod tests will be easier and ornamentation heavier.

Two main types of polymorphism in ornamentation may therefore be distinguished (Text-fig. 1):

—*a "degrading" polymorphism, i.e.* morphs (Peypouqet *et al.*, 1980, 1981) having become smoother, less reticulate and thinner. These morphs are adapted to a minimal bioprecipitation during which the ostacod will have to use up a lot of energy and achieve a "metabolic economy" in order to survive within an environment unfavourable to the precipitation of carbonates.

—*an "agrading polymorphism"* (Peypouquet *et al.*, 1980, 1981), *i.e.* morphs where the test becomes more reticulate, thicker and inter-reticulate spinosities may occur. These morphs are adapted to a maximal bioprecipitation, easy to realise and within which the organism will not have to spend a lot of energy in building its test; the metabolic effort will comply with that of the hydrological environment.

Thus, from a morphological point of view, polymorphism is likely to follow two opposing directions, corresponding to completely different environmental conditions. This is environmentally cued polymorphism.

Apparently, ostracods may be easily subjected to seasonal and cyclical environmental changes. During the building of its test, the ostracod functions to a certain extent as a polymetallic nodule without, however, losing control of a calcareous overcharge during "agradation" nor control of reduction of reticulation during "degradation". There is, therefore, control and choice in the modalities of "agradation" (preferential thickening of certain costae, orientation of intra-reticulate spinosities etc.) and "degradation" (smooth parts of the shell).

These "agradation and degradation" trends suggest "environmentally cued polymorphism" which may occur in parthenogenetic forms (Williams and Mitton, 1973); this is a frequently occurring phenomenon in ostracods of seasonally contrasting environments (summer and winter forms). A typical example was given by Szczechura (1970), with regard to *Limnocythere* in Lake Bogoria (Africa) (Carbonel *et al.,* 1983).

On the basis of the above discussion, answers may be given to the four questions posed at the beginning of chapter II.

Chromosomic polymorphism of somatic cells is a fundamental element accounting for the intense polymorphism of ostracod valves. It is all the more important in that the functioning of the test depends upon the following conditions:

a) epidermic cells must build up the test;

b) the form of the test reticulation must reproduce that of the epidermic cells;

c) the storage of the tests' constitutive elements (alkaline earth elements Ca^+ and Mg^{++}) must be impossible between moulting stages; these must therefore derive directly from the water surrounding the animal during the formation of its shell;

d) the carbonate equilibrium in the water may affect the bioprecipitation of the test in a positive manner when the environment tends to precipitate carbonates (agradation) and in a negative manner when the environment tends to dissolve the carbonates present (degradation);

e) there is therefore induction and direction of polymorphism dependent on the equilibrium of carbonates within the environment.

BIOGEOCHEMICAL MODELS LIABLE TO INDUCE POLYMORPHISM

From the preceding discussion it is apparent that the carbonate equilibrium in water is a determining factor inducing an "agrading or degrading polymorphism" of the reticulation of valves. All environmental physico-chemical parameters subsequently liable to affect the carbonate equilibrium are inductors of polymorphism.

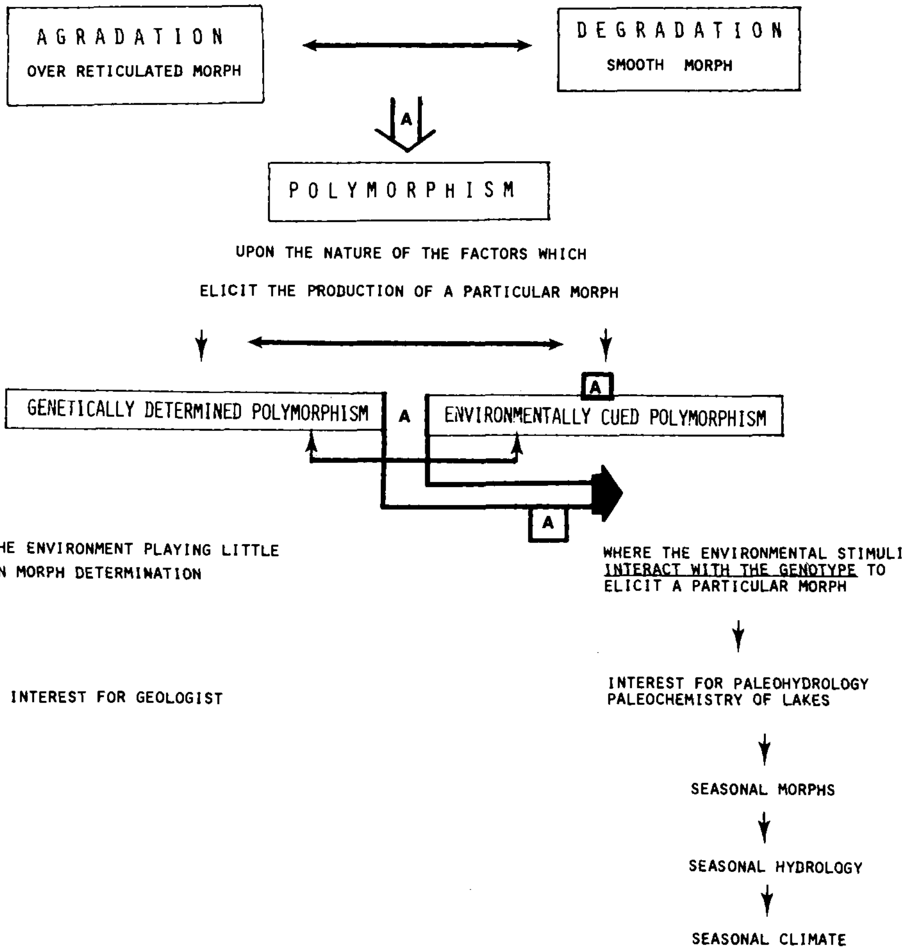
Simple Parameters: Temperature and Depth

In addition to the physico-chemical factors governing equilibrium of the carbonates, there are two other parameters exerting a most influential role:

a) *temperature:* when high, it favours deposition and bioprecipitation of calcareous organisms and thereby encourages the "agradation" of thermophile species; in contrast, when low, it delays drastically the development of costae and reticulations.

b) *depth:* a parameter often linked to temperature, and progressing in the same way with the approach to the abyssal plains. In these regions, temperature decreases, and CO_2 – as ΣCO_2 – increases with depth. The $CaCO_3$ saturation weakens, attaining a lysocline limit, where the carbonate test cannot develop.

Through time (*e.g.* subsidence), littoral species tolerating a deep environment should become progressively "degraded" (Text-fig. 2). This is the case for *Hazelina* sp. *54* of the Rockall plateau between the early lower (NP10) and middle Eocene (NP16) (Peypouquet and Leblé, in prep.). In this lapse of time, the Rockall plateau environment changed from warm infra-littoral (climatic optimum Eocene 10 m depth–NP10) into a continental shelf environment (150 m–NP12) attaining a depth of $>$1000 m (NP16) where the temperature was about 10° C (Text-fig. 1). In addition to the obvious "degradation" of the test from *H.* sp. *54* to *H.* sp. *51* (Text-fig. 1) the loss of the ocular tubercle (in conformity with Benson's ideas, 1975) was also noted. It must be pointed out that the initial species *Hazelina* sp. *59* (48 million years) changes into *Hazelina* sp. *52* or *53* (46 million years) and later into *Hazelina* sp. *51* (39 million years) within a 9 million year interval. The reason for this evolution is the species capacity to tolerate:



TEXT-FIG. 1—Biological model supporting agradation-degradation concept (Peypouquet *et al.*, 1981).Environmetally cued polymorphism produces morphs congruent with current ecological conditions and fluctuating or alternating environment its avoids the worst effect of selection for the previously existing conditions. (Clark, 1976).

—a subsidence greater than 1000 m,

—an important deficit of light (it becomes blind) (*Hazelina* sp. *51*),

—an undersaturation of $CaCO_3$ linked with a drop in $T° >$ to about 10° C and an increase in depth >1000 m.

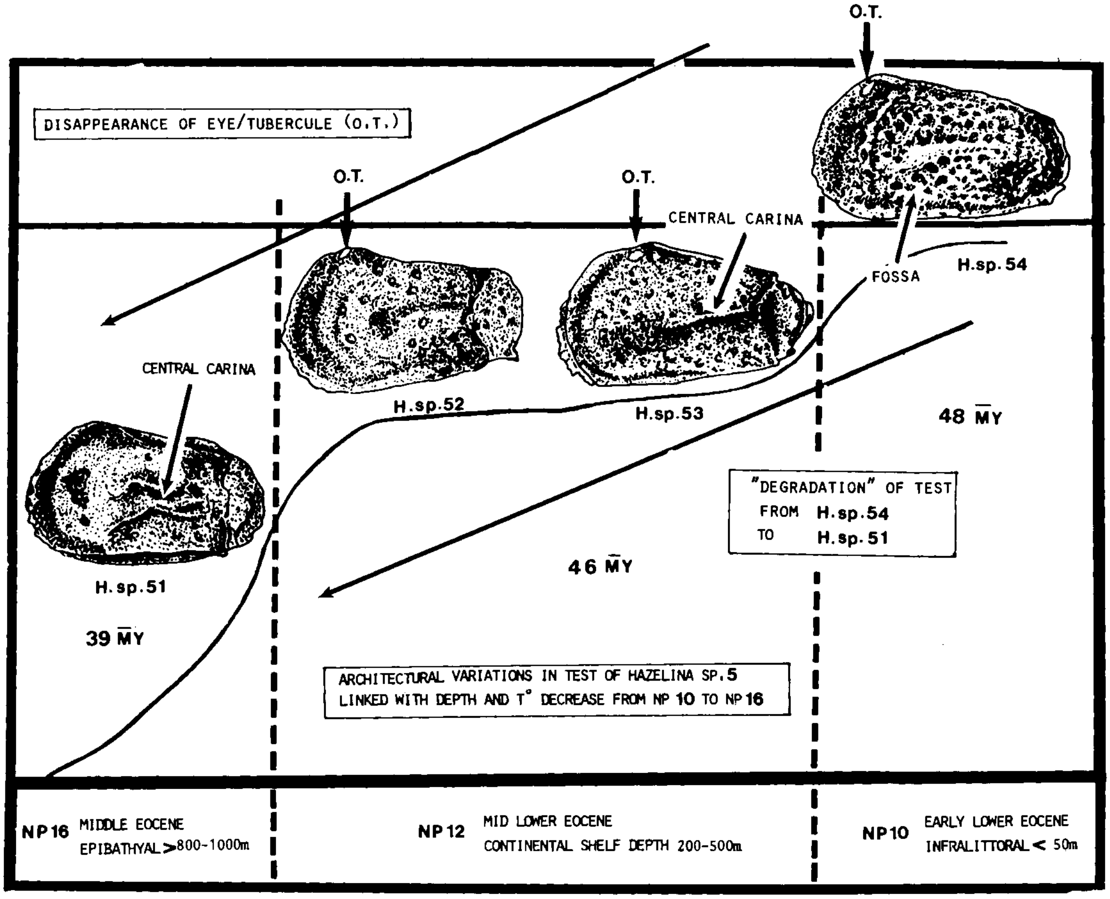
Under these circumstances, the species lineage may be preserved only if the test is "degraded" through time, *i.e.* only if they manage to bioprecipitate the least possible $CaCO_3$ content.

Any further arguments should be superfluous to demonstrate the "degradation" impact of tests. This phenomenon undoubtedly ensures the evolution of a certain number of ostracods under particular environmental conditions.

The places likely to be affected by these two parameters are:

—*for temperature:* littoral areas, rivers, bays, lagoons having varying salinity. Regions of contrasting climatic conditions where both agraded and degraded morphs may occur.

—*for depth:* areas subjected to subsidence or progradation of continental margins.



TEXT-FIG. 2—Architectural variations in test of *Hazelina* sp. ×5 linked with depth and temperature decrease from NP10 to NP16 in the Rockall plateau.

Complex Parameters: The Impact of Organic Matter at the Water/Sediment Interface Biogeochemical Model (Text-fig. 3)

There presently exist on the Senegal continental shelf (100–200 m deep) polymorphic "agraded and degraded" species of *Chrysocythere* which develop within an environment where the temperature and depth parameters are of little, if any, importance. Nevertheless, these forms are situated in seasonal upwelling (Farmer, 1985, thesis in prep.) zones which ensure the occurrence of large amounts of biodegradable organic matter. These quantities of organic matter control the equilibrium of carbonates at the water/sediment interface.

With the occurrence of upwelling, part of the organic matter derived from phytoplankton and zooplankton is consumed, another part dissolved and decomposed in the water column and the rest degraded on the bottom by bacterial action. The outcome at the water/sediment interface is fermentation releasing sugar, vitamins, amino acids and various carbon products. The organic matter decomposition occurs in a more or less oxidysing and reducing environment. The bacterial solution will release CO_2 which in its turn will have three main effects: it will a) diminish pH; b) acidify the environment and c) release the Ca^{++}, Mg^{++}, Na^{+} and K ions (Berner, 1971, 1981; Suess, 1978; Trichet, 1967; Lalou, 1957a,b). The experiment by Lalou is particularly instructive for it classifies the phenomena observed through time in two successive, diametrically opposed, phases.

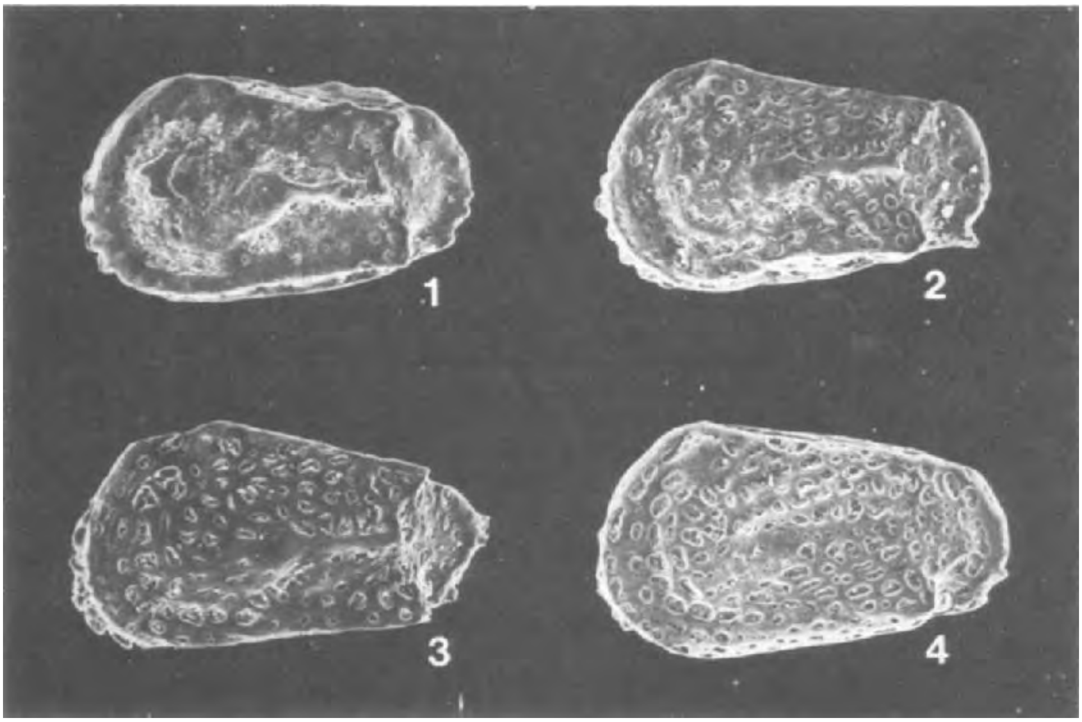


PLATE 1—Fig. 1. *Hazelina* sp. *51*, Left valve (× 75); Leg 81-Site 553 A-Core C 10-Section S 3; NP16 (nannofossil)-Middle Eocene. Fig. 2. *Hazelina* sp. *52* = *53*. Left valve (×75); Leg 81-Site 553 A-Core C 12-Section S 1; NP12 (nannofossil)- Mid-Lower Eocene. Fig. 3. *Hazelina* sp. *53* = *52*. Left valve (×75); Leg 81-Site 553 A-Core C 12-Section S 1; NP12 (nannofossil)- Mid-Lower Eocene. Fig. 4. *Hazelina* sp. *54*. Left valve (×75); Leg 81-Site 555—Core 58-Section S 2; NP10 (nannofossil)- Early-Lower Eocene.

The overall organic matter input (glucose) within a bucket filled with sea water and containing calcareous mud, produces the following effects:

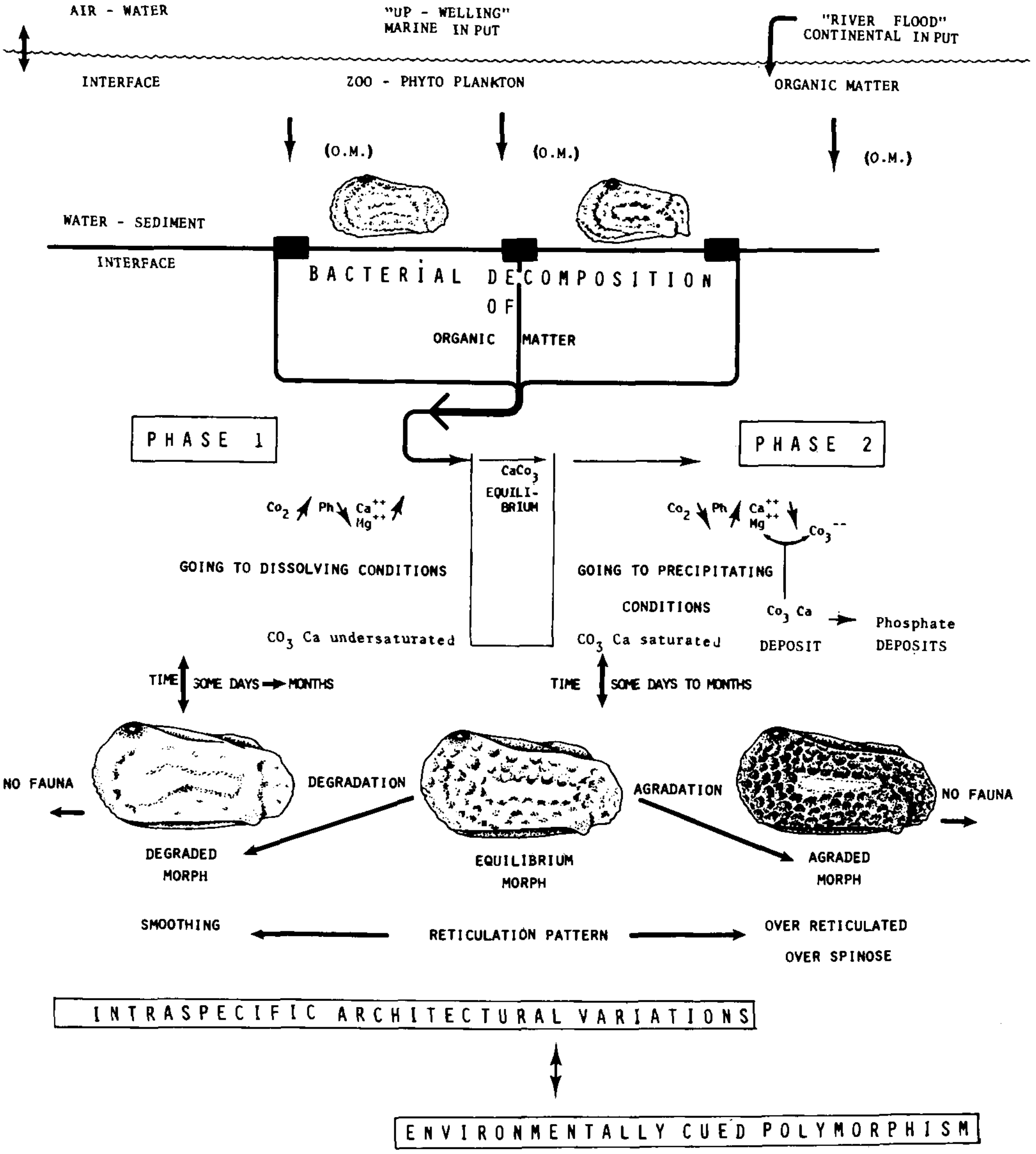
—*firstly*, the environment is acidified inducing, with regard to the carbonates, dissolving conditions ($Ph \downarrow CO_2 \uparrow Ca^{++} \uparrow Mg^{++} \uparrow$) (Text-fig. 3).

—*secondly*, (a few days later) the environment is, on the contrary, characterized by the precipitation of carbonates, by reduction in the alkaline reserve and an important increase in Ph. If further quantities of organic matter are added, a similar phenomenon to the one above will recur. Dissolution and later precipitating trends with regard to carbonates develop as many times as organic matter is introduced.

This experiment, briefly described here, is fundamental for it can account for the morphological variations observed in the ostracod carapace. In accordance with the diagram (see Text-fig. 3), it is tempting to speculate on the following polymoprhic features induced by the environment:

If phase 1 is much too intense, no test building will be achieved during this period. The energy spent by the ostracod during bioprecipitation of its test is far too high with respect to an environment with negative physico-chemical trends.

If the dissolving phase 1 is tolerated by the animal, the difficulty for the test to precipitate is overshadowed by the reduction to a minimum of the precipitable amounts of $CaCO_3$ and $MgCO_3$.



TEXT-FIG. 3—Biogeochemical model for intraspecific architectural variations in ostracoda.

The ostracod will, in this way, become rather smooth, poorly reticulated and poorly ornamented.

If the precipitating phase 2 is moderate or rather insignificant, the bioprecipitation of the test will be indicated by some increase in ornamentation; if this phase is more intense and compatible with the ecological limits of the ostracod's life, the latter will be able to secrete even better developed and thicker reticulation.

If phase 2 is excessively intense, for instance, the deposition of phosphate deposits in situ, the physico-chemical conditions at the water/sediment interface will be incompatible with the development of ostracods.

All the morphological variants may be envisaged depending on the variability of the physico-chemical conditions, changing from dissolving to precipitating, and also on ecological and genetical comparabilities of the organisms studied.

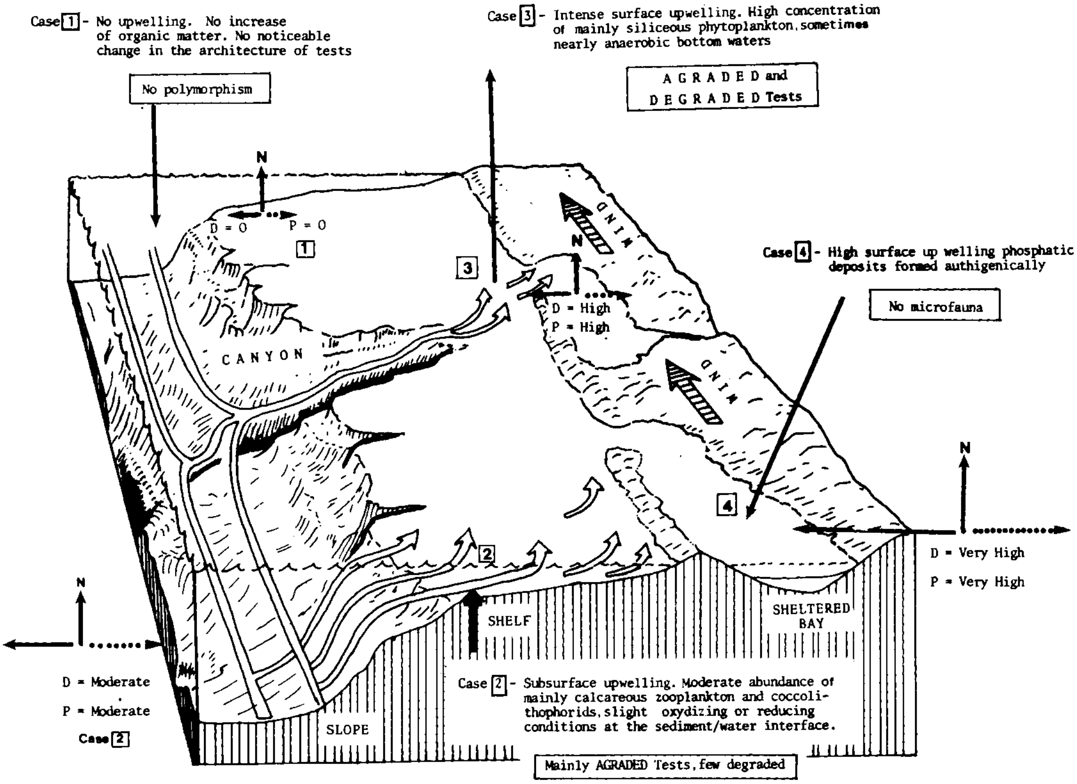
A. The places where organic matter can be most determinant with regard to the carbonate equilibirum at the water/sediment interface and thereby induce an agrading-degrading ostracod polymorphism are the areas of high surficial oceanic productivity, the continental shelf from the outer shelf to the littoral zone (Peypouquet *et al.,* 1985, this symposium). In this case, at least four situations (McKenzie and Peypouquet, 1984) may be envisaged (Text-fig. 4):

Situation n° 1

At the edge of continental shelves there is no evidence of oceanic resurgences. This suggests an insignificant enrichment in the organic matter and a relatively stenothermal and stenohaline environment. The architectural variations in tests will be practically non-existent. If the thermocline is weak, the fauna will be relatively diverse; if the thermocline is strong, the fauna will be scarcer and the Minimum Oxygen Zone (M.O.Z.) relatively high.

Situation n° 2

Again at the edge of the continental shelf, if subsurface upwelling is moderate, an increase in calcareous zooplankton and coccoliths, in particular, will normally take place. Depending on the amounts of organic matter deposited on the bottom (decomposed by bacteria), poorly oxidizing and reducing conditions will result; ostracods building their tests during phase 2, the most favourable to precipitation, will show markedly evident signs of "agradation".



TEXT–FIG. 4—Schematic diagram depicting the different hypothetical cases of the influence of organic matter of upwelling origin on the carbonate equilibrium at the water/sediment interface and the polymorphism of ostracods.

↑ N = Normality of carbonate equilibrium

D = Dissolving conditions for carbonates ←——→ P = Precipitating conditions for carbonates

A far more intense upwelling could develop, however, at the edge of the continental shelf in which case bottom physico-chemical conditions will be those of situation n° 3. Tests will be essentially agraded and only sometimes degraded. If there is an even greater increase in upwelling (*e.g.* Perou) physico-chemical conditions will prevent the development of 2 benthic fauna (dissolved O_2 is far too low) (see situation n° 4). Mineralogical precipitation then occurs (*e.g.* phosphates).

Situation n° 3

In optimum conditions coastal upwelling occurs. There is generally a very high concentration of phytoplankton followed by a high productivity rate of zooplankton and thus an organic matter flux. Physico-chemical conditions above the bottom become highly variable; they change from strongly dissolving to highly precipitating and vice versa. If anoxic conditions are not markedly high, tests become both agraded and degraded. Conversely, if anoxia is high, mineralogical precipitation develops and ostracods cannot survive.

Situation n° 4

Evidence of intense coastal upwelling extends to the middle, sheltered area—the shallow bay area which is more or less confined. Here physico-chemical conditions exceed the ostracod survival limits. There is, in fact, a succession of very intense dissolving and precipitating conditions. The critical drop in dissolved O_2 at the substrate level becomes an obstacle to the development of the benthic life while phosphate deposits flourish.

B. An area rich in organic matter continentally derived and transported by rivers either 1) in the margina-littoral domain where prodeltaic zones are shallow or 2) on the platform or continental margin.

a) *In the shallow marginal–littoral domains* of the inter-tropical zones, all areas receiving large continental inputs (estuary and delta front, Text-fig. 5) are subjected to considerable organic sedimentation. The water column being insignificant, most of the bacterial decomposition of degradable organic matter occurs over the substratum. Consequently, acidification of the water/sediment interface is relatively higher than elsewhere and dissolving environmental conditions predominate over precipitating conditions; this results in a very high "degraded morph" percentage. An area characteristic of this situation is the prodeltaic area of the Mahakam River in Indonesia (Hoibian, 1984; Caronel and Hoibian, 1985, this symposium).

b) *Further off, on the continental shelf and on the slope* (Text-fig. 5), the water column is higher and the organic matter impact on the substratum is more moderate. Subsequently, the most frequently occurring phenomenon is M.O.Z. triggered by the halopycnocline effect of continental inputs. In this case, one may envisage the occurrence of both agraded and degraded forms dependent upon the intensity of the degradable organic matter.

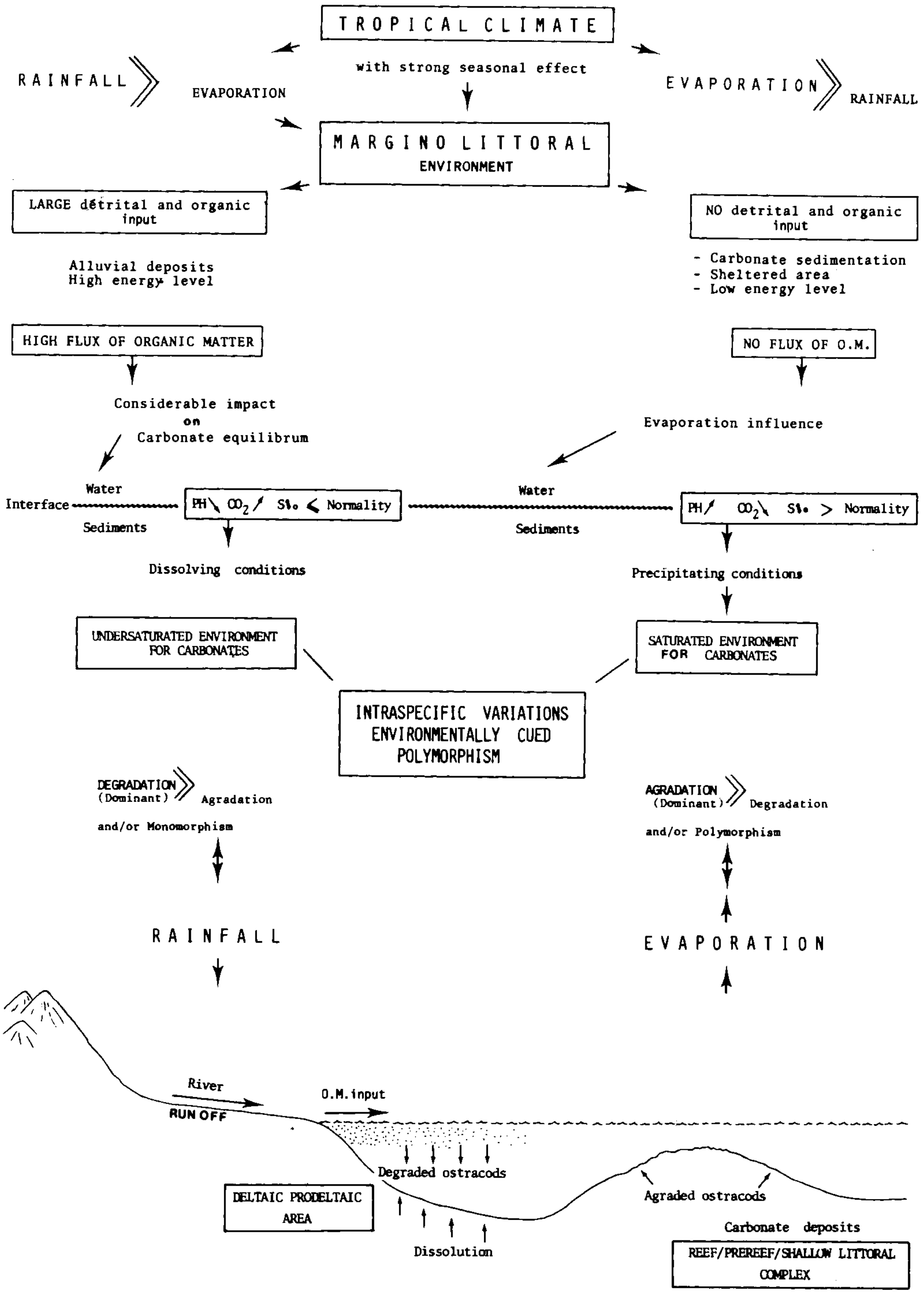
THE "ENVIRONMENTALLY CUED POLYMORPHISM" CONTRIBUTION

Environmentally controlled ostracods, *i.e.* "agraded and degraded" morphs, may be a great source of valuable information in three different fundamental types of investigations:

a) solution of ostracod evolution problems,
b) search for palaeoenvironmental definitions,
c) determination of economic interest: search for phosphatic substances.

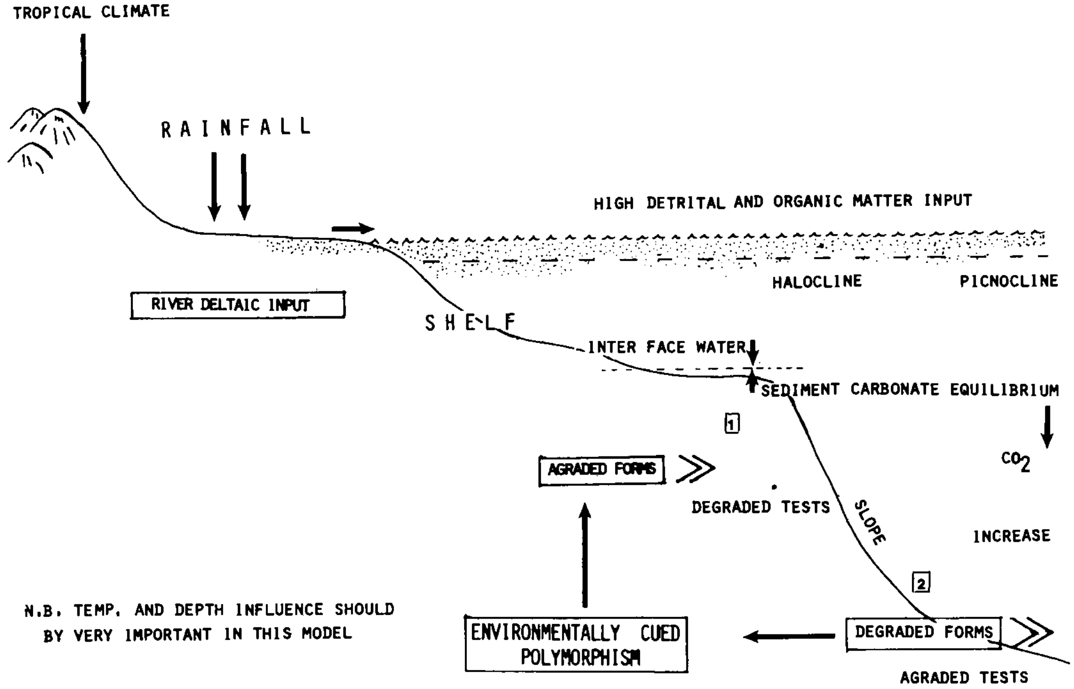
a) Ostracod evolution problems

The intention here is far from grouping all ostracods under the heading of "environmentally



TEXT-FIG. 5—A physiographical and climatic model of marginal-littoral environments; relationship with environmentally cued polymorphism of ostracoda.

N.B.: The temperature impact is highly significant in this model.



TEXT-FIG. 6—Schematic model depicting the case of high detrital organic matter influence on the continental shelf and slope and the hypothetical relationship with environmentally cued polymorphism in ostracoda.

cued polymorphism," but it must be pointed out that their evolutionary success through time (from the Cambrian to the Present) is due to the fact that they proved to be "economic" and highly adaptable to fluctuating environmental conditions. On the one hand, the genetically determined polymorphism includes those expressions of the genotype in which the influence of the environment is minimal or even undetectable. Thus, as chance will be the determining factor, most individuals will be maladapted.

On the other hand, "environmentally cued polymorphism" implies that organisms are recipients of the environmental impact and adapted to the overall selective pressure. Their genetic panoply allows ostracods to react rapidly and positively to diametrically opposed situations. It is evident that the first evolutionary trend is the most costly and will be highly effective as rightly noted by Lewontin (1975), Levins (1961) and Mayr (1963).

An illustration of environmentally controlled ploymorphism with respect to evolution is to be found at the Eocene/Oligocene boundary in the Aquitatine basin which contains "agraded and degraded morphs" (Ducasse *et al.*, 1985, this symposium).

Interesting suggestions to solve the architectural variation problem characterising the transformation (speciation) of *Ortiella? tarfayaensis* into *Ortiella? chouberti* during the basal Turonian within the Moroccan Tarfaya basin, were put forward by Reyment (1982). This author attempted to explain the evolutionary pattern (*O. ?tarfayaensi* (reticulate)→*O. ?chouberti* "degraded", smooth) with the following 4 solutions:

a) a mutation which occurred late in the history of the species,
b) a case of environmentally cued polymorphism,
c) immigrants from a peripheral isolate of *O. ?tarfayaensis,*
d) genetic drift supported by selection.

Examination of the work of Einsele and Wiedmann (1982) showed that in the Tarfaya basin it is possible to consider the appearance of basal Turonian upwelling on the Moroccan shelf. Initiation of "degradation" for *O. ? tarfayaensis* is therefore due to the organic matter inputs induced by upwelling and to the resulting carbonate equilibrium. Such observations are in perfect agreement with our theoretical models and hypothesis (b) proposed by Reyment (1982) appears to be the most convincing one.

In conclusion, to solve this problem, we think it best to agree with Clark's opinion: "Because environmentally cued polymorphism is attuned to environmental conditions and approximately at least to selective pressures, it is unlikely to prove as expensive as chance dependent genetically determined polymorphism. To the extent that the system avoids the production of overtly maladapted morphs it could conceivably be more advantageous than genetically determined polymorphism".

b) The search for paleoenvironmental definitions

Encountering "degraded and agraded morphs" in marine and lacustrine sediments provides research workers with valuable palaeohydrological information which can be used in the reconstruction of palaeoenvironments. An inventory of these polymorphic species gives information about the instability of carbonates within a hydrological environment and on the hydrological oceanic basin structures such as:

—upwelling phenomena and their degree of intensity (Peypouquet *et al.,* 1985, this symposium);
—the intensity of the M.O.Z.

In margina–littoral environments, an evaluation of the river-borne continental input is possible, leading to the determination of evaporation/precipitation relationships in the basin (Peypouquet *et al.,* 1980, 1981).

In lacustrine environments, the haline concentration of lakes contributes to the understanding of palaeoclimatology (Peypouquet *et al.,* 1983). The seasonal factor of lacustrine systems is also determined by the presence of polymorphic populations (summer/winter or dry/damp season) (Carbonel and Peypouquet, 1983).

c) Economic interest-relationship with phosphate deposits

From the information given in this paragraph and in the biogeochemical model linking "environmentally cued polymorphism" of ostracods to the equilibrium of carbonates at the water/sediment interface, it is evident that intraspecific architectural variations in tests are the biological answer to what might be called a "prephosphatic" environment. Thus, the model proposed (Text-fig. 1) concerning the induction of variations is very similar, in many points, to those proposed by sedimentologists studying phosphatic deposits. The economic interest is thus important. It is presently acknowledged that during deposition of phosphates within marine environments two successive geochemical phases occur, the first one dissolving and the second one precipitating. As indicated by Lucas (1977) phsophate is "essentially derived from the initial calcite". It is probable that calcite dissolves slowly and that the calcium released is immediately used by the available phosphorus to replace *in situ* carbonate. The outlines may be preserved by this subtle phenomenon, provoking true epigenesis. Lucas's colleagues (*e.g.* Manheim *et al.,* 1975; Burnett, 1977; Birch, 1980) fully agree with this statement.

As has been rightly noted by Bentor (1980) conditions favourable to the precipitation of apatite are also favourable to the precipitation of $CaCO_3$. Thus, very frequently occurring "agraded-degraded" tests suggest the existence of levels more or less rich in phosphate deposits.

GENERAL CONCLUSIONS

1—Ostracods are crustacea that seem to be physiologically and genetically predisposed to polymorphism. The reasons are:

a) ostracods are often endowed with a chromosomic polymorphism of somatic cells which apparently contribute to their development;

b) ostracods cannot ensure storage of alkaline-early elements (Ca^{++} and Mg^{++}) necessary for the building of their tests between moults. They are, therefore, dependent on the prevailing environmental conditions.

2—The "agradation and degradation" of tests are two characteristic phenomena of an "environmentally cued polymorphism".

3—The state of carbonate equilibrium at the water/sediment interface appears as a major factor in determining, the orientation of the polymorphism (towards agradation or degradation).

4—Regarding carbonates, it may be stated that when the hydrological environment is dissolving, the tests tend to be "degraded"; when it is precipitating, the tests are rather "agraded", and when the milieu is alternating seasonally or cyclically, both "agraded and degraded" population morphs occur.

5—The decomposition of organic matter at the water/sediment interface is one of the most important determining factors in the carbonate equilibrium in the water and over the substrate. This development often leads to alternating or cyclic environments.

6—Parameters such as temperature, depth or oxygenation may intervene and accentuate or diminish the "agrading" or "degrading" polymorphism of Ostracoda.

7—A very detailed survey of polymorphic ostracods provides answers to the questions raised by the reconstruction of marine and lacustine palaeoenvironments, namely hydrological structures (upwelling, M.O.Z., stratification, oligotrophic/mesotrophic seasonal phenomena, impact of run off water masses, etc . . .).

8—Polymorphism being independent of the geological series studied, it may be assumed that the methods applied here may be used in the study of Mesozoic and Cenozoic sequences as well as in marine and lacustrine Palaeozoic ones. Upper Cretaceous marine series from the southern Tethyan margin should yield very important paleooceanographic results.

9—The biogeochemical model eliciting the polymorphism of "agraded and "degraded" tests is identical with the sedimentological models leading to the genesis of phosphates. Hence the economic interest in the recognition of agraded and degraded morphs.

10—It is suggested that for reasons of convenience two broad categories of polymorphism should be recognized:

a) genetically determined polymorphism;

b) environmentally cued polymorphism, when the environment interacts with the genome to evoke a phenotype which is attuned to the environmental circumstances. The latter, through differential gene activity, constitues an important part of normal processes of development, differentiation and the most "economic" and well adapted for evolution in ostracoda.

11—The different models proposed in this paper are hypothetical and should, of course, always be tested, questioned and continuously improved. They are merely intend to stimulate ostracod workers' reactions.

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DISCUSSION

Henning Uffenorde: Does the term "degradation" have the same meaning as "celation" in the sense of Benson and Sylvester-Bradley? If this is the case, the term "acelation" I used in my 1981 paper, may be synonymous with the term "agradation" in your terminology.

Peypouquet: The concept of "agradation-degradation" was established in 1981 (see bibliography). "Agradation" means an increase of reticulation pattern which could be thicker or more reticulated. The murus of the principal reticulation should be higher or thicker and the fossae smaller. "Degradation" means a decrease of reticulation pattern which could be thinner or disappear completely, giving a smooth test. These phenomena are related to bioprecipitation of the test in ostracods and imply "environmentally cued polymorphism". This could be linked with the "celation" concept you proposed in 1981 but "agradation and degradation" should only be used for the morphological change in the valves (see Text-fig. 3).

Patterns and Rates of Evolution among Mesozoic Ostracoda

ROBIN C. WHATLEY
University College of Wales, Aberystwyth, Wales

ABSTRACT

The author has abstracted data from 1267 references on Mesozoic Ostracoda. A total of 6797 species belonging to 739 genera (excluding subgenera) are recorded and grouped into the following suprafamilial categories: Cytheracea, Cypridacea, Bairdiacea, Darwinulacea, Platycopina, Metacopina, Cladocopina, Myodocopina and Palaeocopida. The distribution of the species and genera of these categories by stage through the Mesozoic is illustrated graphically. The diversity of all Ostracoda is shown to be much higher in the Cretaceous, particularly the Upper Cretaceous, than elsewhere in the Mesozoic. Triassic diversity is substantially higher than that of the Jurassic. A measure of evolutionary activity is given by a comparison of both specific and generic origination and extinction rates. High extinction levels occur immediately prior to major Mesozoic division boundaries and are almost immediately succeeded by high absolute or percentage origination levels. High rates of turnover of taxa seem to be correlated with major geological events. The Turonian is unique in the Mesozoic in maintaining its diversity while being a time of extremely low extinction and origination. This is not well understood but appears to correlate with a major anoxic event. An attempt is made to account for changing diversity levels and extinction rates invoking both biotic and abiotic factors. The significance of the evolution of Mesozoic Ostracoda with respect to macroevolutionary heory is discussed.

INTRODUCTION

This paper is a sequel to that presented by Whatley and Stephens at the 5th International Symposium on Ostracoda in Hamburg in 1975 (Whatley and Stephens, 1976). In that paper, entitled "The Mesozoic Explosion of the Cytheracea", the taxonomic evolution of the superfamily Cytheracea was discussed in detail. It was demonstrated that cytherid ostracods in the Mesozoic did not evolve at a regular rate during the interval studied. Rather, it was shown that at certain periods, diversity, both generic and specific, fluctuated considerably as did origination and extinction rates.

In the present paper, the author presents updated data for the Cytheracea and also data for all other ostracod groups recorded from the Mesozoic.

Whatley and Stephens (1976) abstracted data from 638 publications for their study of the Mesozoic Cytheracea. Since 1975, the present author has continued to abstract data and in the preparation of this work has seen no less than 1267 publications on Mesozoic Ostracoda. Whatley and Stephens were confident that "any deficiencies in our knowledge of the literature are not biased towards or against any part of the Mesozic nor for or against any one or more cytheracean families. Thus we feel that these deficiencies do not substantially subtract from the value of our results". (1976, pp. 63, 64). The present paper demonstrates (Text-fig. 7) that, with respect to the Cytheracea, Whatley and Stephens were certainly biased against the Triassic, although the updated figures for both genera and species elsewhere in the Mesozoic generally confirm the trends they originally reported. The present author is confident that, to the date of writing (April, 1985), he has abstracted data from virtually all published works on the ostracods of the Mesozoic.

Of the 1267 references employed in the compilation of data for the present study, only 17 or 1.3% were published prior to 1850. Between 1850 and 1899, 83 papers or 6.5% were published and between 1900 and 1850, 151 papers, representing 12% of the total. Between 1951 and 1975, no less than 793 papers (63%) were published and since 1975 (the date of Whatley and Stephens' presentation was 1976) 223 papers on Mesozoic ostracods have been encountered by the author, representing 18% of the total.

TABLE 1—STRATIGRAPHICAL AND HISTORICAL DISTRIBUTION OF PUBLICATIONS ON MESOZOIC OSTRACODA.

	Triassic		Jurassic		Cretaceous		Mesozoic	
	No	%	No	%	No	%	No	%
Pre 1850	0	0	11	2.8	15	2.1	17	1.3
1850-1899	11	6.3	29	7.4	43	6.0	83	6.5
1900-1950	4	2.2	32	8.2	115	16.1	151	11.9
1951-1975	137	79.8	251	64.3	405	56.8	793	63.5
Post 1975	22	12.6	67	17.1	134	18.8	223	17.6
	174		390		712		1267	

Any study of this nature is rendered difficult to a degree by a variety of problems. For example, it is often difficult to relate stratigraphical data on the ranges of species and genera to currently accepted International Standards for the Mesozoic. This problem is particularly acute when using older literature, but a surprisingly high number of more modern papers refer to the ranges of taxa as being "Jurassic" or "Cretaceous", for example. However in such cases it is usually possible to refine the given ranges by reference to other publications on either the Ostracoda or the strata.

In the various figures and tables it can be seen that a number of stratigraphical compromises have been made. For ease of illustration, the Upper Cretaceous stages Coniacian, Santonian and Campanian have been incorporated within a single entity, the Senonian. Also, the Cretaceous is herein regarded as a bipartite entity rather than separating the Aptian and Albian stages as "Middle Cretaceous". The stages of the Neocomian have been retained despite the difficulty of dealing with the numerous records of species whose stratigraphical range is given as "Wealden". Tithonian and Volgian records have been accommodated within the "Portlandian" and "Purbeckian" although this has caused some difficulties particularly with respect to the occurrence of the Jurassic/Cretaceous boundary within the latter "stage". There are, in fact, many fewer records which are "Tithonian" or "Volgian" than there are for the two "stages" employed here.

With respect to the Triassic, for ease of illustration, the divisions Lower, Middle and Upper (which includes the Rhaetian) have been employed. Relatively little difficulty was experienced in accommodating records of taxa from the "Bunter", "Muschelkalk" and "Keuper" into these divisions.

Without doubt, synonyms and homonyms created the greatest difficulty and consumed the largest proportion of time during the preparation of this work. There may be some which have slipped through the net, but the author is confident that he has eliminated the vast majority of them. The time scale employed in the construction of the various figures is taken from Harland *et al.* (1982).

THE DISTRIBUTION OF THE TOTAL OSTRACOD FAUNA

The total number of species encountered in the literature search was 6797 belonging to 739 genera (excluding subgenera). These taxa have been grouped into the following suprafamilial categories: Cytheracea, Cypridacea, Bairdiacea, Darwinulacea, Platycopina, Metacopina, Cladocopina, Myodocopina and Palaeocopida. The classification employed is essentially *sensu* Moore

TABLE 2—NUMBER OF SPECIES AND GENERA OCCURRING AND APPEARING FOR THE FIRST TIME IN EACH STAGE. (*First appearances of taxa in brackets*).

			SPECIES			GENERA		
			No. of species and No. of new species per stage	Mean No. of species, No. of new species and % of new species per division	Mean No. of species, No. of new species and % of new species per system	No. of genera and No. of new genera per stage	Mean No. of genera, No. of new genera and % of new genera per division	Mean No. of genera, No. of new genera and % of new genera per system
CRETACEOUS	Upper	Maastrichtian	1311 (678)	1048 (2211) (32.5%)	899 (3985) (58.6%)	233 (70)	202 (230) (31.1%)	173 (388) (52.5%)
		Senonian	1181 (664)			213 (87)		
		Turonian	794 (188)			171 (8)		
		Cenomanian	907 (681)			190 (65)		
	Lower	Albian	864 (371)	799 (1774) (26.1%)		167 (28)	154 (158) (21.4%)	
		Aptian	669 (275)			154 (26)		
		Barremian	786 (91)			143 (9)		
		Hauterivian	825 (163)			156 (8)		
		Valanginian	789 (117)			139 (7)		
		Berriasian	860 (757)			162 (80)		
JURASSIC	Upper	Purbeckian	512 (211)	396 (793) (11.7%)	296 (1950) (28.7%)	91 (5)	97 (52) (7.0%)	81 (189) (25.6%)
		Portlandian	367 (176)			95 (5)		
		Kimmeridigian	346 (170)			97 (13)		
		Oxfordian	360 (236)			105 (29)		
	Middle	Callovian	340 (250)	276 (794) (11.7%)		97 (17)	86 (99) (13.4%)	
		Bathonian	396 (316)			110 (40)		
		Bajocian	235 (133)			81 (26)		
		Aalenian	131 (95)			56 (16)		
	Lower	Toarcian	126 (59)	214 (363) (5.3%)		56 (12)	59 (38) (5.1%)	
		Pliensbachian	257 (51)			58 (3)		
		Sinemurian	277 (76)			61 (5)		
		Hettangian	199 (177)			59 (18)		
TRIASSIC		Upper	552 (308)	431 (862) (12.7%)	431 (862) (12.7%)	103 (39)	102 (162) (21.9%)	102 (162) (21.9%)
		Middle	456 (268)			115 (35)		
		Lower	286 (296)			88 (88)		

1961 with certain necessary modifications. Although a more sophisticated classification could have been employed, given the current somewhat fluid state of ostracod taxonomy, the author has chosen not to pre-empt the *Treatise* revision.

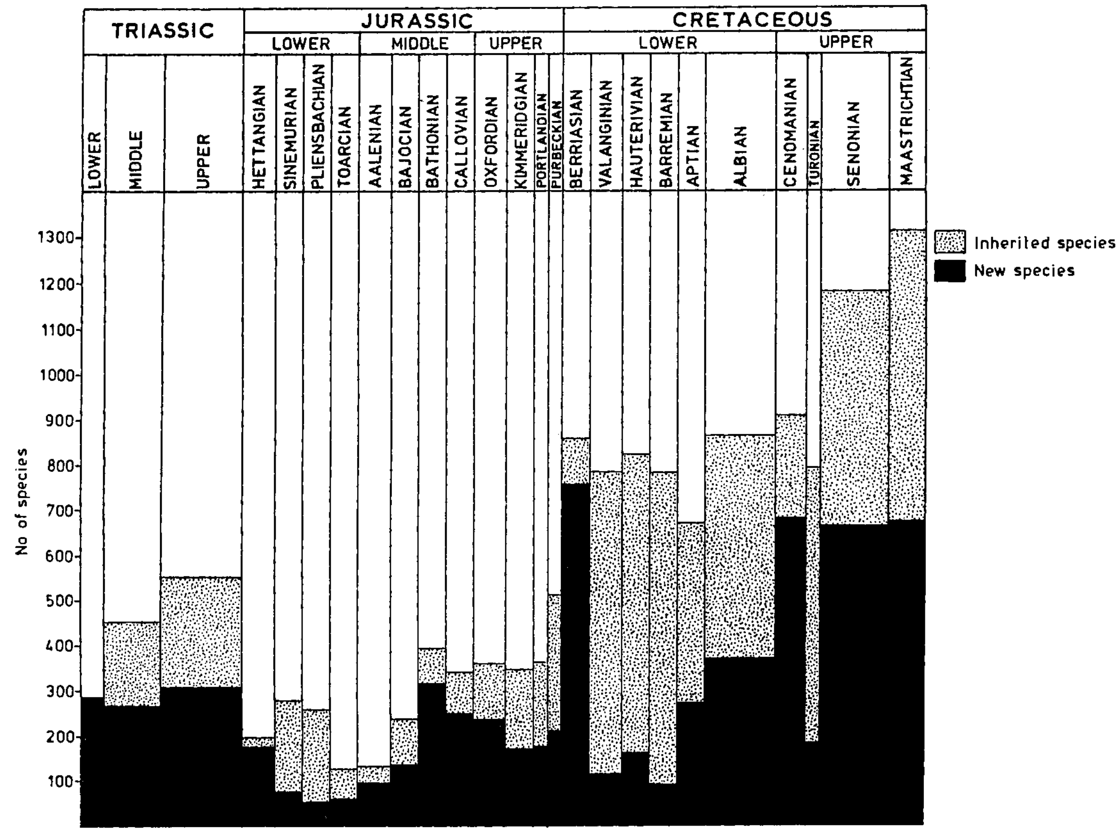
Table 2 shows the distribution of all species and genera of ostracods in the Mesozoic in terms of number of taxa per stage, division and system. The table also gives, as a measure of evolutionary activity, the number of new taxa first appearing in each unit and also the percentage of new taxa.

Numbers of genera and species in the Triassic are higher than in the Jurassic, although a significant increase in the number of taxa is shown to take place throughout the Jurassic. The number of genera and species in the Lower Cretaceous is higher than in any part of the Jurassic. Upper Cretaceous ostracod diversity, however, is significantly higher than that of the Lower Cretaceous.

These general trends are very clearly illustrated by the mean number of species per stage (in the case of the Triassic the tripartite divisions are used).

	Mean No. of Species per Stage	Increment
Upper Cretaceous	1048	249
Lower Cretaceous	799	403
Upper Jurassic	396	120
Middle Jurassic	276	62
Lower Jurassic	214	minus 217
Triassic	431	

As will be demonstrated later in this paper, the decline from a relatively high number of species



TEXT-FIG. 1—Histograms illustrating the simple species diversity and the inherited versus new component of all ostracod species for each stage of the Mesozoic.

to the lowest number for the Mesozoic in the Liassic, is due to a number of factors. Among them is the virtual extinction of the Palaeocopida in the Triassic. Other groups, such as the Cytheracea and the Bairdiacea, which flourished subsequently in the Mesozoic, underwent a crisis at the Triassic/Liassic boundary as witnessed by the sharp decline in their diversity. Several families of the former superfamily became extinct at this time, an almost unique event in the Mesozoic.

The largest increment in the mean number of species per stage takes place from the Upper Jurassic to the Lower Cretaceous and the second largest increment is between the Lower and Upper Cretaceous. The former is largely accounted for by the appearance in the Neocomian of large numbers of nonmarine cyprids; the latter is largely due to a major adaptive radiation of the Cytheracea.

The mean number of species per stage for each system also clearly reveals the same trend with a mean number of 431 species for the Triassic, 296 for the Jurassic and 899 for the Cretaceous.

In Text-fig. 1, the total number of ostracod species per stage for the entire Mesozoic is plotted, showing the relationship between new and inherited species. All species in the Lower Triassic are assumed to be new. The following 12 stages have less new than inherited species:

Sinemurian	27%	Valanginian	15%
Pliensbachian	20%	Hauterivian	20%
Toarcian	46%	Barremian	12%
Kimmeridgian	49%	Aptian	41%
Portlandian	47%	Albian	43%
Purbeckian	41%	Turonian	24%

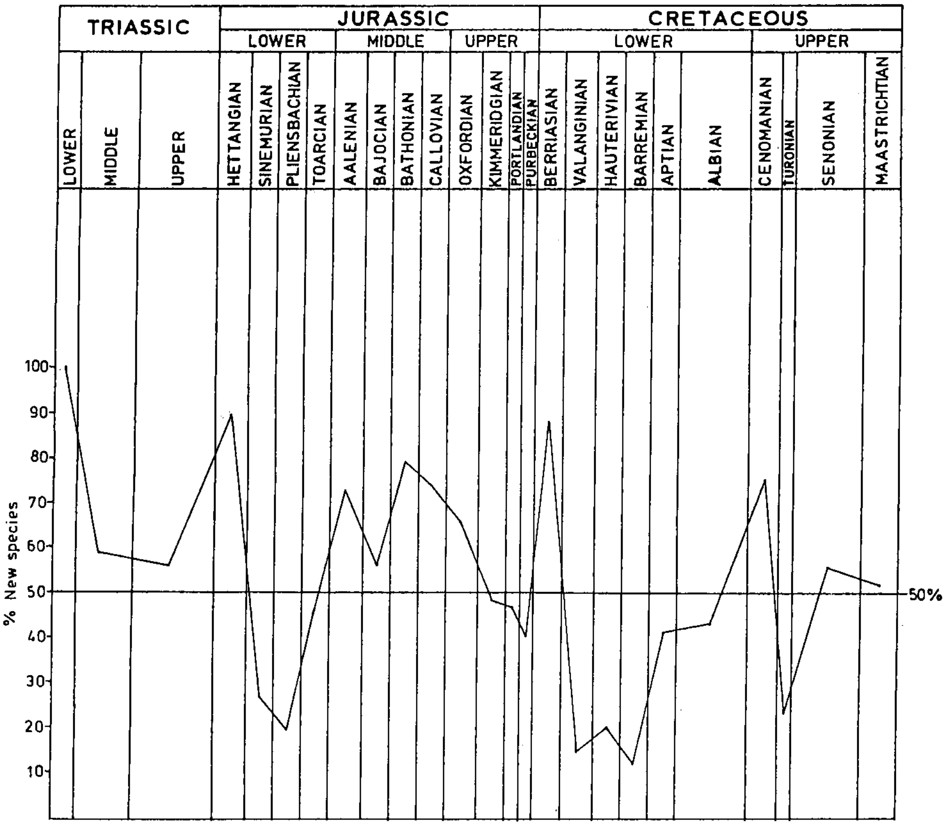
The following 13 stages have more new than inherited species:

Lower Triassic	100%	Callovian	74%
Middle Triassic	59%	Oxfordian	66%
Upper Triassic	56%	Berriasian	88%
Hettangian	89%	Cenomanian	75%
Aalenian	73%	Senonian	56%
Bajocian	57%	Maastrichtian	52%
Bathonian	79%		

This is illustrated graphically in Text-fig. 2. Origination rates almost always increase notably in the first stage of a system or major system division *viz.* Lower Triassic, Hettangian, Aalenian, Berriasian and Cenomanian. From such relatively high origination rates, there is an immediate and often dramatic decline to much lower levels of first appearances of species, *e.g.* Middle Triassic, Sinemurian, Bajocian, Valanginian and Turonian. This low level is generally continued until the next major boundary. The only boundary which is not associated with an increase in origination rates is the Middle/Upper Jurassic, there being a decline from the Callovian to the Oxfordian.

As Text-figs. 1 and 2 show, there is a complex relationship between the total number of species per stage and the percentage of those species which are new. For example, although there is a high percentage of new species in the Lower Triassic, the total number of species is the lowest of the three Triassic divisions. Similarly, the low number of total species in the Hettangian and Aalenian does not match the high percentage origination levels of these stages. However, the Berriasian has the highest number of species and the highest proportion of new species of any of the Neocomian stages. In the case of the Cenomanian, the number of species, although higher than at any previous time in the Mesozoic and higher than the succeeding Turonian, is relatively low for the Upper Cretaceous, despite the fact that 3/4 of its species are new.

Although the major system and intra-system boundaries for the Mesozoic were established on the stratigraphical distribution of other fossil organisms, notably ammonoids, both Text-figs 1 and 2 demonstrate the validity of these boundaries and their ability to be recognized on the basis of the distribution of Ostracoda.



TEXT–FIG. 2—The percentage of newly appearing species in each stage of the Mesozoic for all Ostracoda.

Text-fig. 3 illustrates graphically the relationship between the number of species which first appear and which become extinct in each stage.

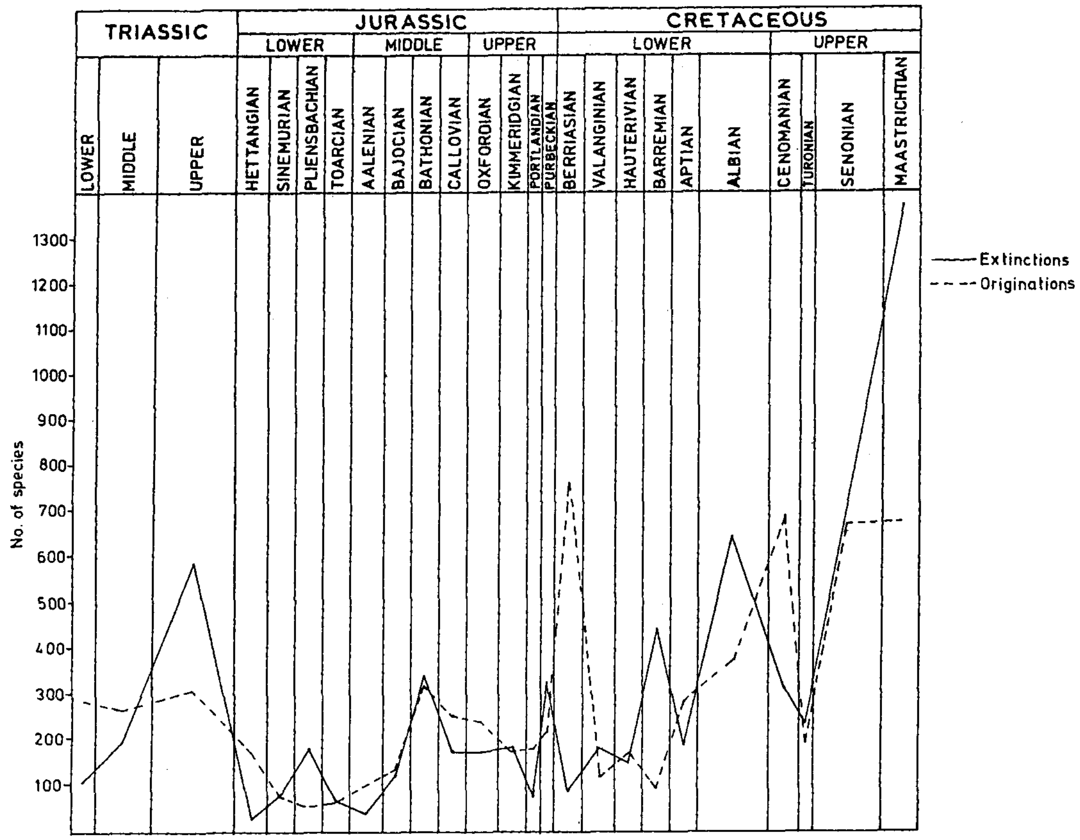
In the following 12 stages, extinctions exceed originations:

Upper Triassic	+274	Purbeckian	+110
Sinemurian	+ 1	Valanginian	+ 61
Pliensbachian	+128	Barremian	+343
Toarcian	+ 5	Albian	+270
Bathonian	+ 20	Turonian	+ 43
Kimmeridgian	+ 10	Maastrichtian	+694

The probably invalid assumption is made that all Mesozoic species became extinct at the Cretaceous/Tertiary boundary.

In the following 13 stages, originations exceed extinctions:

Lower Triassic	+182	Portlandian	+ 98
Middle Triassic	+ 74	Berriasian	+672
Hettangian	+153	Hauterivian	+ 17
Aalenian	+ 62	Aptian	+ 91
Bajocian	+ 15	Cenomanian	+375
Callovian	+ 79	Senonian	+ 50
Oxfordian	+ 69		



TEXT-FIG. 3—The relationship between originations and extinctions of species for all Mesozoic stages and all Ostracoda.

High rates of extinction in either absolute or proportional terms can be seen to precede the major divisions of the Mesozoic. The extinction rate rises in the Triassic to an Upper Triassic climax and this is succeeded by a low rate in the Hettangian, the lowest for the Mesozoic. Similar phenomena can be seen when one compares extinction rates for the Pliensbachian and Aalenian, Bathonian and Oxfordian, Tithonian and Berriasian, Barremian and Aptian, Albian and Cenomanian and the Maastrichtian high also probably precedes a very low extinction rate for the Danian.

As Text-figs. 1–3 show, in most of the instances cited above, the low level of extinction of species which follow the absolute or proportional high levels correlate well with proportional or absolute high origination rates. These have already been noted with respect to the Hettangian, Aalenian, Berriasian, and Cenomanian.

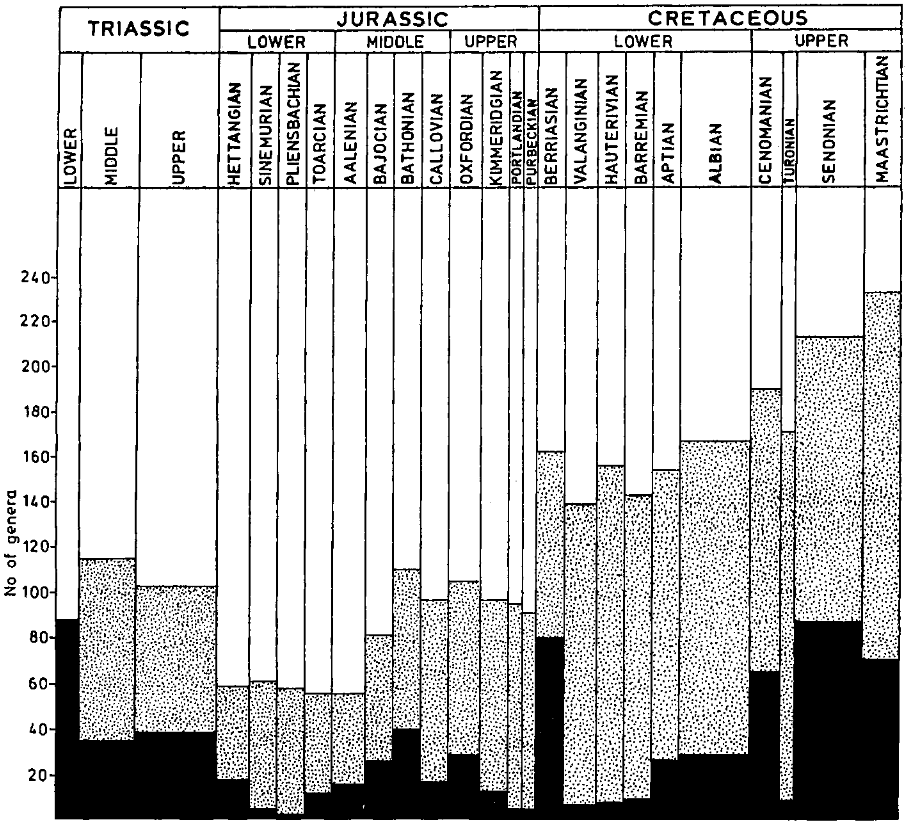
The relationship between the level of origination and extinction is not only a measure of the rate of evolution, it is also a reflection of mechanisms of regulation by which diversity levels are maintained. Text-figure 1, however, demonstrates very clearly that simple species diversity fluctuated considerably during the Mesozoic. In simple terms, it was higher in the Upper Triassic than at any time in the Jurassic and considerably higher throughout the Cretaceous than at any previous time in the Mesozoic. The simple species diversity of the Neocomian, for example, is approximately 70% higher than that of the Upper Triassic, while that of the Maastrichtian is approximately double that of the Upper Triassic and approximately 10.5 times greater than that of the Toarcian, in which stage the lowest diversity of the Mesozoic is recorded.

There are many factors which can influence results such as these. Taphonomy must always be considered, but this alone could not possibly be responsible for the differing diversites of Ostracoda through the Mesozoic. Intensity of research is another possibility, but, as Table 1 shows, for example, more studies have been carried out on Jurassic than on Triassic Ostracoda. Variable levels of research activity may somewhat prejudice the results in favour of the Cretaceous but, as Whatley and Stephens (1976, fig. 6) demonstrate for the Cytheracea, this is not likely to introduce major discrepancies. The reasons for changes in diversity are discussed later.

THE EVOLUTIONARY DISTRIBUTION OF MESOZOIC GENERA

For the most part, the distribution in terms of originations, extinctions and diversity of genera reflect those of species. The greater longevity of genera being the principal difference between the taxa.

The same major trends in generic diversity as in species occur, as can be seen when the mean number of genera per stage is considered.

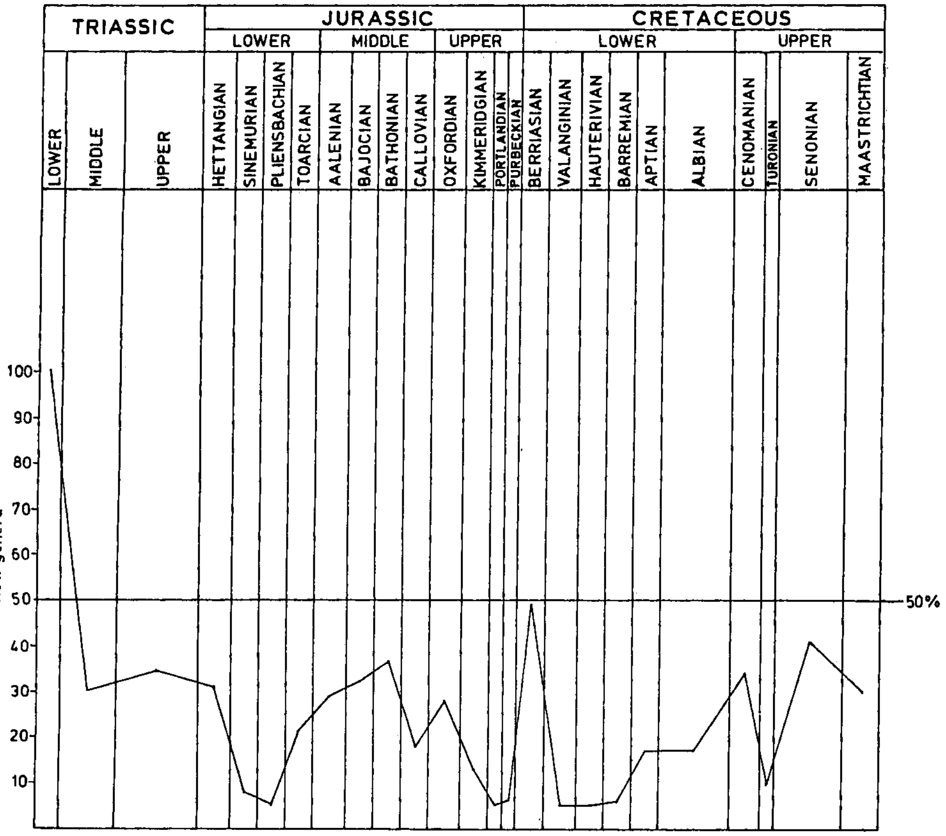


TEXT-FIG. 4—Histograms illustrating the simple generic diversity and the inherited versus new component of all ostracod genera for each stage of the Mesozoic.
☐, Inherited genera; ▨, New genera

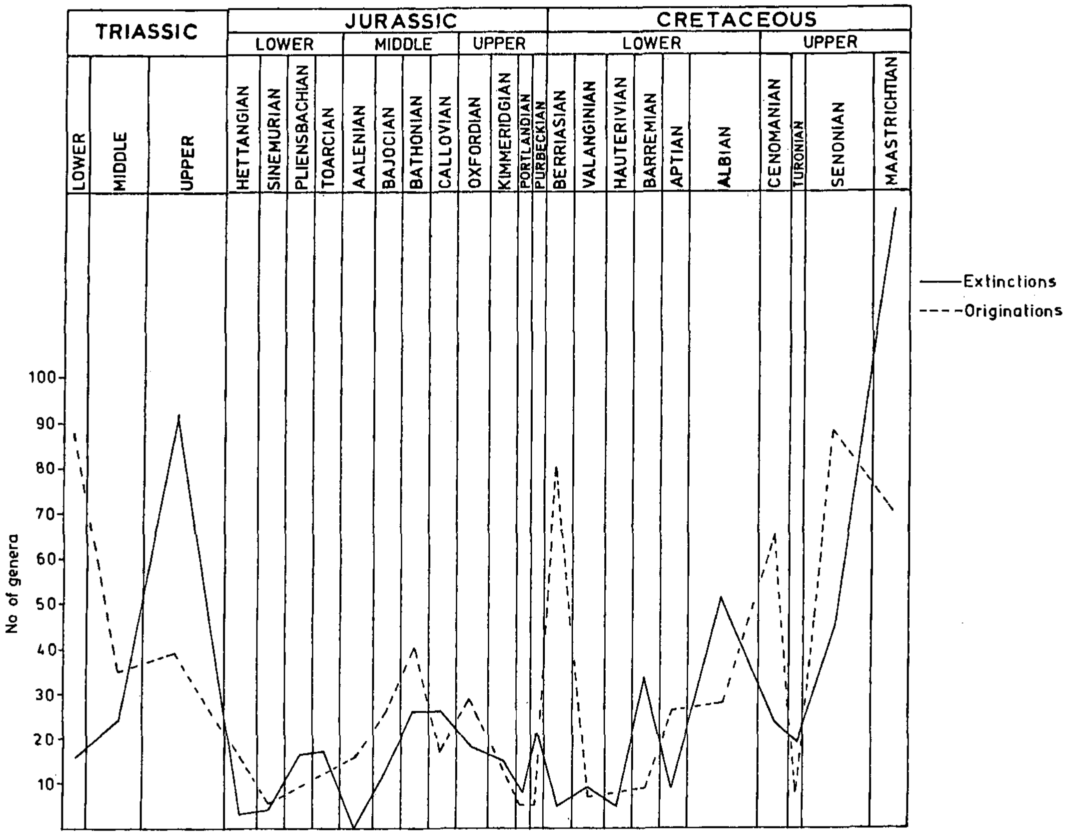
	Mean No. Genera per Stage	Increment
Upper Cretaceous	202	48
Lower Cretaceous	154	57
Upper Jurassic	97	11
Middle Jurassic	86	27
Lower Jurassic	59	minus 53
Triassic	102	

A sharp decrease in mean generic diversity from the Triassic to the Liassic is followed by an increase in mean diversity to the Upper Cretaceous. The trend for genera differs from that of species only in that the incremental difference between Lower Jurassic/Middle Jurassic and Middle Jurassic/Upper Jurassic is reversed. This difference is a function of the greater longevity of genera, coupled with the fact that a large number of Jurassic genera make their first appearance in the Aalenian-Bathonian interval (Table 2). When considered at the system level, the mean generic diversity trend is 102 for each Triassic division and 81 and 173 for the Jurassic and Cretaceous stages respectively.

In Text-fig. 4, plotted as a series of histograms, the relationships between new and inherited genera is given by stage. All genera in the Lower Triassic are, for convenience, assumed to be new. When compared to Text-fig. 1 which demonstrates the same distribution for species, a number of features become apparent:



TEXT-FIG. 5—The percentage of new genera in each stage of the Mesozoic for all Ostracoda.



TEXT-FIG. 6—The relationship between originations and extinctions of genera for all Mesozoic stages and all Ostracoda.

1) The major trends for species are mirrored by genera.
2) Because of the greater longevity of genera, the inherited component of the histograms is larger.
3) Although generic diversity in the Hettangian-Aalenian interval is much lower than that of the preceeding Triassic, that of the Bajocian–Purbeckian is more similar to that of the Triassic than was the case with species.
4) The generic diversity for all Cretaceous stages is higher than at any preceeding interval in the Mesozoic.

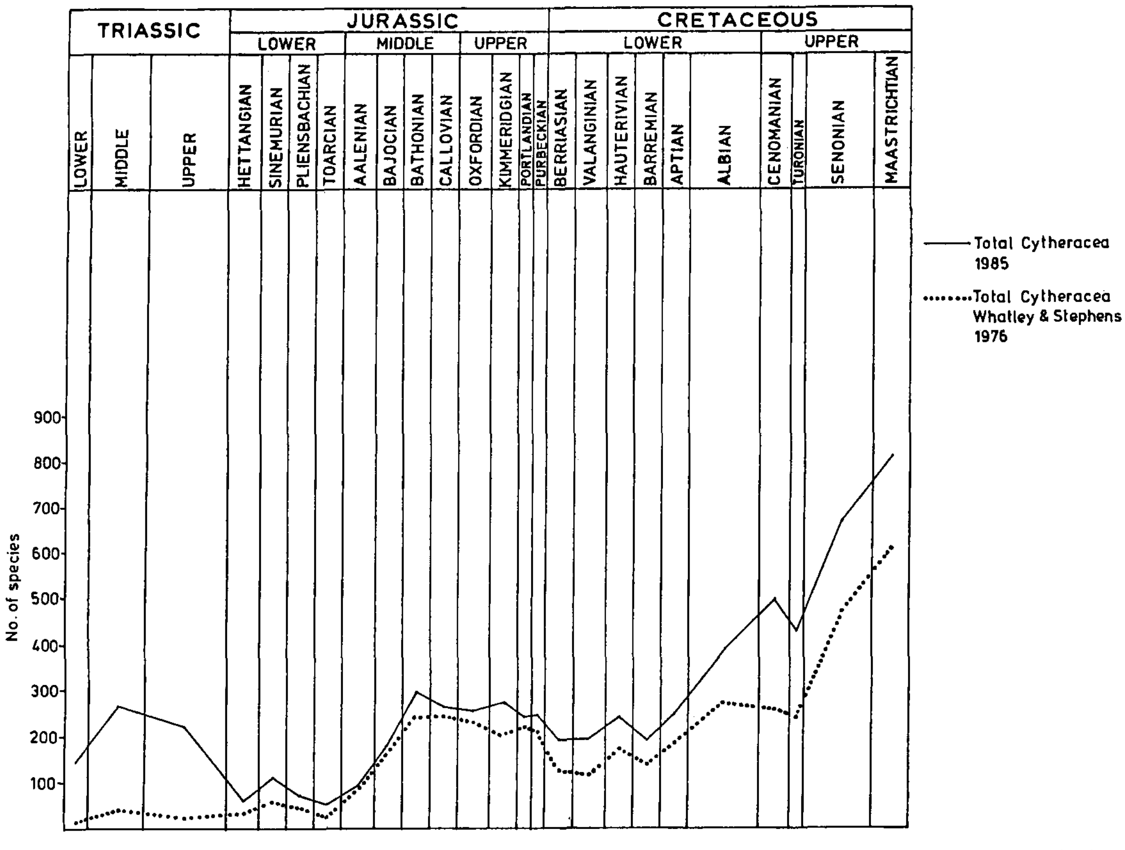
The percentage of new genera per stage is plotted in Text-fig. 5. Although in Text-fig. 2, which plots the same percentage for species, no less than 13 stages have more than 50% new species, apart from the Lower Triassic (where all genera are assumed to be new) no other Mesozic stage has more than 50% new genera. With respect to species, highest levels of origination occur in the first stage after a system or major infra-system boundary. This effect is less clear with respect to genera, but the generic origination level is higher in the Hettangian than in any other Liassic stage and also that of the Berriasian, with 49%, is higher than at any subsequent stage in the Cretaceous.

The relationship between originations and extinctions of genera is given in Text-fig. 6. As with species (Text-fig. 3), enhanced extinction rates take place immediately prior to major boundaries within the Mesozoic *viz.* Upper Triassic, Toarcian, Callovian, Purbeckian, Barremian, Albian and Maastrichtian. As Text-figs. 5 and 6 show, in many instances, these elevated extinction rates are followed by enhanced origination rates; the best examples are the Berriasian, Aptian and Cenomanian.

THE EVOLUTIONARY DISTRIBUTION OF THE MAJOR GROUPS OF MESOZOIC OSTRACODA

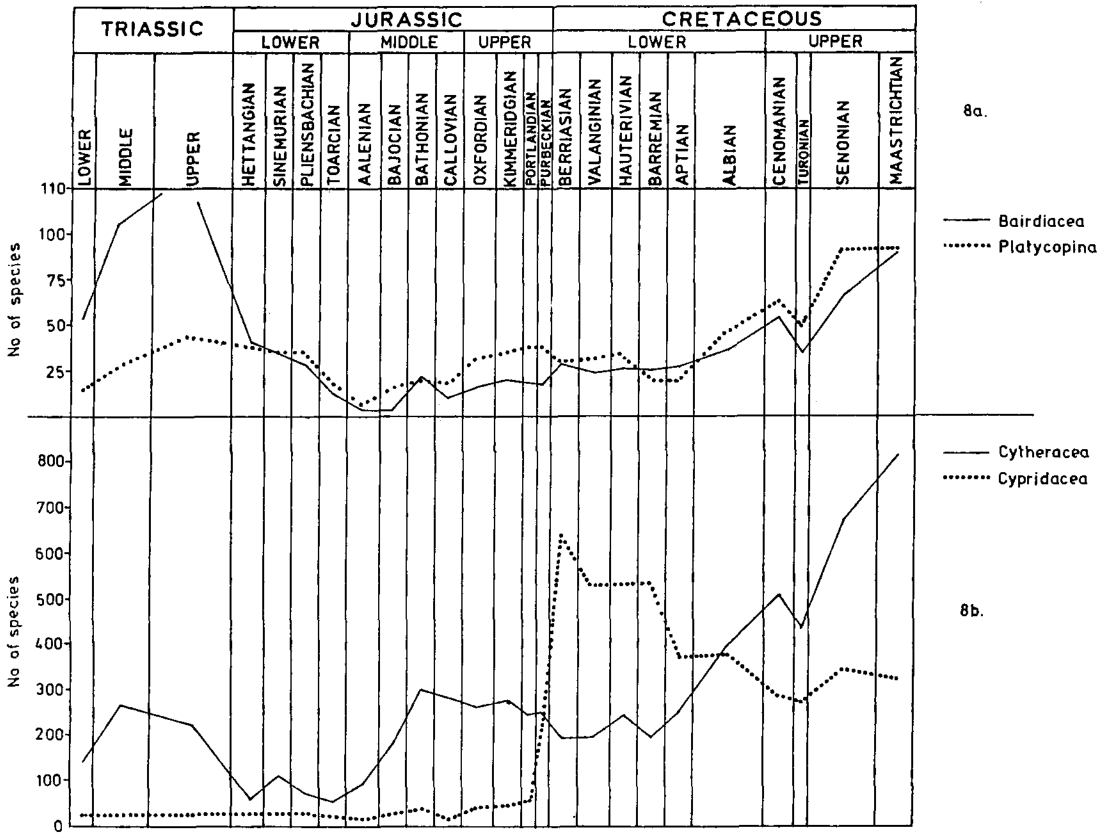
The distribution of genera and species of 9 suprafamilial groups of Ostracoda has been analysed. These comprise the superfamilies Cytheracea, Cypridacea, Bairdiacea and Darwinulacea, the suborders Platycopina, Metacopina, Myodocopina and Cladocopina and the order Palaeocopida.

The largest Mesozoic category (by both species and genera) is the Cytheracea. Text-fig. 7 compares graphically the results produced by Whatley and Stephens (1976, fig. 6) with those calculated to April 1985 for the distribution of cytheracean species. The 1976 figures for the Triassic were much too low. This was due to the fact that the authors of that paper did not have access to a number of important papers on Eastern European Triassic faunas. The 1985 figures for Triassic species are also a reflection of a considerable degree of research activity in the system post 1975 (Table 1). For the remainder of the Mesozoic, the graph for 1985 closely follows that for 1976, the only divergence being in the Cenomanian. In all stages, the 9 years since the publication by Whatley and Stephens has seen the description of new species.



TEXT-FIG. 7—Graphs showing the simple species diversity of Cytheracea for each Mesozoic stage for 1976 (Whatley and Stephens) and 1985.

The distribution of cytheracean species departs somewhat from that of all Mesozoic ostracod species (Text-fig. 1). The principal difference is that, although Triassic diversity levels are higher than those of the Hettangian-Bajocian interval, those of the Upper Jurassic are as high or higher than those of the Triassic and also higher than those of the Neocomian. The Liassic was the time of lowest species diversity among the Cytheracea. Although many of the Triassic taxa described in the literature are thought to have been brackish, given the restricted extent of marine environments in the Triassic as opposed to the extensive marine transgressions of the Liassic, it is surprising that an essentially marine superfamily such as the Cytheracea should not have proliferated in the Lower Jurassic. Elsewhere in the Mesozoic, an overall relationship between cytheracean diversity and palaeoenvironment can be seen. A good example is the decline in diversity from the marine dominant Upper Jurassic to the Neocomian, a period of widespread global regression. This is followed by a major transgressive event initiated in the Aptian, at which time most Wealden non-marine basins were eliminated, and culminating in the Upper Cretaceous. The response to this event is clearly seen in Text-fig. 7 with (apart from a decline in the Turonian which will be discussed later) a fairly regular increase in cytherid diversity from Aptian to Maastrichtian. Cytherid species diversity for this last stage of the Mesozoic is 7 times higher than that of the Berriasian, the least diverse part of the Cretaceous and 15 times greater than that of the Toarcian, the least diverse part of the Jurassic (and the Mesozoic). Maastrichtian cytherid diversity is also 2.7 times higher than

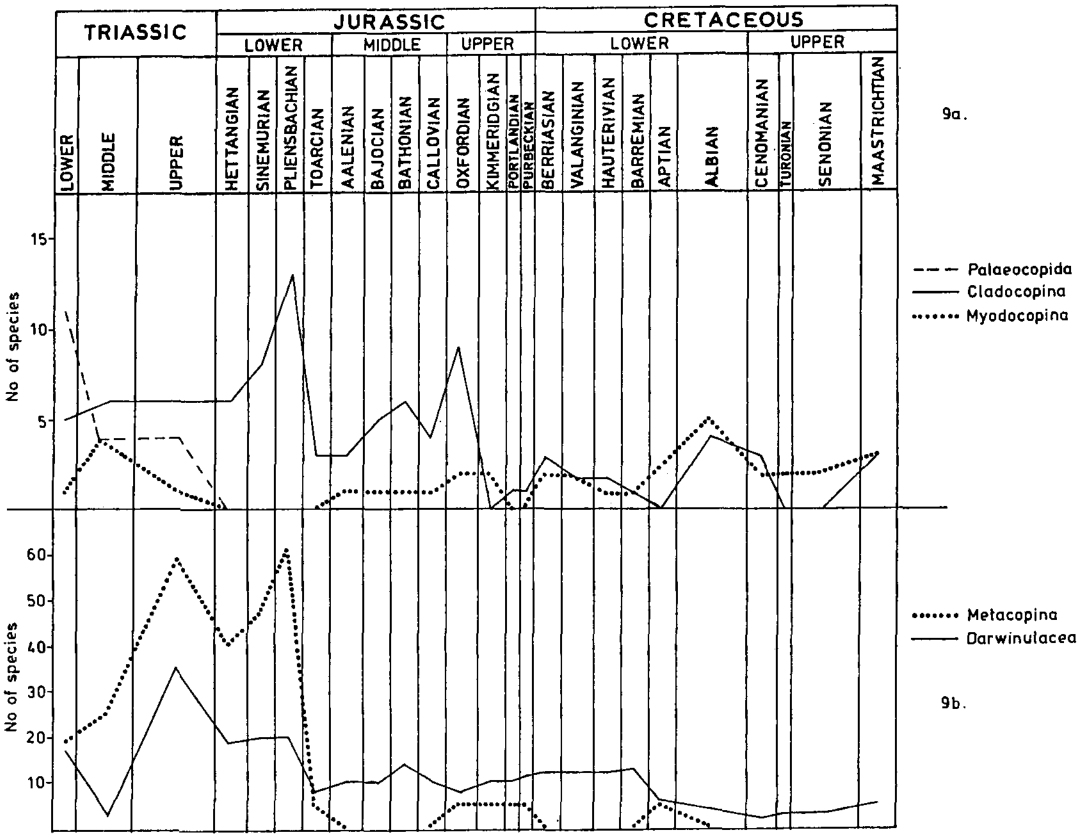


TEXT-FIG. 8—a. The numerical distribution of species of Bairdiacea and Platycopina through the Mesozoic. b. The numerical distribution of species of Cytheracea and Cypridacea through the Mesozoic.

that of the Bathonian, the highest for the Jurassic and 3 times higher than the Middle Triassic, the highest for the Triassic.

In Text-fig. 8b, the number of species per stage for the Cytheracea and the Cypridacea are compared. Only in the Berriasian-Aptian interval does cyprid diversity exceed that of the cytherids. Most, if not all, Triassic and Lower Jurassic cyprids were marine. The first non-marine cyprids of the Mesozoic are of Bathonian age, but they remain relatively unimportant and subordinate in non-marine environments to the Limnocytheridae until the close of the Jurassic where in the Purbeckian, their numbers begin to undergo an increase. Pre-Purbeckian cyprid diversity is regularly low. The adaptive radiation of non-marine cyprids, notably of the genus *Cypirdea* and its allies, is clearly seen in Text-fig. 8b in the Neocomian. This is clearly related to the global abundance of "Wealden" environments. The wholescale elimination of these non-marine environments from the Aptian onwards is reflected in the steep decline in cyprid diversity. It is, however, largely due to the persistence in China and Mongolia of "Wealden" type facies into the Upper Cretaceous which is responsible for the maintenance of relatively high cyprid diversity to the end of the Mesozoic.

Text-figure 8a illustrates graphically the species diversity by stage of two marine groups, the Bairdiacea and the Platycopina. In the Triassic, the Bairdiacea clearly dominate, largely due to the large number of taxa recorded from Tethyan carbonate environments in the Triassic. From their major peak in the Triassic, the Bairdiacea decline through the Lower Jurassic and maintain (with



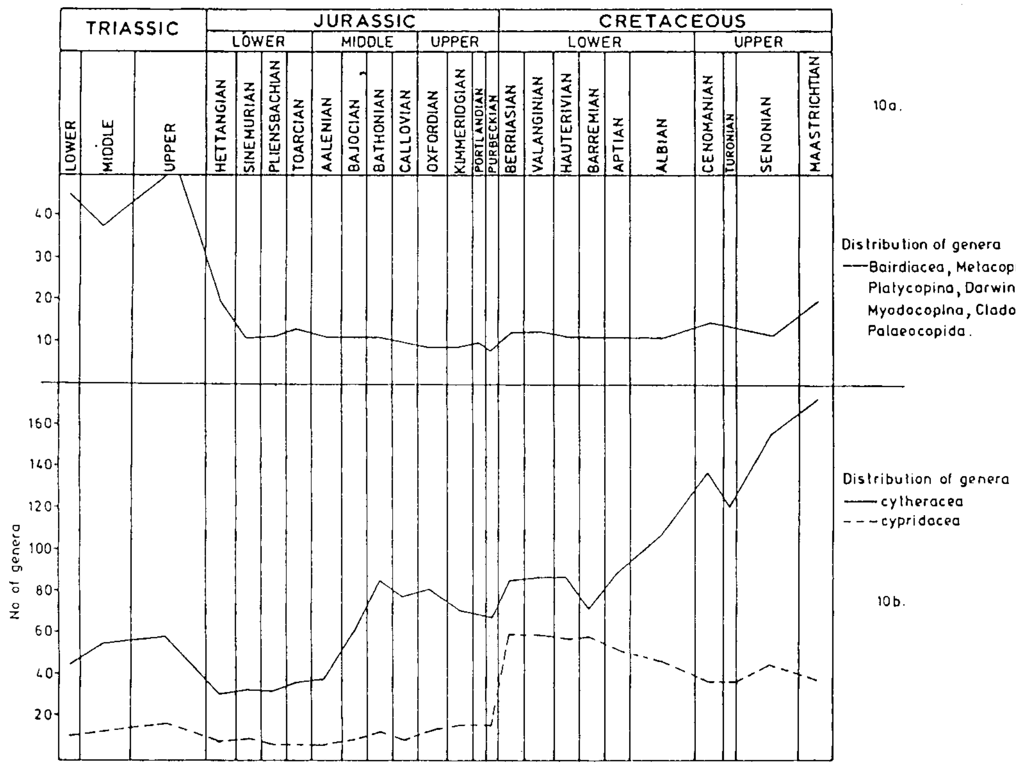
Text-fig. 9—a. The numerical distribution of species of Palaeocopida, Cladocopina and Myodocopina through the Mesozoic. b. The numerical distribution of species of Metacopina and Darwinulacea through the Mesozoic.

the exception of the Bathonian) generally low levels in the Middle and Upper Jurassic. Neocomian levels are higher than at any time in the Jurassic and, with the exception of a sharp decline in the Turonian, increase regularly through the remainder of the Cretaceous.

Platycope species diversity increases through the Triassic and maintains a high level to the Pliensbachian, before declining to the lowest level for the Mesozoic in the Aalenian. With the single exception of the Bathonian, the species diversity of the Platycopina exceeds that of the Bairdiacea throughout the Jurassic and is also higher throughout the Cretaceous with the exception of the Barremian and Aptian. Platycope diversity is also substantially reduced in the Turonian.

The species diversity by stage for the remaining 5 groups of Mesozoic Ostracoda is illustrated in Text-fig. 9. The virtual demise of the essentially Palaeozoic "Palaeocopida" is documented in the Triassic (Text-fig. 9a). Despite the fact that Tertiary and Recent species of at least two genera are known from the Southwest Pacific, no genuine records of this group are known from Mesozoic strata younger than Upper Triassic. (Records from the Upper Jurassic of North America are almost certainly of reworked Palaeozoic material). The order is placed in quotation marks because some of the taxa which linger on into the Triassic would be classified by certain authors in a separate new order (Gramm, 1984).

Text-figure 9a also clearly demonstrates the low number of species of the Myodocopida recorded from the Mesozoic. The highest diversity for the Myodocopina is in the Albian, with 5 spe-



TEXT-FIG. 10—a. The numerical distribution of genera of Bairdiacea, Metacopina, Platycopina, Darwinulacea, Myodocopina, Cladocopina and Palaeocopida through the Mesozoic. b. The numerical distribution of genera of Cytheracea and Cypridacea through the Mesozoic.

cies. However, taphonomy is probably more important in this than in any other group of Mesozoic ostracods, in that with their rather weakly calcified carapaces, they will only be preserved in the most favourable circumstances. The absence of myodocopes from the entire Lower Jurassic is clearly an artefact of preservation.

Text-figure 9a also illustrates that cladocope diversity is higher in the Triassic and Jurassic than in the Cretaceous, with diversity peaks in the Pleinsbachian and Oxfordian. The rather "patchy" distribution of this suborder largely confirms Neale's (1983) observations on the group.

Text-figure 9b plots the distribution of species of Metacopina and Darwinulacea in the Mesozoic. Somewhat surprisingly, the diversity of the Metacopina more than doubles from Lower to Upper Triassic. It then declines into the Hettangian, recovers in the Sinemurian and then declines very steeply into the Toarcian. There are no Aalenian records of the suborder and subsequent Mesozoic records, although plotted on Text-fig. 9b, are very old and incapable of being checked. They are almost certainly erroneous. The significance of the decline of the Metacopina with respect to subsequent proliferation of other marine groups is discussed later.

The entirely non-marine Darwinulacea are most diverse in the Upper Triassic. They maintain a relatively high diversity in the Lower Liassic of some 20 species per stage, but this is approximately halved for the remainder of the Jurassic. The mean Neocomian diversity of the Darwinulacea is some 12 species per stage, declining to less than 5 per stage for most of the remainder of the Cretaceous.

Text-figure 10a plots the generic diversity by stage of the Bairdiacea, Darwinulacea, Metacopina, Platycopina, Myodocopina, Cladocopina and Palaeocopida, while the diversity of Mesozoic genera of the Cytheracea and Cypridacea is given in Text-fig. 10b. The former group are most diverse in the Triassic and subsequently decline markedly, Jurassic and Lower Cretaceous diversity being only approximately 1/5 as high, although the mean for the Upper Cretaceous is a little higher. The high Triassic generic diversity of these 7 groups is principally occasioned by the Bairdiacea and the Metacopina.

In Text-fig. 10b, the generic diversity for the Cytheracea and Cypridacea can be compared. The former always exceed the latter, despite the fact that in the Neocomian and Aptian, cyprid species exceed cytherids (Text-fig. 8b). Apart from this, the trends for genera for the two superfamilies confirm those for species.

DISCUSSION

The data presented above poses a number of questions which require consideration.

A. Diversity

Both specific and generic diversity has been shown to fluctuate considerably throughout the Mesozoic, with respect to all ostracods and also to most of the 9 suprafamilial groups studied. Why should diversity of species have been so much higher in the Triassic and Cretaceous than it was in the Jurassic? Why should the simple species diversity of the Maastrichtian be 10.5 times that of the Toarcian?

The author has not found any simple answer to these and related questions. He is convinced, however, that these diversity fluctuations are real and not artefacts due to differential preservation or research activity, etc. What is not known, however, is the extent to which ostracod biomass per unit area or volume may have changed during the Mesozoic. Attempts to collate and compare data from various levels in the Mesozoic were frustrated by time considerations, the lack of standardized techniques between authors, sedimentary dilution, taphonomy, etc. Despite this, however, the general impression gained by the author from his own studies of Mesozoic ostracods and those of his students, together with what could be abstracted from the literature, is that although mean ostracod incidence seems to have fluctuated throughout the Mesozoic, it has not done so nearly to the extent that diversity has.

Frequently in the fossil record it is possible to correlate the increased diversity of one group of organisms with the decline in another. No obvious correlation is apparent, however, with respect to the Mesozoic Ostracoda. Little enough data exists with respect to competition between Recent ostracoda and other organisms to allow one to extrapolate any meaningful interrelationships back so far into the past.

The collapse of high Upper Triassic ostracod diversity levels into the Lower Jurassic is difficult to explain. Since most Triassic and Liassic ostracods were marine, on first principles one would expect that, since globally more epicontinental shallow marine environments were available in the Liassic than in the Triassic, that Lower Jurassic diversity would more nearly approach (if not exceed) that of the Triassic. In fact, were it not for a considerable proliferation in the Lower and Middle Liassic of the Metacopina (Text-fig. 9b) immediately prior to the virtual extinction of the suborder, then Lower Jurassic faunas would be of much lower diversity.

The Triassic witnessed a considerable adaptive radiation of the Cytheracea, Bairdiacea, Darwinulacea and Metacopina. All of these groups decline radically into the Hettangian and of them, only the latter can be said to "do well" in the Lower Jurassic despite virtual extinction before its close. The "Palaeocopida" also disappear from the Mesozoic Fossil Record at the end of the Triassic.

Considering diversity alone, it is evident that a crisis occurred at the Triasic/Jurassic boundary. This is not unique to ostracods, since possibly the most dramatic reductions in amonoid diversity and incidence also occur at this time.

Only the metacopes recover rapidly in the Lower Liassic. Other groups such as the Cytheracea and Bairdiacea fail to recover their Triassic diversity levels in the Liassic; the recovery of the former is delayed until the Middle Jurassic and the latter until the Upper Cretaceous. It is possible that the post-Triassic radiation of the Cytheracea was supressed in the Liassic by that of the Metacopina. This seems unlikely given the high diversity of both groups in the Upper Triassic. Also, in the Toarcian, when the metacopes have all but gone, cytherid diversity also declines to its nadir for the Mesozoic.

The Middle Jurassic sees an increase in diversity of all ostracods (Text-fig. 1), but this is principally the consequence of an increase in the number of cytherid species (Text-figs. 7, 8b). By Bathonian times the composition of cytheracean faunas has changed considerably with members of the progonocytheridae undergoing a major adaptive radiation, accompanied by other "new" cytherids, notably the Schulerideidae and Protocytheridae. Strongly calcified progonocytherids with the newly evolved entomodont hinge were possibly capable of occupying niches, particularly those in high energy environments, which had previously been denied to most cytherids. This factor alone could account for enhanced diversity levels in the Bathonian-Oxfordian interval. High Bathonian diversity is maintained by the Cytheracea despite the very widespread regression which occurred at the time.

Although a single progonocytherid with an entomodont hinge lingers on into the Kimmerdigian, this group otherwise become extinct in the *Perisphinctes plicatilis* zone of the Upper Oxfordian. In the same zone, the first cytherids with amphidont hingement are encountered in the form of *Amphicythere* and *Macrodentina*. Neither of these events seem to have effected cytherid diversity levels at this time, any more than does the acme of Jurassic transgressive activity which occurs during the Callovian–Kimmeridgian interval. As in the case of the Liassic, in the Upper Jurassic there is no apparent correlation between ostracod diversity and sea-level curves of the sort published by Hallam (1978, 1981), Vail and Todd (1981) or Vail *et al.* (1977).

Diversity increase in the Purbeckian-Neocomian is largely accounted for by the proliferation of non-marine cyprid taxa at this time in response to the large scale availability of Purbeckian–Wealden environments (Text-figs. 1, 8b). The large scale diversity increase in total ostracod species in the Aptian–Maastrichtian interval is principally due to the Cytheracea, but the Bairdiacea and Platycopina also contribute significantly (Text-figs. 1, 8a,b). This interval was one of protracted and almost uninterrupted transgression culminating in the Upper Cretaceous in one of the highest sea level rises of the Phanerozoic. The increase in diversity of ostracods over this interval is, with the exception of the Turonian, regular and this represents the only time in the Mesozoic when it is possible to correlate a transgressive event with increased diversity.

In the Cytheracea, however, which are the group principally responsible for this diversity increase in Aptian to Maastrichtian times, evolutionary events of major significance took place at this time. The amphidont hinge which first appeared in the Oxfordian does not seem to have been a particularly successful character in the Jurassic. In the marine Cretaceous, however, particulary from the Aptian onwards, this hinge type is found in more and more ostracod taxa. The interval saw this hinge type evolve from the primitive hemiamphidont to the more sophisticated holampphidont and in Cretaceous times, with the exception of *Protocythere* and its alies, almost all thick-shelled ornate ostracods were articulated by this hinge. There is probably a correlation between this wholesale adoption fo the amphidont hinge and the ability of such ostracods to occupy new environmental niches. The consequent adaptive radiation of the Trachyleberididae, Brachycytheridae and the first appearance of the Cytherettidae and Hemicytheridae (Whatley and Stephens, 1976 p. 66, fig. 1) are all related to the high diversity levels of the Senonian and Maastrichtian.

Whatley and Stephens (1976) noted that the Turonian was a time when origination and extinction levels were abnormally low for the Upper Cretaceous. This can be seen in the present study in Text-figs. 1-7, 8a, 8b and 10b. This possibly correlates with a major global anoxic event at the Cenomanian-Turonian boundary. (Arthur and Schlanger 1979; Schlanger and Jenkyns, 1976; Hart and Bigg, 1981). It is, nonetheless, difficult to equate low extinction and origination rates to such an event.

B. Origination and Extinction Rates as a Measure of Evolutionary Activity

The overall turnover of Mesozoic genera and species was considerable. Not only did the era see the virtual extinction of the "Palaeocopida" and the Metacopina and many genera and species of the other groups, it also witnessed the first appearance of many families of Ostracoda which survive to the Recent and other groups typical of the Mesozoic.

This study demonstrates that rates of evolution were very variable in the Mesozoic, a phenomenon which Whatley and Stephens commented on in 1976. They also demonstrated, (Table 4, Text-fig. 5, Table 5) that different cytherid families evolved at different rates at different times. In the present paper, Text-figs. 1, 2 and 3 all indicate that the rate of origination of new species is very variable. Text-figure 1 compares the actual number of new species per stage with the number of inherited species. Large numbers of new species per stage (more than 250) evolved in the following: Triassic, Bathonian, Callovian, Aptian and Albian. Very large numbers of new species (more than 500) evolved in the Berriasian, Cenomanian, Senonian and Maastrichtian. Very low numbers of new species (less than 100) originated in the Sinemurian, Pliensbachian, Toarcian, Aalenian and Barremian. Although there are 188 new species in the Turonian, compared to the other Upper Cretaceous stages (all over 600) this is a very low figure. Low or relatively low origination levels are usually associated with large numbers of inherited species. This is also the case, however, for some stages where high levels of origination of species occur, particularly in the Upper Cretaceous.

Such consideration of absolute rates of origination of new species are, of course, very strongly influenced by the prevailing diversity level. It is natural, therefore, that the highest absolute numbers of new species occur in the Upper Cretaceous, where diversity levels are overwhelmingly higher than elsewhere in the Mesozoic. For this reason, it is important to also consider the percentage of originations. This is given in Text-fig. 2 and has been discussed above, as has the relationship between originations and extinctions as shown in Text-fig. 3. These two figures indicate that high extinction levels precede major geological boundaries, within the Mesozoic and that these are followed almost immediately by absolute or proportional "highs" in originations. Excellent examples of these phenomena can be seen at the Triassic/Liassic, Jurassic/Cretaceous, Neocomian/Aptian and Lower Cretaceous/Upper Cretaceous boundaries. Similar events took place at the Lower Jurassic/Middle Jurassic boundary, but here there are two peaks and a time lag in originations. The only major post-Triassic Mesozoic boundary not marked by high extinction rates followed by high origination rates is the Middle Jurassic/Upper Jurassic boundary, between the Callovian and Oxfordian stages.

Most of the boundaries preceeded by high extinctions and followed by high originations can be correlated with more or less major global geological events. Among these are:

1) The ending of the generally restricted marine conditions of the Triassic by the transgressions of the Liassic, which, in many places, were initiated in the Rhaetian.

2) The widespread creation of non-marine aquatic environments in the Neocomian in a major global regressive phase, initiated in the late Tithonian.

3) The virtual eradication of Wealden environments in most parts of the globe (except China and Mongolia) by the Aptian transgression.

4) The Cenomanian onset of the Upper Cretaceous transgression, the greatest transgressive event and the attainment of the highest eustatic sea level rises of the Mesozoic.

These four events seem to have a more than coincidental correlation with enhanced evolutionary activity in Mesozoic Ostracoda. It is, however, difficult to explain why evolutionary activity was also high in the Toarcian/Aalenian interval. Indeed it is difficult to explain with certainty how these periods of environmental stability *directly* affected ostracod evolution since, on theoretical grounds, long periods of stability can, by allowing the establishment of climax (or near climax) communities, enhance diversity and therefore be responsible for enhanced rates of evolution by the need of many species to mutually avoid competition among themselves.

The fact that the late Cenomanian anoxic event produced in Ostracoda not an increase but a decrease in extinction and origination rates in the Turonian, does not seem to allow the recognition of similar events elsewhere in the Mesozoic. Everything about the Turonian "event" seems to defy logic.

It is virtually impossible to distinguish in detail the influence of biotic and abiotic factors in the various evolutionary patterns described above. Clearly, biotic factors caused by the interaction of evolving lineages of Ostracoda and other organisms must have exerted an influence as must the changes in the morhology of the carapace of many groups through the Mesozoic. These biotic factors, however, are likely to have produced effects of a more gradualistic nature, and therefore more difficult to detect, than the more abrupt "punctuated" effects associated with global environmental changes.

MESOZOIC OSTRACODA AND EVOLUTIONARY THEORY

The author has shown (Whatley, 1985) that certain lineages of Ostracoda seem to exhibit, all in the same lineage, elements of their evolution which may be described as gradualistic and punctuated equilibrium coupled with virtual stasis.

On the scale at which the present study has been undertaken, stasis would not be detectable. However, the rapid bursts of evolutionary activity immediately before and after the major division boundaries of the Mesozoic seem to imply relatively rapid evolution of the punctuated equilibrium model in a number of lineages. The reduced level of extinction and speciation which separates these events is possibly the product of more gradualistic evolutionary change in the same lineages. The data presented for the various groups in Text-figs. 7 to 9b tends to support this suggestion.

Because of the difficulty in the evolutionary history of any group of distinguishing the effects of biotic and abiotic events and of placing a quantitative value on either, using data as presented here to test models of evolution put forward by the theorists is always problematical. For example, to what extent can the Red Queen hypothesis (Van Valen, 1973) be demonstrated to apply to the present case? The Red Queen hypothesis, in a sense, seeks to explain the Law of Constant Extinction—that the probability of extinction of taxa is constant through time and not related to the antiquity (duration) of taxa. According to the Red Queen model, various taxa within an evolving community maintain their relationships one to another and these relationships evolve to maintain the same level of interaction between taxa, *i.e.* predator and prey etc. This hypothesis predicts that whatever the level of diversity and whatever the degree of enironmental stability, rates of extinction and origination and the progress of phyletic evolution are constant.

The Red Queen hypothesis is currently opposed by the Stationary Model of Stenseth and Maynard-Smith (1984). In this they seek to explain the Law of Constant Extinctions not, as in the case of the Red Queen primarily by the system being driven by a biotic dynamo, but rather by invoking one in which extrinsic factors, geological and climatic etc. provide the impetus. *Reductio ad absurdam*, the Red Queen model would deny that major global geological and palaeoclimatic changes, whether due to terrestrial or extra-terrestrial causes, could substantially affect phyletic evolution and the Stationary Model implies that evolutionary activity will only take place at times of environmental change with stasis in between.

Both extremes are, or course, nonsense. Neither alone is capable of explaining any evolutionary lineage known to the author from his own studies or from published literature. Not all environmental changes leave evidence in the strata and when they do, their nature is always the subject of great controversy. Not all major evolutionary events can be correlated with environmental changes.

The Law of Constant Extinctions is itself highly suspect. In the context of Mesozoic Ostracoda, the probability of extinction of taxa varies widely according to family. Whatley and Stephens (1976, table 4) have clearly shown this to be the case with respect to the Cytheracea. A bythocytherid species enjoys a much lower extinction probability than does a trachyleberid or a progonocytherid. Many more species and genera of the Bythocytheridae and Limnocytheridae, for example, survive the major Mesozoic extinction events than do taxa belonging to the Trachyleberididae, Progonocytheridae, Cytherideidae and Cytheruridae. At times of crisis in evolution more specialized forms are less likely to survive than the "old fashioned" models.

Common sense dictates that the Red Queen and Stationary Models do not and cannot operate in isolation, they are both part and parcel of one phenomenon—evolution. Some may wish to claim that the acceleration of evolutionary activity at major Mesozoic division boundaries, which seems to correlate with major geological events, is a justification of the Stationary Model. Others may claim that the relatively "steady state" evolution seen in the relatively stable Neocomian favours the Red Queen. The author, however, remains convinced of the dual role of biotic and abiotic events in all evolution.

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Homeomorphy, Phylogeny and Natural Classification: Case Studies Involving Palaeozoic Ostracods

ROGER E. SCHALLREUTER
University of Hamburg, F. R. Germany

I

Homeomorphy is particularly common in ostracodes, thus often obscuring true relationships within the group (Triebel 1950; McKenzie, 1982). Homeomorphy in Palaeozoic ostracodes has been recognized and documented only rarely, a fact which has hindered the development of a natural classification and has led to grave taxonomic (and thus geologic) misinterpretations. A basic requirement for the recognition of homeomorphies is a reasonably sound natural system of classification, which has often been lacking in many Palaeozoic ostracod groups. On the other hand, it is impossible to establish a natural system if homeomorphies are not recognized. To emerge from this blind alley one needs a detailed and exact species description and special attention must be paid to generic assignment. Following generic assignment, the interpretation of phylogeny can proceed; phylogeny and natural systematics are inseparably interwoven.

II

As with nearly all other groups of animals and plants, the first classificatory systems applied to Palaeozoic ostracodes were based on (unrecognised) homeomorphs. Most genera were so-called "sack" genera, as in the case of *'Aparchites'* for nonsulcate forms and *'Primitia'* for simple unisulcate species. In the same way, distinctly quadrilobate representatives without an anterodorsal (speral) spine or similar process were placed in *Tetradella,* and those with such a spine or process in *Ceratopsis* (Jaanusson, 1957: 225). *Ctenobolbina* has been a typical sack genus for bisulcate forms having S2+S3 sulci as well as for unisulcate species which did not fit into *Primitia* (Henningsmoen, 1953: 211), and *Beyrichia* was formerly used as a sack genus for trilobate members having S1+S2 sulci. The classificatory system based on lobal and sulcal (L-S) sculptures (which are also often expressed just as well on steinkerns) was established by Ulrich and Bassiler (1923) and later modified by Swartz (1936) and E. A. Schmidt (1941). This system was discredited in the period 1949–1957, mainly by the work of Scandinavian scientists who stressed that features associated with sexual dimorphism reflected a more natural system and should be given priority in systematics. In 1937 Opik had already established different genera on the basis of dimorphic features. Hessland (1949) also recognized differences caused by sexual dimorphism but, trying to adhere to the old system, he still described conspecific dimorphs as different species. It was Henningsmoen (1953) who founded the 'new' system of classification, which was further improved and modified by Jannusson (1957).

Detailed morphological investigations by Schallreuter (since 1964), on extraordinary preserved material gained from glacial erratic boulders of Northern Germany, and phylogenetic studies proposed that any natural systematics must take both the L-S sculptures and dimorphism into consideration. The L-S sculptures are particularly important in classifying lower taxa (genus and family categories), while sexual dimorphism is especially important for higher taxa (family and order categories).

The system built up on this basis is currently widely assumed to be a natural one. It provides many homeomorphies which are 'proof' of a natural system.

III

In principal, all features of the ostracod shell can be possible homeomorphic features. Homeomorphy affects both lobal-sulcal features as well as ornamental (including sexually dimorphic) sculptures, as shown by the following examples.

A well-known example of homeomorphic lobal-sulcal features (L-S sculptures) is quadrilobation, which occurs in many Lower Palaeozoic ostracods. In the example illustrated (Pl. 1, figs. 1, 6) the main difference between the two figured Ordovician species is expressed in their dimorphic adventral sculptures, especially the development of a histium in *Sigmoopsoides*. Modifications in quadrilobation at first led to the distinction of separate genera (for example, *Ceratopsis, Kiesowia*), which soon became sack genera too.

A general phylogenetical trend in Lower Palaeozoic ostracodes is the reduction of quadrilobation, a trend which can apparantly occur in many different lines. Its occurrence in different lines, often simultaneously, implies the existence of homeomorphies. One form of lobal reduction is the dissolution of the lobes into single nodes. Such forms were formerly united in the genus *Kiesowia,* now recognized as a classical example of homeomorphy.

Of the 7 species assigned by Henningsmoen (1953) to *Kiesowia*, only the type-species now remains in the genus. The other species are now assigned to 5 or 6 different genera and subgenera of various families and subfamilies. Two of these species and some similar species are illustrated herein (Pl. 1, figs. 2–5, 7, 8).

Kiesowia is, by its almost perfect homeomorphy, a very good example of how difficult it is to

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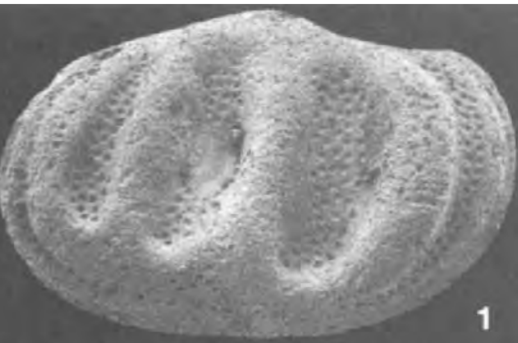
PLATE 1—Fig. 1. *Tetrada memorabilis* (Neckaja, 1953), ♀ left valve (GPIMH 2595), ×70. Backsteinkalk erratic boulder (no. G29) from the beach of the Isle of Gotland (Baltic Sea), S. of Klintehamn. Fig. 2. *Homeokiesowia frigida* (Sarv, 1959), ♀ right valve (GPIMH 2023a), ×60. Backsteinkalk erratic boulder (no. Ho2) of the beach of Klein-Horst, Pomerania. Fig. 3. *Snaidar radians* (Krause, 1892), ♀ right valve (SGWG 33/183), ×25. Backsteinkalk erratic boulder (no. 5B2) from the beach of the Klein-Zicker, Peninsula Mönchgut, Isle of Rügen (Baltic Sea), Pomerania. Fig. 4. *Quadritia* (*Krutatia*) *iunior* Schallreuter, 1981, right valve (GPIMH 2468), ×65. Öjle myrflint erratic boulder (no. G30) from the same locality as in fig. 1. Fig. 5. *Polyceratellal sexpapillosa* (Troedsson, 1918), left valve (GPIMH 2697 = Silcoset cast of: Lunds Univ. Geologiska Institutionen, Avd. f. Historisk geologi och paleontologi LO 2886t), ×65. Brachiopodskiffer (upper Harjuan) of Röstånga, Central Scania. Fig. 6. *Sigmoopsoides sigmoopsoides* (Schallreuter, 1964), ♀ right valve (GPIMH 2984), ×60. Some boulder as in fig. 1. Fig. 7. *Kiesowia (Kiesowia) dissecta* (Krause, 1892), ♀ right valve (GPIMH 2194), ×45. Same boulder as in fig. 4. Fig. 8. *Polyceratella aluverensis* Sarv, 1959, ♀ right valve (GPIMH 2986), ×70. Backsteinkalk erratic boulder (no. G39), locality as in fig. 1. Fig. 9. *Uvonhachtia botulata* g. n. sp. n., holotype, ♀ left valve (GPIMH 3263), ×75. Upper Viruan Hornstein erratic boulder (no. Sy225A) from the Upper Kaolinsand (Lower Pleistocene) near Braderup, Isle of Sylt (N. Sea). Fig. 10. *Pleurodella pentaloculata* (Schallreuter, 1978), ♂ right valve (GPI MH 2004), ×65. Öjlemyrflint erratic boulder (no. 789) from the beach of Visby, Isle of Gotland (Baltic Sea). All figures in lateral view and SEM micrographs (except fig. 3). GPIMH = Geologisch-Paläontologisches Institut und Museum, University of Hamburg; SGWG = Sektion Geologische Wissenschaften, University of Greifswald; Age of Backsteinkalk: Upper Viruan (upper Middle Ordovician); Age of Öjlemyrflint: Upper Harjuan (upper Upper Ordovician).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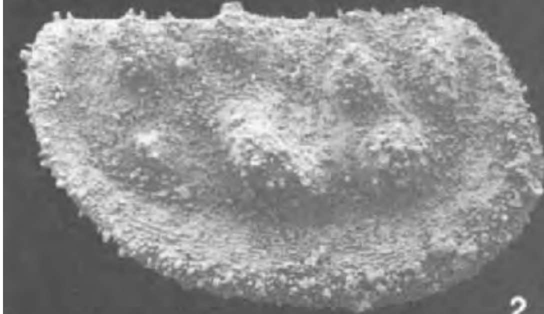
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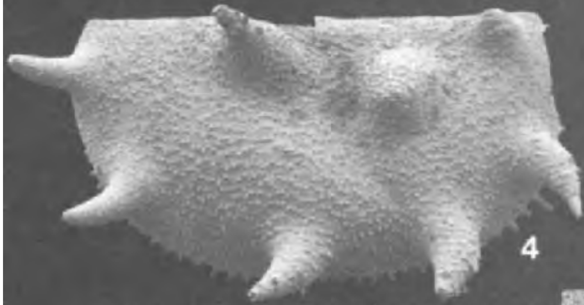
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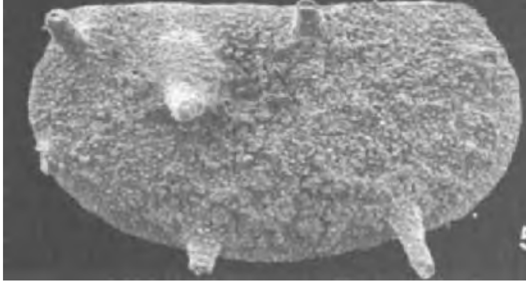
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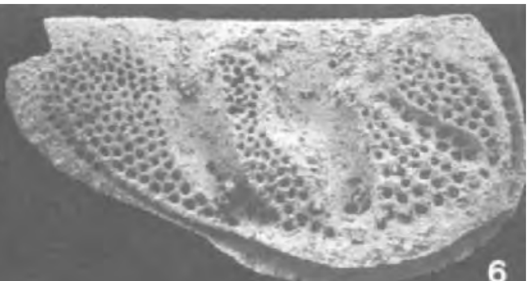
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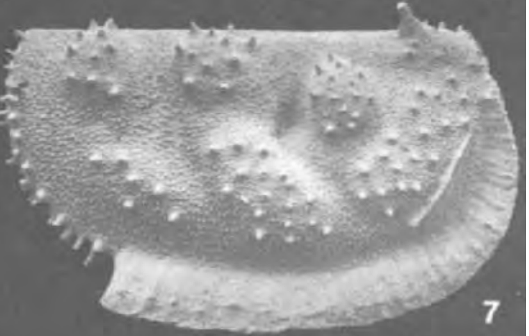
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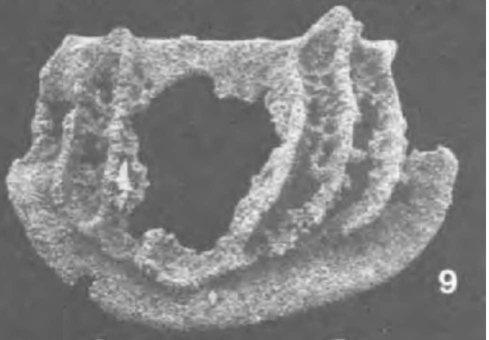
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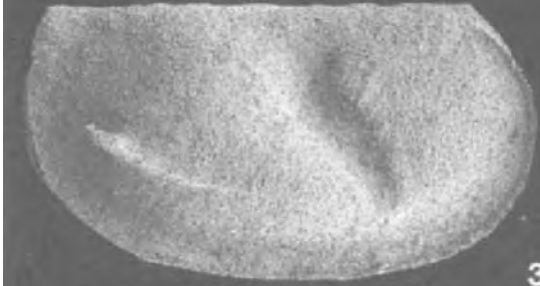

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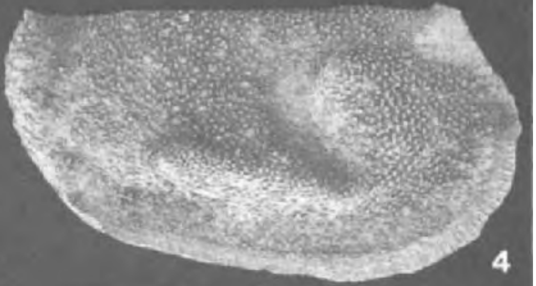

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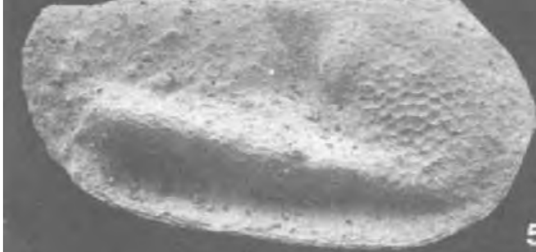

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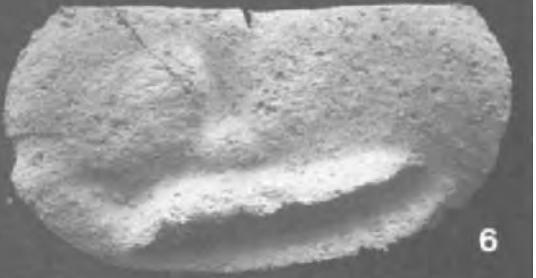

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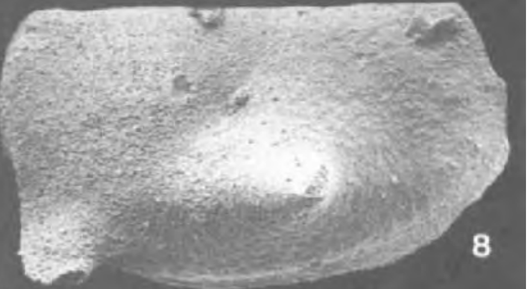

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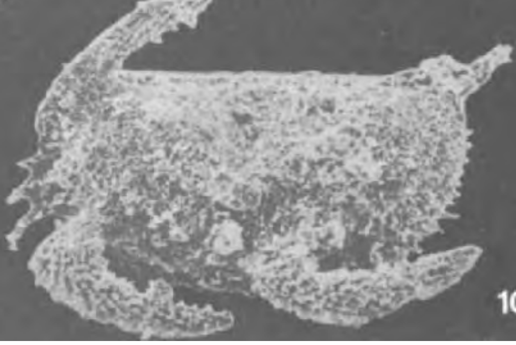

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decide the correct systematic position for some genera. The affiliation of the type-species (*K. dissecta*) to the Sigmoopsinae is demonstrated mainly by its (rudimentary) histium, a feature which is completely developed in the older *Sigmoopsoides* (Pl. 1, figs. 6–7). On the other hand, the rudimentary histium is sometimes missing completely in *Kiesowia* specimens (Schallreuter 1979: Pls. 6, 86, fig. 5) and then there are no principial differences from the homeomorphic *Homeokiesowia* and a generic separation becomes difficult or even impossible.

Another form of reduction of quadrilobation is the lobal dissolution into cristae, which can sometimes copy the pattern of the quadrilobate precursor. This trend has produced homeomorphies such as that shown by the examples illustrated on Pl. 1, figs. 9, 10.

The reduction of the quadrilobation has often led to uni- or nonsulcate forms which may or may not exhibit similarities to their more markedly lobate ancestors. Among such forms there are many potential cases of homeomorphy and also evolutionary convergences.

An excellent example of convergence are the beyrichiomorphs with 'diffuse' cruminal dimorphism. These forms are so similar to primary nonsulcate Aparchitidae that they were, even recently, still placed together (Rozhdestvenskaya, 1972, cf. Jones, 1985: 158).

In examples of homeomorphic unisulcate representatives (Pl. 2, figs. 1–4) the systematic differentiation of separate species is possible on the basis of the nature of the dimorphic adventral sculptures. They are, in part, so similar that some of them were formerly placed in a single genus; for example, *Henningsoenia gunnari* and *Sigmobolbina porchowiensis* were assigned to the genus *Ordovicia* and *Henningsmoenia* (cf. Schallreuter, 1976: 199; 1982: 36).

Equally, the dimorphic adventral sculptures which permitted a 'correct' classification of the examples cited can also be homeomorphic features, as for example in *Severobolbina* (Sigmoopsinae) and *Pentagona* (Perspicillinae) (Pl. 2, figs. 5, 6). In both cases the histial dolon is united anteriorly with the velar dolon and both genera are also similar in being unisulcate. However, differences exist in their marginal sculptures (row of spines in *Severobolbina;* ridge in *Pentagona*) and in their tecnomorphic vela (nearly missing in *Severobolbina;* keel-like ridge in *Pentagona*).

A much better case of homeomorphy affecting the adventral sculptures is the well-known example of locular dimorphism of many lower Palaeozoic ostracodes. Jaanusson and Martinsson (1956) established the subfamily Ctenoloculininae (within the family Hollinidae) for such forms. Bless and Jordan (1971) transferred this subfamily to a family of its own, expanded and modified the family and considered locular dimorphism as its main feature. However, already Henningsmoen (1965: 386) and Schallreuter (1966: 846) had considered that locular dimorphism at this systematic level was a homeomorphic feature. Moreover, Schallreuter (1974) drew the corresponding conclu-

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PLATE 2—Fig. 1. *Henningsmoenia gunnari* (Thorslund, 1948), ♀ right valve (GPIMH 2596), ×65. Backsteinkalk erratic boulder (no. 1B1), beach of the Dornbusch, Isle of Hiddensee (Baltic Sea), Pomerania. Fig. 2. *Sigmobolbina porchowiensis* (Neckaja, 1958), pre-adult ♀ left valve (SGWG 33/115), ×70. Backsteinkalk erratic boulder (no. 1B74), locality as in fig. 1. Fig. 3. *Sigmobolbina eichbaumi* Schallreuter, 1980, tecnomorphic right valve (GPIMH 2278), ×65. Local erratic boulder of Sularp shale (no. Gis29) (Upper Viruan), beach of Gislövshammar, SE-Scania. Fig. 4. *Naevhithis naevus* Schallreuter, 1981, ♀ carapace (GPIMH 2486) from the left side, ×60. Öjlemyrflint erratic boulder (no. Sy106). Locality as in Pl. 1, fig. 9. Fig. 5. *Pentagona joehviensis* (Sarv, 1959), ♀ right valve (GPIMH 2030a), ×90. Same boulder as in Pl. 1, fig. 2. Fig. 6. *Severobolbina elliptica* (Steusloff, 1895), ♀ left valve (GPIMH 2985), ×40. Same boulder as in Pl. 1, fig. 1. Fig. 7. *Eolomatella bicuspidata* Schallreuter, 1981, tecnomorphic left valve (GPIMH 2478), ×80. Upper Viruan Hornstein erratic boulder (no. Sy108), same locality as in Pl. 1, fig. 9. Fig. 8. *Semibolbina ordoviciana* Schallreuter, 1977, tecnomorphic left valve (GPIMH 2644), ×80. Öjlemyrflint erratic boulder (no. G6), beach N of Lickershamn, Isle of Gotland (Baltic Sea). Fig. 9. *Thuringobolbina*? *australis* Reynolds, 1978 (Pl. 2, fig. 2), tecnomorphic left valve (lost), ×70. Devonian of New South Wales, Australia. Fig. 10. *Acinacibolbina anteropinnata* Reynolds, 1978 (Pl. 3, fig. 6b), holotype, tecnomorphic left valve (Australian National University Canberra 36862/1/1), ×60. Locality as in fig. 9.

All figures in lateral view and SEM micrographs (except fig. 2).

sions in the systematics of the family Hollinidae. The genera united by Jaanusson and Martinsson in the Ctenoloculininae were thereby distributed in three subfamilies, each of which contains locular and non-locular (=botulate) dimorphic forms. The basis for distinguishing the three subfamilies is a combination of the L-S sculptures and/or the nature of the tecnomorphic adventral sculptures; the presumed systematics were supported by phylogenetic considerations. Within and between these subfamilies homeomorphies exist not only involving locular dimorphism but also between the respective tecnomorphs and involving the development of two tecnomorpic ventral spurs (Pl. 2, figs. 7–10). The anterior spur is in any case a velar spur, the posterior spur can also either be a velar spur or a posteroventral lobal spine. That it is in one case a velar spur and in the other case a lobal feature is demonstrated in the females: the spur is either incorporated in the dolon, or it lies above the velum [cf. Reynolds, 1978: Pl. 2, figs. 1, 2 (fig. 2=this paper: Pl. 2, fig. 9), Pl. 3, figs. 6b, 7b (fig. 6b=this paper: Pl. 2, fig. 10) or Schallreuter, 1977: Pl. 5, figs. 1, 7 (fig. 7=this paper: Pl. 2, fig. 8) and Lethiers *et al.*, 1985: Pl. 9, figs. 26–29]. For the latter forms (with a spine-like/distinct posteroventral lobe) the subfamily Tetrasacculinae was established. The forms with a velar spur were placed in the subfamilies Hollininae and Triemilomatellinae. In most Tetrasacculinae the velum is developed ventrally (behind the anterior spur) as a keel-like ridge but, as shown by *Thuringobolbina*? *australis*, it could also be developed as a spur (Pl. 2, fig. 9).

Examples of homeomorphies exist not only within the beyrichiocopes but also in the other orders of Palaeozoic ostracodes. For example, after demonstrating that the two stoppegs in the left valve of metacopes (order Podocopa) is a very important and characteristic taxonomic feature, some species which were formerly united in special genera were unmasked as good examples for homeomorphy (Schallreuter, 1979: 26). The two stoppegs are a very characteristic feature within the metacopes but, on the other hand, they themselves could be homeomorphic: they also occur within the leperditiocope family Kiaeriidae Schallreuter, 1984, but in the larger right valve (Copeland, 1974: Pl. 9. fig. 18).

IV

Similar to a children's puzzle in which numbered points must be connected to show a figure, for reconstructions of phylogeny ('evolutionary lines') a certain number of points must be given (basic number) to come to a solution approximating the probable path of evolution. Below the basic number, attaining the real derivation is more or less accidental. The correct sorting of the correct points is in this respect, of course, very important, especially at the beginning and this is dependent to some degree on the 'form feeling' of the palaeontologist. The 'sorting' procedure could be helped by recognising characteristically important features, such as dimorphic adventral sculptures as in the examples mentioned above, or (in the case of the Ordovician metacopes) the two stoppegs. In other groups such features may not be recognized or are maybe not present at all; the deciphering of such sack genera (for example *Bollia* or *Ulrichia*) is therefore especially difficult. In such cases more 'points' are necessary to connect the correct points, i.e. the basis number is higher and more species (than in other groups) must be known. Unfortunately, the relatively featureless forms present special problems and are especially neglected; they tend to be more seldom and less well described than the more 'beautiful' species rich in features. Furthermore, the more featureless ('simpler'), the more danger of homeomorphic trends exists.

V

The examples cited above demonstrate that, on one hand, uncritical hasty, wholesale generic assignment or the aversion to erecting new monotypic genera both hinder the process of achieving scientific 'truth'; pragmatical 'paths' must be 'refused' as unscientific. On the other hand, the over-hasty and uncritical establishment of new genera can sometimes also veil 'real' relationships and other (for example palaeobiogeographic) connections (Schallreuter and Kruta, 1984; Schallreuter, Siveter and Kruta, 1984; Schallreuter and Siveter, 1985). Though time and energy consuming and often viewed as relatively unattractive and unspectacular, careful taxonomy is absolutely essentially to any serious palaeontological work. It is the basis for many further conclusions and the edifice built on these conclusions stands or falls with the quality of the taxonomy.

VI (APPENDIX)

Sometimes in some hollinids an additional spur occurs in the anterocentral region, besides the anteroventral spur (Lethiers *et al.*, 1985: Pl. 9, figs. 25, 29). Such an isolated spur was observed first by Becker (1968) in *Nodella hamata.* Becker called this spur a hamus, considered its occurrence as a special kind of dimorphism (hamal dimorphism) and founded a whole suborder (Nodellocopina) on this kind of dimorphism. The assignment of the nodellids to the Palaeocopa or the Hollininae was considered by Schallreuter (1972: 140; 1976: 234, 235). The evidence cited strengthened the understanding that the hamus and hamal dimorphism is only a special modification or rudimentary form of the well documented hollinomorph antral dimorphism and is in this respect comparable with the perimarginal dimorphism of the Primitiopsacea (Schallreuter, 1979: 735).

Thuringobolbina australis Reynolds, 1978 is very similar to *Semibolbina* (cf. Reynolds, 1978: Pl. 2, fig. 1 and Schallreuter, 1977: Pl. 6, fig. 2). According to Reynolds (1978: 160) *Thuringobolbina australis* possesses a dolonate (botulate) antrum whereas in *Semibolbina* it is locular. Schallreuter (1974) placed *Semibolbina* in the Tetrasacculinae because of its spine-like posteroventral lobe; *Thuringobolbina* was placed within the Hollinini. *T. australis* possesses (like *Semibolbina*) a spine-like posteroventral lobe and belongs, therefore, in the Tetrasacculinae. The holotype of the type-species of *Thuringobolbina*, *T. thuringica,* (Zagora, 1967: Pl. 6, fig. 2) seems not to be (as stated) a female valve, but a tecnomorph (or perhaps male) valve if compared with corresponding figures in Reynolds (1978: Pl. 2, fig. 2). The assumed male of Zagora (*op. cit.* Pl. 6, fig. 2) presumably represents a larval valve. In larvae spine-like sculptures are often more persistent than flange-like sculptures. The dimorphism of *Thuringobolbina* is therefore unknown. The possibility exists that this genus is a junior synonym of *Semibolbina.* The designation of *T. australis* is therefore questionable. A distinct difference between *T. thuringica* and *T.*? *australis* is the development of a second velar spur behind the anteroventral spur in front and ventrally of the posteroventral spine in *T.*? *australis* (Pl. 2, fig. 9).

UVONHACHTIA BOTULATA n. gen., n. sp.

Derivatio nominis.—In honour of Ulrich Von Hacht, Hamburg, collector of the boulder with the holotype (Pl. 1, fig. 9) and alluding to the botulate antrum.

Diagnosis.—Unisulcate. With cristae copying the former quadrilobate design: L1 represented by two, L2 (at least ventrally) by one, L3/4 by three vertical ridges. C1 and C3/4 are united dorsally in cusps. Velum in ♀ antero- and centroventrally as a flange-like dolon forming (with the marginal area) an admarginal-dolonate botulus (antrum).

Relations.—The new genus is characterized by a botulate antrum in combination with its pattern of cristae. *Consonopsis* Schallreuter, 1967 possesses a similar antrum, but has distinct lobes (L2, L3) and fewer cristae (*op. cit.* fig. 4). *Pleurodella* resembles *Uvonhachtia* in lobation and cristation but exhibits locular dimorphism (Schallreuter, 1978).

Occurrence.—Known only from an erratic boulder of the Isle of Sylt, Germany (Age: Keila Stage, D2 of Estonia, Upper Viruan, middle Ordovician).

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DISCUSSION

Adamczak: Your Ordovician podocopids with the duplicature are a peculiar fauna in which this element (the duplicature) is presumably an artefact. I have never seen a Silurian podocope ostracod (and I have seen thousands of them in thin sections) with a duplicature.

The stop-ridge is an element which appears in many genera of podocopids but it has, in some only, a selective value.

Schallreuter: The duplicature in my specimens is *certainly not* an artefact. It occurs in certain species only and in these species in nearly all (adult) specimens (sometimes hundreds of valves). whereas in other sympatric podocopes (metacopes) it does not.

The stop-ridges (stop-pegs) in the Ordovician metacopes are so persistent that I consider that this feature is an important one. I observed it in many genera, for example, *Kroemmelbeinia, Balticella, Steusloffina, Duplicristatia, Bulbosclerites, Pachydomelloides, Longiscula, Trianguloschmidtella, Platyrhomboides, Rectella, Medianella* and others.

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Is *Neckajatia* an Ancestor of the Platycope Ostracodes?

Robert F. Lundin
Arizona State University, Tempe, U.S.A.

ABSTRACT

Neckajatia Schallreuter, 1974 and a closely related genus are known from a complex of at least four species from the Silurian of Gotland, Great Britain (where the related genus has been recorded as species of *Primitia*), Podolia and the eastern Baltic states of the U.S.S.R. The oldest of these species, *N. modesta* Neckaja, 1958, occurs in rocks older than the rocks which yield the oldest true platycopes which are from the upper Llandoverian of Gotland and Estonia. *Neckajatia* and the related genus possess characters which are basic to the definition of the platycope ostracodes, but lack others which are equally fundamental to that definition. The combination of characters, which is a) right-over-left overlap, b) a contact groove along all or most of the free margin of the right valve, c) a relatively long straight hinge with a groove in the right valve hinge, d) poorly-developed straguloid processes, but e) the absence of any well-defined dimorphic characters, suggests *Neckajatia* and related forms are a primitive stock from which the platycopes evolved. It is suggested that this occurred through reduction of the straight hinge, improvement of the contact groove (holoselenic groove) in the right valve and introduction of a distinctive domiciliar dimorphism. Present knowledge indicates that this occurred during the Llandoverian.

INTRODUCTION

Neckajatia Schallreuter, 1974 is based upon *Altha modesta* Neckaja, 1958; designated the latter as the types species for the genus *Altha* Neckaja, 1958, which is a junior homonym of *Altha* Walker, 1862, an insect (Schallreuter, 1974; see also Schallreuter, 1975). Neckaja (1958) also described another species, *Altha lata* Neckaja, 1958, but since that time references to the genus have primarily had to do with stratigraphical occurrences of these species. Pranskevichius (1972) added another species, *A. minima,* to the genus. The genus is well-represented in the Silurian of Gotland and the Welsh Borderland and a study of well-preserved materials from these areas as well as from the Soviet Union demonstrates that *Neckajatia* has characteristics which are basic to the definition of the Platycopa, whereas it lacks other characteristics which are equally fundamental to that definition.

In a classical study of the functional morphology of the shell of platycope ostracodes, Jaanusson (1985) has pointed out that the basic shell characteristics of the platycopes were already well established in the earliest (late Llandoverian) true members of the suborder. Since the early Silurian, only minor changes in the adductor muscle scars and extent of the domatium and details of the arrangement of eggs in it have occurred (Jaanusson, 1985, p. 81, 82). Through his analysis of the modern cytherellid platycope *Cytherella abyssorum* G. O. Sars, Jaanusson explained, from the standpoint of the functional morphology of the carapace, the reasons for the very conservative phylogeny of this group once it came into existence. On the other hand, neither Jaanusson (1985) nor other authors have discussed in detail the ancestors of the platycope ostracodes. It has been generally supposed that the kloedenellacean ostracodes represent the roots of the platycopes (see Guber and Jaanusson, 1964, p. 9; Adamczak, 1966, p. 13; and Schallreuter, 1968, p. 128).

REPOSITORIES

Ostracodes illustrated in this paper are housed in the type collections of the Department of Geology at Arizona State University (ASU X). Sample numbers used in the plate explanations have the prefix "MS" or "RFL".

PURPOSE

In view of the above, the purpose of this paper is to evaluate the morphoiogy of *Neckajatia* and a related genus and compare that morphology to the morphology of the platycope ostracods. This will provide a basis for the conclusion arrived at here, that *Neckajatia* is ancestral to the Platycopa. It is not the purpose of this paper to undertake species level taxonomic revision or even to describe and/or illustrate all species of the genera involved. Accordingly, my observations and conclusions are based upon a few forms which demonstrate the important morphological characters.

THE PLATYCOPA

The platycope ostracodes have the following combination of shell characteristics which are diagnostic for the group:

1) The right valve is larger than the left and overlaps it along all or nearly all of the free margin. The overlap may be reduced anteriorly.

2) The contact structure along the free margin consists of a groove in the right valve into which the edge of the left valve fits. The contact groove may be reduced or even absent anteriorly in some species (Adamczak, 1968, p. 30; Jaanusson, 1985, p. 74).

3) The hinge is also an edge and groove arrangement, the groove being in the right valve into which the edge of the left valve hinge fits. The detailed morphology of the hinge is somewhat variable but the hinge groove of the right valve is, in all cases, to a greater or lesser degree a con-

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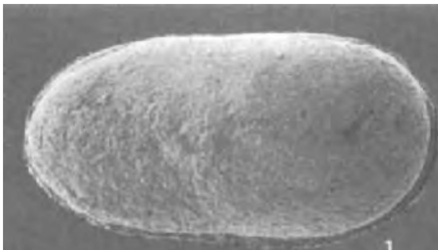
PLATE 1—Figs. 1–3, 5, 6, 9. *Neckajatia modesta* (Neckaja). 1, 2, 9. Right lateral (×71), ventral (×78) and slightly oblique dorsal (anterior two-thirds of specimen, ×126) views of adult carapace (ASU X-73): note R/L overlap and anterior straguloid process (fig. 9). 3. Dorsal view (×83) of adult carapace (ASU X-74). 5. Interior view (×92) of adult left valve (ASU X-75). 6. Interior view (×83) of adult right valve (ASU X-76) to show contact groove and straight hinge. All specimens from the Silurian at Nyhamn, Gotland (MS 17). Figs. 4, 7. *Neckajatia lata* (Neckaja). Dorsal (×56, ASU X-77) and right lateral (×68, ASU X-78) views of adult carapaces from the Silurian (early Wenlockian, Jaani Stage) of Estonia: note R/L overlap and anterior and posterior straguloid processes. Fig. 8. *"Primitia" variolata* Jones and Holl. Ventral view (×72) of adult carapace (ASU X-81) from the Silurian Much Wenlock Ls. Fm. at Lincoln Hill (RFL #13), Welsh Borderland, showing R/L overlap (anterior end abraded). Figs. 10, 11. *Neckajatia* cf. *N. lata* (Neckaja). Interior views of parts of adult left (×123, ASU X-79) and right (×132, ASU X-80) valves from the Silurian Mulde Beds at Däpps, Gotland (RFL 1970) to show hinge details.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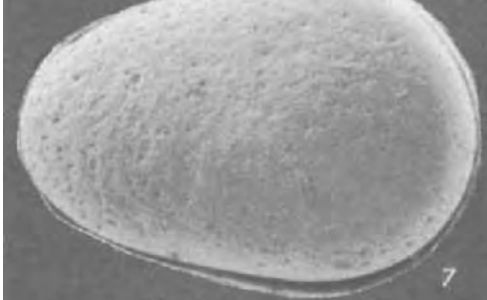
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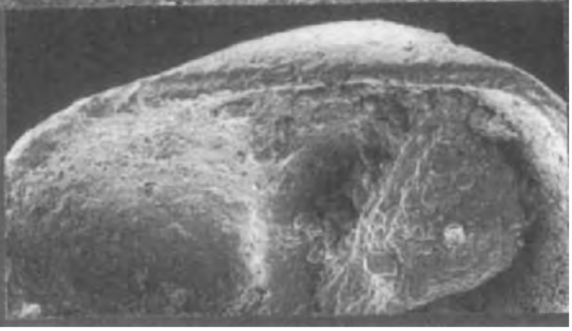
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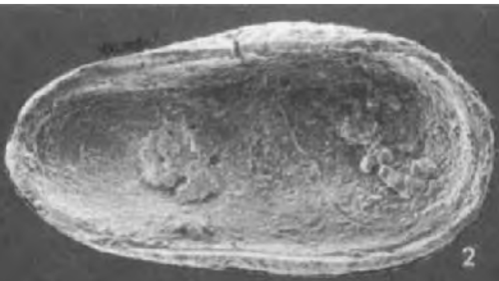

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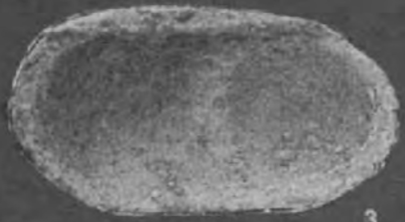

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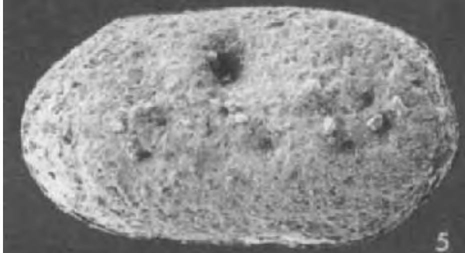

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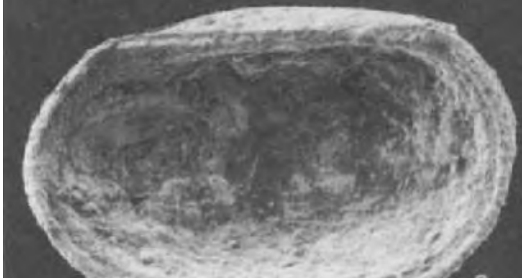

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tinuation of the contact groove of the free margin. Accordingly, in its fullest development, the contact relationship of the platycope valves is described as a holoselenic contact (Pokorny, 1957).

4) Domatial dimorphism (Jaanusson, 1985, p. 80) in which a portion of the posterior part of the carapace forms a chamber for egg care. The extent and shape of the domatium and precise arrangement and number of eggs placed in it is variable, but it is bounded anteriorly by a ridge, the limen (Adamczak, 1966), which is variably developed but distinct in all platycopes.

Some representatives of the platycope ostracods have an anterior straguloid process (Guber and Jaanusson, 1964, p. 3). This feature is variably developed on platycopes and is absent from many of them (*e.g.*, some species of *Cavellina*). I do not consider it to be an important diagnostic character, but it appears to be reduced in those species in which the holoselenic contact condition is well-developed. In such forms longitudinal movement (slippage) of the valves is minimized and an anterior straguloid process serves no purpose in this regard. It is also possible that development of straguloid processes is related to, or partly controls, the degree to which the valves can be opened. In this way, development of the straguloid processes may be related to the position of posterior termination of the intervalvar band (see Jaanusson, 1985). In any case, straguloid processes are not consistently developed in Paleozoic platycopes.

The changes in the adductor muscle scars of the platycope ostracodes has been discussed at length (*e.g.*, Gramm, 1985 and elsewhere; Jaanusson, 1985). Adamczak (1966) has shown that the early platycopes had an oval adductor muscle field with many scars. His illustrations of *Nyhamnella musculimonstrans,* which is a platycope (Sarv, 1977), show that the scars have no special regular arrangement as has been reported by Gramm (1985) for younger cavellinids. The adductor muscle scar of *Nyhamnella* can be considered the primitive condition for platycopes. In any case, the adductor muscle scar pattern is not significant to the issue discussed here because it is not known for *Neckajatia.*

In summary, the characteristics indicated above (numbers 1–4) are the important diagnostic characteristics of the platycope ostracodes. All of these seem to be stable characteristics which have remained essentially unchanged, except for some details, since the late Llandoverian.

THE GENUS *Neckajatia*

Neckajatia modesta, N. lata, N. cf. *N. lata* and *"Primitia" variolata* Jones and Holl, 1865, are four forms which demonstrate the platycope-like morphology of this group. The former is the type species of *Neckajatia* and the latter should be placed in a new genus because it is distinctly unisulcate. There is, however, no doubt about the close relationship between *N. lata, N.* cf. *N. lata,* and *"P." variolata.* In all regards, except for the distinct adductorial sulcus in *"P." variolata* (Pl. 2, figs. 5, 7), these forms are similar. Furthermore, some specimens of *N. lata* and *N.* cf. *N. lata* (Pl. 2, figs. 6, 8) have an incipient adductorial sulcus.

With regard to those characters discussed above which are considered important diagnostic characters for the platycope ostracodes, the following can be stated for *Neckajatia* and the related genus:

PLATE 2—Figs. 1, 2, 4, 6, 8, 10. *Neckjatia* cf. *N. lata* (Neckaja). 1, 8. Interior (×66) and exterior lateral (×77) views of adult right valve (ASU X-80). 2. Interior (×72) view of elongate adult right valve (ASU X-83). 4, 6. Interior (×77) and exterior lateral (×69) views of adult left valve (ASU X-79). 10. Interior (×72) view of adult right valve (ASU X-82). All specimens from the Silurian Mulde Beds at Däpps, Gotland (RFL 1970). Figs. 3, 5, 7, 9. *"Primitia" variolata* Jones and Holl. 3, 5. Interior (×66) and exterior lateral (×74) views of adult left valve (ASU X-84). 7, 9. Exterior lateral (×73) and interior (×82) views of adult right valve (ASU X-85). Both specimens from the Silurian Much Wenlock Ls. Fm. at Lincoln Hill (RFL #13), Welsh Borderland.

1) The right valve is larger than the left and overlaps it along all of the free margin. This is clearly indicated for *N. modesta* (Pl. 1, figs. 1, 2, 9), for *N. lata* (Pl. 1, figs. 4, 7), *N.* cf. *N. lata,* (Pl. 2, figs. 1, 2, 10), and for *"Primitia" variolata* (Pl. 1, fig. 8; Pl. 2, fig. 9).

2) The contact structures of the free margin consist of a contact groove in the right valve into into which the edge of the left valve fits. This is illustrated for *N. modesta* (Pl. 1, figs. 5, 6), *N.* cf *N. lata* (Pl. 2, figs. 1, 2, 4) and *"P" variolata* (Pl. 2, figs. 3, 9).

3) The hinge is generally not well-preserved. The shell of *N. modesta* is relatively thin and, accordingly, fragile. Therefore, the hinge (and free edge) is commonly abraded and details of the hingement which may have been present are not observable. Nevertheless, it is a long straight hinge (Pl. 1, fig. 6). The nature of the hinge is rather well-shown for *N. lata* (Pl. 1, figs. 10, 11) and *"P." variolata* (Pl. 2, figs. 3, 9). The hinge is straight, relatively long, and consists of an edge (left valve) and groove (right valve) which is a continuation of the contact groove along the free margin (Pl. 2, figs. 1, 2).

4) The species studied here show no evidence of domatial dimorphism. Although Neckaja (1958) observed two forms with different height/length ratios among her specimens of *N. lata* for which she suggested sexual dimorphism as a possible explanation, no specimens of any species of *Neckajatia* or the related genus have a limen. *N.* cf. *N. lata* shows the same variation in the development of the posterodorsal portion of the carapace as Neckaja observed for *N. lata.* Neither elongate (Pl. 2, fig. 2) nor foreshortened (Pl. 2, fig. 1) specimens have a limen. Furthermore, I have seen no evidence of bimodality in the shape of adults of *N.* cf. *N. lata.* If the variation is sex-significant, the expression of it in the shell is subtle or absent and dimorphism is of the *Cyprideis*-type (Jaanusson, 1985, p. 80).

DISCUSSION

Similarities.—The species studied here are like typical platycope ostracodes in the following respects:

1) Contact margin structures. The contact groove in the right valve of *N. modesta* (Pl. 1, fig. 6) is reduced along the anterior margin just as indicated for some modern species of *Cytherella* (Jaanusson, 1985, p. 74). In all other regards, the contact margin structures are virtually identical to those of typical platycopes.

2) Valve relationships. *Neckajatia* and *"Primitia" variolata* exhibit right-over-left overlap, just as is the case with all Paleozoic platycopes (I include here only those forms which have domatial dimorphism and exclude forms which exhibit *Cyprideis*-type, or kloedenellid, dimorphism). Numerous authors (*e.g.*, Sohn, 1983) have reported reversal of overlap in species of *Sansabella* Roundy, 1926 and, therefore, discount the significance of the direction of overlap. *Sansabella is* not a platycope ostracod and therefore is not significant to the issue. Until evidence is presented for common variation in direction of overlap among ostracods having platycope-like contact margin structures and domatial dimorphism, I will consider the right-over-left overlap, in combination with the other characters discussed here, to be taxonomically important for the platycopes. I conclude that direction of overlap is strongly controlled by genetics and that it is a very stable character for the platycopes even though it may not be a stable character in some other groups.

3) The hinge. Although there are differences between the hinges of typical platycopes and the hinges of the species studied here (see below), the basic structure of the hinges is the same. Both groups have an edge (left valve) and groove (right valve) arrangement of the hinge and the hinge groove is connected to the contact margin groove, at least at its posterior end (Pl. 2, figs. 1, 2). Furthermore, some specimens of *N.* cf. *N. lata* and *"P." variolata* show evidence of a reduction in

in development of the inner hinge (contact) ridge near the anterior end of the hinge (Pl. 1, fig. 11; Pl. 2, fig. 9). Although the evidence isn't overwhelming, this condition seems to be like that reported by Jaanusson (1985, p. 77, fig. 1) for *Cytherella abyssorum* and by Adamczak (1966, figs. 1, 2) for *Nyhamnella musculimonstrans* and *Gotlandella martinssoni.*,

4) Straguloid processes. *N. modesta* (Pl. 1, figs. 3, 9) and *N. lata* (Pl. 1, fig. 4) have anterior and posterior straguloid processes the former of which is less-well developed than that on *Nyhamnella musculimonstrans* Adamczak, 1966, the earliest known true platycope. Nevertheless, the morphology of the anterior straguloid process of *Neckajatia modesta* and *N. lata,* except for size, is virtually identical to that of *Nyhamnella musculimonstrans.* Furthermore, on the species studied here in which the contact groove is well-developed (*Neckajatia* cf. *lata* and *"P." variolata*), straguloid processes are absent. In short, although I place no great taxonomic value on the presence of straguloid processes, in those species of *Neckajatia* which have them, they are similar to those of the earliest platycopes.

Differences.—The primary differences between the species studied here and true platycope ostracods involves the following characters which are considered significant to the definition of the Platycopa:

1) The hinge. Similarities in the hinges of *Neckajatia, "P." variolata* and the platycopes have been pointed out above. The primary difference is that in *Neckajatia* and *"P." variolata* the hinge is relatively long (compared to the length of the carapace), straight and parallel to the longitudinal axis of the valve. In the early true platycopes, the entire hinge structure (Adamczak, 1966) is arched, but the hinge proper is straight, short and may be inclined to the longitudinal axis of the valve. The orientation of the hinge relative to the longitudinal axis of the valve apparently is not very important because it is quite different in males and females of the same species (see Adamczak, 1966, Pl. 1, figs. 1, 2; Pl. 3, figs. 1, 2). In short, the hinge structure of *Nyhamnella, Gotlandella* and many other Silurian platycopes (see Sarv, 1977) is differentiated into a short, straight posterior part (the hinge proper) and an anterior part, the two of which together form a curved (arched) line along which the valves articulate. No such differentiation can be seen in *Neckajatia* and *"P." variolata.*

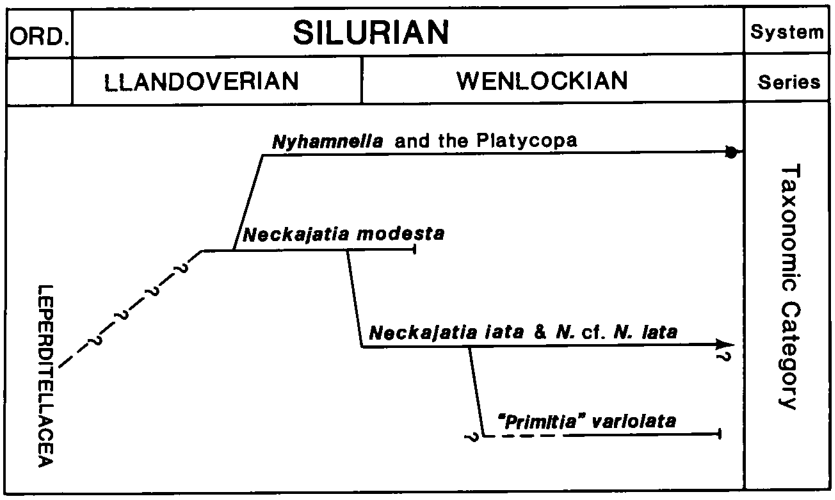
2) Dimorphism. As indicated above, there is no evidence in either *Neckajatia* or *"P." variolata* for domatial dimorphism, a characteristic which is diagnostic for platycopes. I have seen no evidence of a limen in any specimens of either *Neckajatia* or *"P." variolata.* If these forms are dimorphic, the dimorphism is very subtle and could be of the *Cyprideis*-type only.

CONCLUSIONS

Because of the similarities of *Neckajatia* and the true platycope ostracodes, I conclude that the former is an ancestor of the latter. *Neckajatia modesta* is more platycope-like in general appearance than *N. lata, N.* cf. *N. lata* or *"P." variolata.* Therefore, of those species of *Neckajatia* presently known, *N. modesta* is the most likely immediate ancestor of the platycopes. Considering the present state of knowledge, I propose a phylogeny like the one shown in Text-fig. 1.

Text-figure 1 implies that the earliest true platycope (*Nyhamnella musculimonstrans*) was derived from *Neckajatia modesta.* The changes which took place, according to this hypothesis, are as follows:

1) The hinge proper (the straight portion) was shortened (relative to valve length) through posteriorward extension of the anterior portion of the contact margin structures. In this case, there was also an associated elaboration and strengthening of the straguloid processes, especially the anterior one.



TEXT-FIG. 1—Proposed ancestor-descendant relationships among the Leperditellacea, *Neckajatia*, *"Primitia" variolata*, *Nyhamnella* and other platycope ostracodes. The *"Nyhamnella* and the Platycopa" branch is generalized. Phyletic transition is not intended for all Silurian platycopes. Jones and Holl (1865) described *"P." variolata* from the Woolhope Limestone near Malvern, England. This occurrence is stratigraphically lower than for any of my collections, and needs to be checked. The dashed line and question mark indicates the uncertainty of the lower limits of the range of this species. *N.* cf. *N. lata* is presently known from only one locality in the Mulde Beds of Gotland. Accordingly, the limits of the range of this form are not firmly established, but it is clear that *N. lata* ranges lower than *N.* cf. *N. lata.*

2) Introduction of domatial dimorphism through the development, in the female, of a posterior chamber for egg care, bounded anteriorly by a limen.

Present evidence indicates that these changes occurred in late Llandoverian time. Jaanusson (1985) has emphasized that once the changes occurred, the combination of characters became stable and only minor changes have occurred since the Silurian.

Finally, it is interesting, under this hypothesis, to speculate about the Ordovician ancestors of *Neckajatia.* The morphology of *N. modesta* suggests that it was derived from a morphologically rather generalized group of ostracods with a relatively long, straight hinge. The Leperditellacea qualify in this regard. Indeed the *Neckajatia* species studied here, as well as *"P." variolata*, are reminiscent of the Ordovician *Milleratia* and *Schmidtella* (Adamczak, pers. commun., 1985). On the other hand, Schallreuter (pers. commun., 1985) has suggested that *Karinutatia* Schallreuter, 1978, a monotiopleurid, could be ancestral to *Neckajatia.* Although the hinge of *Karinutatia* is long and straight and similar to that of *Neckajatia, Karinutatia* seems to have left-overright overlap (not entirely certain from Schallreuter's 1978 material) and is distinctly dimorphic. I favor an interpretation which derives *Neckajatia* and the platycope ostracodes from a morphologically more generalized group than is represented by the monotiopleurids.

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DISCUSSION

Sohn: Are the pits on *Neckajatia lata* artifacts or real? If real, they suggest that *Nakajatia* may not be related to Carboniferous to Recent Platycopida.

Reversal of overlap is common in upper Paleozoic and younger ostracodes in several stocks (*Sansabella*).

Lundin: The pits on *Neckajatia lata* are real. I would not place any major taxonomic value on that characteristic because pits are absent from *N. modesta.*

My experience with other groups of ostracodes indicates that direction of overlap is strongly controlled by genetics. It is not common for reversal of overlap to occur and where it does it seems to be a genetic accident within a species. If you know of platycopes in which direction of overlap seems to be commonly variable then we must change our diagnosis of the group. In that case, domatial dimorphism, the contact margin features and the hinge are the only characters which distinguish this group. For additional comment see the section of text entitled "Discussion".

Neale: I can add something to this question of valve overlap in the Platycopa with respect to the higher deposits in the Mesozoic. Here valve reversal has been shown to occur on occasion in the Cretaceous of the Middle East. I would certainly not regard valve reversal in this instance as being of more than specific significance. Anderson recorded a similar concluson on the significance of valve reversal in the genus *Cypridea* although these are, of course, members of a very different group.

Lundin: It seems clear that the entire topic of reversal of overlap needs additional study. It is equally clear that the vast majority of kloedenellaceans (forms with *Cyprideis*–type dimorphism) have left-over-right overlap and the vast majority of Paleozoic cytherellaceans (forms with domatial dimorphism) have right-over-left overlap. For the present I must consider this to be a significant characteristic for higher level taxonomy.

Adamczak: The genus *Neckajatia,* it seems to me, has some relation with *Schmidtella* and *Milleratia* in which (in the Ordovician) the left or the right valve is the longer and the interior of the valves very much resembles the *Neckajatia,* which is a Leperditellid ostracod.

Lundin: For my reply see the section of text entitled "Conclusions".

Schallreuter: Which taxon is the ancestor of *Neckajatia*?

Lundin: I do not know the answer to that question, but judging from comments just made by Dr. Adamczak, certain leperditellacean genera may qualify. The other obvious option would be to look toward the monotiopleurids for an ancestor. For additional comment see the section of text entitled "Conclusions".

XI
Biostratigraphy and Exploration

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Some Quaternary Ostracods of the Pannonian Basin with a review of a few neglectoida

NADEŽDA KRSTIĆ
Geoinstitut, Beograd, Yugoslavia

The Pannonian basin is more or less filled by Quaternary sediments. On the whole, this is a permanently subsiding basin, but its different parts sink differently through time. Therefore, the thickness of the Quaternary varies from 50–200 m. In some parts, the basin part of the succession may be absent; sometimes it is the Lower Pleistocene and often the lower part of the Upper Pleistocene.

This big basin is filled by fluviatile, lacustrine, marsh and aeolian sediments, arranged in 6 cycles, every cycle consisting of all or the first three sedimentary types. The coarse grained fluviatile sediments are slowly replaced upwards by sandy-silty, often finely-bedded, lacustrine deposits. Filled-in lakes become marshes in which, and beside which, aeolian silt (loess) is deposited at the end of an ideal cycle. In the Pannonian basin, the Upper Pleistocene loess is preserved. Older loess may be eroded (if deposited?) as is the case with the youngest one in many places.

The ostracods of the Pannonian Quaternary have not yet been studied in detail. Kollmann (1960) described the first fossil occurrences and there are articles by Szeles (1968) and Gagić (1968–1972). Gagić also determined ostracods for some sheets of the geological map of Yugoslavia (1973–1984), as well as Šikić (1980–1984). Sokač published a number of papers (1971–1978) and a single palaeontological monograph (1978) for this region. In addition, there are a few articles by the author (Krstić, 1981–1985) on this topic.

Among ostracods which are of stratigraphical importance in the Quaternary are *Scottia*, some *Candona* from the *neglecta* group and *Virgatocypris*. *Ilyocypris* species also seem to have stratigraphical value. Unfortunately, the occurrences of the *Ilyocypris* species are not continuous. Different species replace one an other through space and time. This is the reason that one still cannot define the key-species in the genus *Ilyocypris*. In the following text not only the ostracods of the Pannonian Quaternary, but also their environment and other geological conditions will be discussed.

The *Pliocene-Pleistocene boundary* is still under discussion (IGCP project no. 41). In the Pannonian basin it was drawn above the last ornamented viviparids and unionids, and is now placed a little below the disappearance of the ornamented unionids (but still above the ornamented viviparids). For the Lower Pleistocene, key-molluscs are the smooth *Viviparus boeckhi*, and *Bithynia crassitesta*, most numerous in the sequence where *Potomida sturi*, *Hyriopsis fuchsi* and other ornamented unionids are still present.

Most of the ostracods cross the Pliocene-Pleistocene boundary unchanged, like *Scottia browniana*, *S. tumida*, and many other still living species (see Table 1). It is not clear if the coarsely reticulate *Ilyocypris caspiensis* remains unchanged from the uppermost Pliocene to the Middle Pleistocene because of its rarity (it is also not clear whether the slender Pliocene form should be regarded as the male of this species or a different species).

In the Pliocene there are other species apparently different from those in the Pleistocene. They are not yet described and include a *Candona* from the *neglecta* group, a triangulate *Cypria*, some

Table 1

	OSTRACODS OF THREE BOREHOLES (150–200 m deep)	PLEISTOCENE												PLIOCENE				
		MIDDLE			LOWER									UPPER				
		single cycle			upper cycle			middle cycle			lower cycle			ultim. cycle		penultimate cycle		
		10	11	1	10	11	1	10	11	1	10	11	1	10	1	10	1	1
Recent species	*Eucypris pigra*							+										
	Metacypris crodata			+														
	Eucandona lewanderi							+										
	Candonopsis kingsleii			+													+	
	Candona candida			+				+				+						
	Candona weltneri					+					+	+						
	Cyclocypris laevis	+	+	+		+		+			+	+						
	Pseudocandona compressa	/+/		+		+		+		+	+	+		/+/		+	+	
	Ilyocypris monstrifica					+				+			+					
	Cyclocypris ovum									+								
	Cypris ophthalamica		+	+		+					/+/							
	Fabaefromiscandona fabaeformis		/+/	+		+		/+/			/+/						/+/	
	Hungarocypris madaraszi			+		+						+						
	Fabaeformiscandona protzi			+		+												
	Cyrpidopsis vidua			+						+		+				+		
	Cyclocypris serena		+			+			+		+							
	Pseudocandona marchica		+	+	+	+		+		+	+	+			+	+	+	
	Cyclocypris cf. *ovum*	+		+				+										
	Paracandona euplectella		+															
	Ilyocypris gibba			+														
	Paralimnocythere compressa		+	+		+		+				+						
	Slerrocypris? *clavata*			+		+			+								?	
	Cypris pubera		/+/	+						+	+	+					+	
	Cyprois marginata		+								/?/							
	Cyclocypris globosa		+			+					+	+						
	Eucandona balatonica			+		+					+							
	Stanchevia crassa							+										
Pleistocene	*Ilyocypris* aff. *bradyi*		+	+		+		+		+		+	+					
	Herpetocypris indet.			+		+		+		+	/+/							
	Scottia browniana	+	+	+		+				+			+		+			+
	*Candona permanenta**		+	+						+	+				?		?	
	*Ilyocypris sokaŏi**		+	+		+					+							
	Scottia tumida					+				+					+			
	Ilyocypris salebr. salebrosa		+															
	Virgatocypris cf. *elongata*			+							/+/							
	Cyclocypris taubachensis			+														
	Ilyocypris caspiensis			+														?
	Limnocythere aff. *inopinata*										+	+						
	Ilyocypris biplicata			+														
	*Candona banatica**					+				+								
	Limnocythere aff. *stationis*									+		+						
	Candona cf. *montenegrina*					+				+		+	+					
	*Ilyocypris inermis minuta**					+												
	Cyclocypris diebeli							+										

(Continued)

TABLE 1—*Continued.*

		10	11	1	10	11	1	10	11	1	10	11	1	10	1	10	1	1
Pleistocene	*Cyprinotus magnus**							+										
	Ilyocypris aff. *biplicata*/ n.sp./								+						+	+	+	
	Ilyocypris n.sp. /cylindrical/								+									
	Cyprinotus n. sp. /smooth/									+	+	+						+
	Cypridoptis aff. *newtoni*										+							
	Cypris sp. /tuberculate species/												+					
	Typholocypris sp.												+					
Pliocene	*Ilyocypris* gr. *decipiens*															+	+	
	Pseudocandona aff. *crispata*																+	
	Candona sp. /high neglectoid/																+	
	Ilyocypris gr. *gibba* /small/																+	
	Eucypris cf. *famosa*																+	
	Cypridopsis aff. *vid''a*																+	
	Cypria sp. /triangulate species/																+	
	Ilyocypris gr. *bradyi* /small/																	+

* New species and subspecies described from this region (Krstić, 1985).

Ilyocypris from the *gibba* group and *bradyi* group etc. It is not possible to establish for certain which species appear at the Pliocene-Pleistocene boundary. In Table 1 only three boreholes are shown (BT-10, Ž-11 and JT-1), in which ostracods were carefully studied and other evidence was also complete. Two of them reached the Pliocene (depth of boreholes is 150 m.), while the third one (with a depth of 200 m) did not.

Three main sedimentary cycles belong to the *Lower Pleistocene s.l.* (*Boeckhi* Beds). According to the climatic theory, they should be Biber-Danube (Tiglian?) and Danube, Danube-Günz (Waalian?) and Günz, and Günz-Mindel (Cromerian?) and Mindel in age. Apart from *Viviparus boeckhi* and *Bithynia crassi testa,* which are present mostly in the lower part of the Lower Pleistocene, there are micromammals-*Arvicola greeni* (Upper Biharium) and *Microtus* gr. *arvalis-agrestis* (uppermost Upper Biharium-Upponium to early Oldenburgium) showing affinities to Mindel. The different thicknesses of the same cycles in different boreholes depends on the tectonics-slow or fast sinking or even uplift(?) as well.

In the ostracod associations there are plenty of species which are still living as well as extinct ones. At present it is not possible to name key ostracods. A possible key-species could be *Ilyocypris malezi* (Sokač, 1978, determined as Middle Pleistocene in a few cycles, some of which should be Lower Pleistocene in age), and some other *Ilyocypris* species from the *bradyi* group. *Cyprinotus magnus* (Krstić, in press) has been found in the Waalian?–Günz. The genus *Cyprinotus* is not common in the Quaternary of the Pannonian basin, but there are more *Cyprinotus* in the rheophile environment of the lower cycle (Tiglian?-Danube) with its warmer climate. The first records of *Ilyocypris sokači* and *Virgatocypris* are from the lower cycle of Lower Pleistocene. *Virgatocypris* is a Tertiary relic (known from the Middle Miocene).

The whole association from the three bore holes is given in Table 1. Here the change between rheophile and stagnophile species through a single sedimentary cycle should be noted. In the lowermost part of every cycle, where *Lithoglyphus* and similar molluscs representative of a high-energy environment (coarse sand, sometimes with pebbles) are present, there are no ostracods. Just above it, in the moderate energy environment (medium to fine-grained sand), *Scottia browniana* is most numerous, and sometimes forms a monospecific assemblage. Towards the top of the ideal cycle, *Scottia* is slowly replaced by other ostracods, mostly *Candona, Pseudocandona, Cyclocypris* (mainly *C. laevis*), *Ilyocypris* and others indicating a lacustrine environment. This pic-

TABLE 2

ENVI-RON-MENT	Ostracods of the MIDDLE PLEISTOCENE in SE of Pannonian basin	NE Bačka			NW Banat			NE Banat			Middle Banat			Srem		
		SF	Sl	S	SF	Sl	S	SF	Sl	S	SF	Sl	S	SF	Sl	S
	Mixtacandona transleithanica						•									
	Typhlocypris cf. *szöcsi*					○	•								○	
	Candona aff. *breuili*						•									•
A	*Typhlocypris* cf. *hvarnensis*														•	
	Mixtacandona botosaneanui						•			•						
	Typhlocypris cf. *eremita*		•		•	•					•			•		•
	Pseudocandona cf. *profundicola*						•									
Q	*Potamocypris zschokkei*										•			○	•	
	Cypridopsis subterranea germanica										•					
	Scottia browniana	○			●			●			●			○		
F	*Ilyocypris salebrosa*				•			•						•		
	Eucypris pigra		●	•		●	○			○		•		○	○	
	Cytherissa lacustris				•				•			●			○	
	Metacypris cordata			•								•			●	
	Scottia tumida				○	●	•	•								
	Eucandona levanderi				○	●	●	○	●	○		●				●
	Cyclocypris taubachensis			•			○	○	○			○	•			
Sl	*Candona permanenta*				●	○		●	●	●	●	●	●		●	
	Ilyocypris decipiens baczkae				●	●	●	•	○	○		●	○			
	Candona banatica				○		○	•		●		●	●			
	Limnocythere aff. *inopinata*			•		○	○	○	○	○		○	○	○	•	
	Candona cf. *wegelini*						•									
	Ilyocypris inermis minuta									○		○	○			
	Candona candida		○	●	○	○	●	●		●		●	●			●
	Cyclocypris laevis		●	●	●	●	●	●	○	●		●	●		●	●
	Candona weltneri obtusa		•			○	•									
	Ilyocypris biplicata									•		●	●			•
	Candona cf. *neglecta*		○	○	●	●	○	●		●		●	●		●	●
	Pseudocandona cf. *crispata*					•						•			●	
	Candona cf. *candida*					•	•					•				
	Ilyocypris monstrifica				○	○	•	•		○		○	○		○	●
	Candona cf. *paionica*									●		●	○	○	○	
	Ilyocypris sokači				●	○	●	•		●		○	○			
	Cyclocypris cf. *serena*	○	•	•	○	●	●			○		○	○			
	Candona rawsoni			•												
	Pseudocandona compressa	●	○	●	○	●	●	●		●		●	●		○	○
	Candona ložeki			○												
S	*Ilyocypris* aff. *bradyi* /div./			●		○	○	•	○	●		○	○	●	●	
	Notodromas monacha												•			
	Virgatocypris cf. *elongata*			•			○			•		○	○			
	Fabaeformiscandona fabaeformis		•	•			○			●		○	○		○	○
	Cypira ophthalamica		•	•			•	○		○		○	○		○	
	Candona cf. *montenegrina*		○	○			○	○		○				○	○	○
	Candona lobipes						○									
	Limnocythere aff. *stationis*						•								•	•
	Pseudocandona cf. *insculpta*		•												○	
	Cyclocypris ovum				○	●	●									
	Fabaeformiscandona protzi			•			•					○	•	•		
	Limnocythere cf. *baltica*											•				
	Candonopsis kingsleii														○	

(Continued)

TABLE 2—*Continued.*

ENVI-RON-MENT	Ostracods of the MIDDLE PLEISTOCENE in SE of Pannonian basin	NE Bačka			NW Banat			NE Banat			Middle Banat			Srem		
		SF	Sl	S	SF	Sl	S	SF	Sl	S	SF	Sl	S	SF	Sl	S
	Darwinula stevensoni				•		•					•				
	Ilyocypris aff. *gibba*									○		•	•			
	Herpetocypris reptans			•?			•			•?		○?		•?		○
	Candona weltneri			○				●		○		○	●		●	○
S	*Cyclocypris* cf. *ovum*		○	●		○	○		○	○		○	○			○
	Fabaeformiscandona hyalina											○				
	Hungarocypris madaraszi			•											○	
	Cypridopsis vidua									•		○				•
	Pseudocandona marchica			○	●	○	○	•		●		○	●		●	○
	Paracandona euplectella			•			○			○		○	○			
	Pseudocandona albicans			•								○			○	○
	Ilyocypris gibba				●		●			○		○	○		○	●
	Physocypria cf. *kraepelini*				●		●									
P	*Cyprinotus bulgaricus*														○	
	Paralimnocythere compressa			○	•		○			○		○	○		○	
	Cyclocypris diebeli						•					•				
	Sclerocypris? *clavata*			•				•	•	•	•	○	○		○	○
	Cypris pubera				•		○	○		●		○	○		○	○
	Stanchevia crassa						○			•		•	•			
	Candona sp. /gigant/						•									
Pp	*Eucandona balatonica*			•			○			•			●		○	○
	Cyclocypris globosa			•	○		●			○		○	○		○	●
	Cyprois marginata						•			○			•			•
	number of positive samples	1	9	7	11	13	27	9	1	60	2	26	44	4	5	14

Explanation: ● > 10%; ○ 2–10%; • < 2% most in any of the samples. A=underground species, Q=spring species, F=fluviatile species, Sl=stagnophile/lacustrine/species, S=stagnophile species, P=palustrine species, Pp=species of periodic swamp.

ture is repeated in every cycle. It is also seen in the Middle Pleistocene, but not in the Upper Pleistocene because *Scottia browniana* has disappeared.

The *Middle Pleistocene* (Makiš Beds) is the most widespread unit at the surface in the Pannonian basin, although it is represented by a single sedimentary cycle. Consequently, it was possible to study it in detail and to distinguish three ecological groups of assemblages: fluvio-lacustrine, lacustrine and stagnophile. In order to distinguish these two ecologically, key-species were used: *Scottia browniana* and *Cytherissa lacustris,* the basis being Absolon's species distribution (1973). From an ecological point of view, *Scottia browniana* appears in moderate energy environments. The second ecologically important species, *Cytherissa lacustris,* which now lives in the deeper parts of lakes, was used to distinguish a true lacustrine biofacies. In cases where *C. lacustris* was absent (first two columns of Table 2), the absence of any palustrine species suggested a stagnant biofacies, mainly lacustrine but from the shallow parts of the lakes (the true palustrine biofacies is not yet known from the Middle Pleistocene of the Pannonian basin). The presence of assemblages with *Typhlocypris, Mixtacandona* and the like, need to be explained since they should belong to the nearshore environment. An explanation is also needed for the presence of rare species such as *Ilyocypris salebrosa* Stepanaytis, *Virgatocypris* cf. *V. elongata* (Schneider), *Candona rawsoni* Traessler and *Caclocypris diebeli* Absolon, as well as *Cyprois marginata, Notodromas monacha* and even *Pseudocandona albicans.* It is possible that they are climatically conditioned as the first two belong to warm, and the others to cold, climatic zones. Stratigraphically, the cycle described here belongs to the great Mindel-Riss interglacial period. There are many records of mammals such as *Elephas trogontherii* from it. At the upper boundary of this cycle, many species known from the Lower Pleistocene and even Upper Pliocene, disappear, including *Scottia browniana, S. tumida, Virgatocypris* (as a genus), *Candona permanenta, Ilyocypris salebros salebrosa, I. sokači* and other ostracods, as well as some molluscs like *Pisidium clessini.*

The *Upper Pleistocene* is the second most widespread unit in the Pannonian basin. Unfortunately for ostracod research, it consists of aeolian and swampy loess, the latter with a very scarce microfauna. Riss loesses (not yet documented palaeontologically) are developed only in the southernmost part of the Pannonian basin which at that time was sinking and was not much exposed to later erosion. The Riss-Würm interglacial (Eemian) sediments on the southern rim of the Pannonian basin are known as the Bulbulder terrace sediments. They consist of reworked loess-like silt, with rare, well rounded (many times reworked) pebbles and, near the Neogene limestone on the bank, intercalcations of breccia. Further north, in Bačka there are also some records of rare, well-rounded pebbles in the base of the Würm loess and above the Middle Pleistocene. The Würm silt is spread out on wide loess sheets. It seems that in Würm-2, the climate was more humid so that small water bodies had grown bigger and had ostracods living in them, not only molluscs as was the case before and after this time. The picture is complicated by synsedimentary and later tectonic movements which produced the fluvio-lacustrine Szentes unit, preserved in some places, and of proven Würm-2 age.

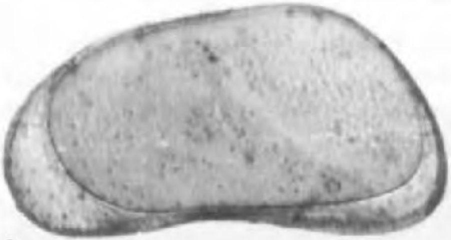
Ostracods are very rare in the Upper Pleistocene. Scarce finds of solitary valves in swampy loess are of little help in reconstructing the biotope. The more or less rich ostracod associations were only found in the level attributed to Würm-2. There two types of associations could be distinguished, namely the *Candona-Ilyocypris* assemblage and the *Typhlocypris-P. albicans* assemblage. The *Candona-Ilyocypris* assemblage belongs to a kind of lacustrine biotope (the middle part of the Szentes unit). Together with *Elephas primigenius* of the Würm-2 evolutionary level, the ostracod association consists of: *Candona paionica, Ilyocypris biplicata, Eucandona levanderi, Ilyocypris monstrifica, Limnocythere* aff. L. *inopinata, Ilyocypris decipiens.* At the top of the cycle (started by fluviatile crossbedded coarse sand with pebbles at the base), this association is slowly replaced by an assemblage containing *Paralimnocythere compressa, Eucandona balatonica, Cypris pubera* and *Cyprois marginata,* but *Cyclocypris laevis, Candona paionica, C. fasciolata, C. candida, Pseudocandona compressa, Ilyocypris inermis,* etc. are still present. The second assemblage, with *Typhlocypris eremita, Pseudocandona albicans* (*parallela*), *Mixtacandona botosaneanui, M. transleithanica,* and also *Ilyocypris gibba, Candona candida, Eucypris pigra* and others, was found in the second loess horizon, so it should also belong to Würm-2. It is possible that this assemblage belongs to small water bodies, perhaps small lakes. The species *P. albicans* could indicate a cold climatic period, but the other representatives of the second association do not have clear climatic implications.

The *Holocene* sediments form a thin surface sheet about one metre thick. In origin they are overbank fluviatile deposits and consist of silt which is rich in organic matter. Rarely and close to the rivers, there are filled in old river channels which contain plenty of ostracods in the silty parts of the sequence, mainly sandy and pebbly at the base and silty at the top. The ostracod assemblages consist of *Candona paionica, C. candida, Eucandona levanderi, Pseudocandona mar-*

PLATE 1—Female and male left valves. Figs. 1,2. *Candona (Candona) neglecta* Sars, Recent, Mavrovo spring (coll. det. Petkovski). Fig. 3. *Candona (Candona) fasciolata* Petkovski, Würm-2, Kikinda. Figs. 4, 5. *Candona (Candona)* cf. *C. paionica* Petkovski-winter form, Holocene, Gložanj 4. male right valve. Figs. 6, 7. *Candona* (Candona) cf. *C. paionica* Petkovski-summer form, Holocene, Gložanj. Figs. 8, 9. *Candona (Candona)* cf. *C. paionica* Petkovski Würm-2, Kikinda. Figs. 10, 11. *Candona (Candona)* cf. *C. paionica* Petkovski, Middle Pleistocene, Banatsko Karadjordjevo.


1


2


3


4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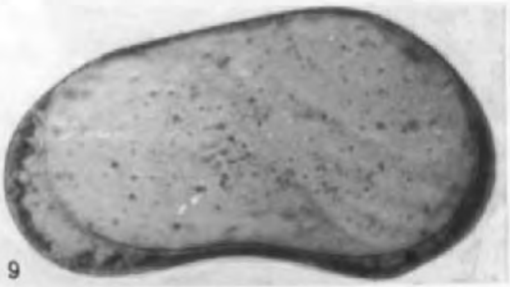
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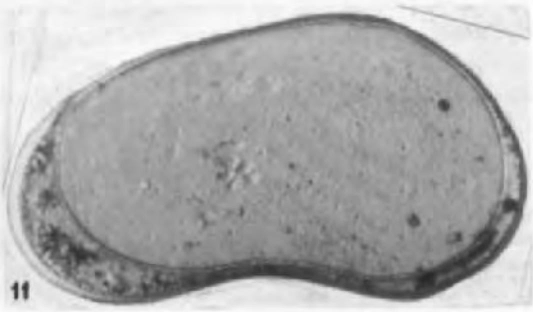
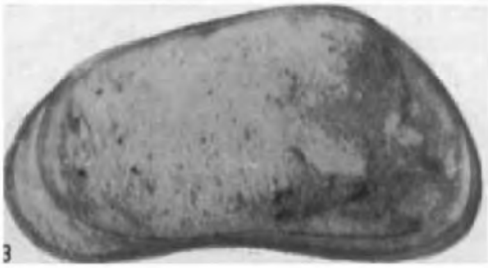
10


11


1


2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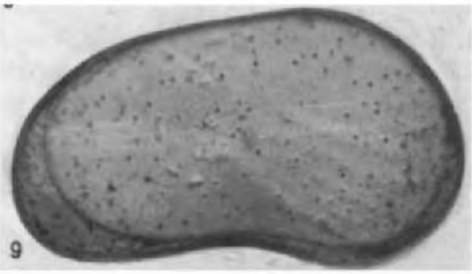
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10


11

chica, P. compressa, Cypris pubera, Physocypria kraepelini, Cypria ophthalamica, Cypridopsis vidua, Ilyocypris salebrosa carinata and others. Such an assemblage again indicates a lacustrine environment, defined as a river lake by geomorphological analysis. At the time when ostracods lived in it, the lake was 1–3 m deep, as determined on the basis of the Charophyta. In the microfauna, warm climate species are represented by *Ilyocypris salebrosa carinata* and *Physocypria kraepelini* (most common species) and perhaps also by *Eucandona levanderi,* an abundant species in the Quaternary of the Pannonian basin.

Candona neglecta and its allies are abundant in the Quaternary of the Pannonian basin. This is a large group of species which is very similar in the form of their shells. Here its features will be discussed and its relationships to the Recent representatives, a discussion that was initiated by Absolon (1978, p. 25–27).

Candona neglecta Sars is a southern species, described from Lake Garda in Italy. It has a bean-shaped shell (Pl. 1, fig. 1) with a curvate, relatively high anterior part, and a moderately rounded posteroventral one.

Candona fasciolata Petkovski, described from the mountain region on the Balkan peninsula, is a form common in central and northern Europe. Its shape is somewhere between that of a bean and a triangle, and it has a less curved posterior margin, a narrower rounded posteroventral margin and a lower anterior than *C. neglecta.* The inflation of the carapace is a little bit more than that of the previous form. The specimens from the cool Würm-2 (Pl. 1, fig. 3) are a little shorter than the Recent ones.

Candona permanenta Kristić (1985), from the Lower-Middle Pleistocene, has an almost evenly curved anterior margin (see Pl. 2, fig. 10). The posterior part of the ventral margin is clearly convex, and the axis of posteroventral roundness directed much higher than in all previously discussed species. Otherwise, in shape it is closest to *C. neglecta,* but straighter whilst *C. neglecta* is somewhat crescent-shaped.

Candona cf. *C. neglecta*, as described by Diebel and Pietrzeniuk (1978, p. 49, fig. 3), is also found in the Pannonian basin in the sediments of the great Mindel-Riss interglacial period. It seems to have developed from *C. permanenta* and in Tables 1 and 2 they are not separated. The main feature of *C.* cf. *C. neglecta* is the low anterior part of the left valve and the deep ventral concavity. Thus, the anterior part of the ventral margin (concavity) is parallel to the dorsal margin as in *C. neglecta,* but more clearly so.

Candona aff. *C. montenegrina* Petkovski, another Quaternary member of the *C. neglecta* group, is crescent-shaped (Pl. 2, fig. 7), because its anterior margin has marked infracurvature and the axis of posteroventral roundness is directed downwards more than in any of previous species. It is not related to *C. montenegrina* from Skadar Lake (Pl. 2, fig. 8) which has a straight carapace, but the previous designation was not changed after studying comparative material. *Candona* aff. *C. montenegrina* is closer to *C. dedelica,* also crescent-shaped, but shorter (Pl. 2, fig. 1).

Candona paionica Pektovski has a large rounded posteroventral margin and is not much inflated (Pl. 2, figs. 5, 7, 8, 10). It seems that the types from Dorjan lake are even more rounded posteroventrally.

Candona banatica Kristić (in press) is a relatively small and high species, easily distinguishable

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PLATE 2—Female and male left valves. Figs. 1, 2. *Candona (Candona) dedelica* Petkovski, Recent, Ohrid lake (coll. det. Petkovski). Figs. 3, 4. *Candona (Candona) natronphila* Petkovski, Recent, Elemir in Panonian basin. Figs. 5,6. *Candona (Candona) altoides* Petkovski, Recent, Gevgelia (coll. det. Petkovski). Fig. 7. *Candona (Candona)* aff. *C. montenegrina* Petkovski, Middle Pleistocene, Bačka Topola. Figs. 8, 9. *Candona (Candona) montenegrina* Petkovski, Recent, Skadar lake (coll. det. Petkovski). Figs. 10, 11. *Candona (Candona) permanenta* Krstić, paratypes, Lower Pleistocene, borehole JT-1 from 65.15 m.

from the other members of the *C. neglecta* group by the short angular concavity of the ventral margin. It is described from the Middle Pleistocene, but it is also present in the Lower Pleistocene.

ACKNOWLEDGEMENT

Without the Recent comparative material of T. Petkovski it would have been impossible to discuss the *C. neglecta* group.

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Preliminary Notes on the Japanese Miocene Ostracoda

MICHIKO YAJIMA
Tokyo Seitoku Gakuen, Tokyo, Japan

ABSTRACT

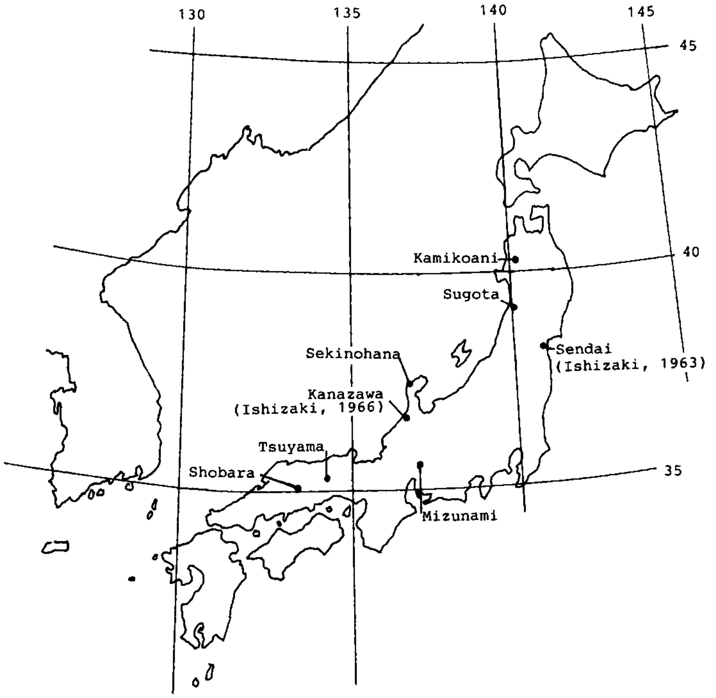
During Early Middle Miocene, 16.5–15.5 Ma, shallow, warm water ostracods lived in the Palaeo-Setouchi Province (Shobara, Tsuyama and Mizunami) and in Northeast Japan (Kanazawa and Sendai). The fauna has close affinities with that of the Pleistocene and Recent, distributed along the Pacific coast of Southwest Japan. During Middle Miocene, 15.5–9 Ma, shallow cold to temperate water ostracods became widespread in Northeast Japan (Sekinohana, Sugota and Kamikoani). The fauna is similar to Pleistocene and Recent faunas distributed along the Japan Sea and Pacific coasts in Northeast Japan. The existence of two faunas in the Middle Miocene, an earlier warm and a later cold one, confirms recent findings of tectonic and palaeogeographical studies.

INTRODUCTION

The biostratigraphy and chronology of the Japanese Miocene have recently been vigorously investigated, and a precise time scale has become available (Tsuchi *et al.*, 1981). Sediments older than the Early Middle Miocene are very scarce in Japan. The sediments of the early Middle Miocene ranging from 16.5–15.5 Ma, Blow's (1969) N 8 zone, are dominated by shallow marine facies rich in mega- and microfossils. *Geloina*-bearing molluscan assemblages of intertidal facies demonstrate the existence of mangrove swamps. Other assemblages of tropical to subtropical, shallow marine molluscan fossils are also present. These sediments are succeeded by offshore muddy or diatomaceous sediments. They represent the beginning phase of a major transgression in Japanese Neogene history. At this time a shallow marine basin, the Palaeo-Setouchi Province, developed in the Chugoku area of Southwest Japan and the Mizunami area of central Japan (Text-fig. 1).

In the Middle Miocene, Southwest Japan was emergent, while in Northeast Japan deposition of thick marine sediments took place (Text-fig. 2).

Although these Miocene sediments are rich in mega- and microfossils, studies of ostracod faunas are rare. Ishizaki (1963) described a small fauna from the Sunakosaka Member of the Yatsuo Formation, east of Kanazawa. Recently this member was correlated with the Kurosedani Formation of Blow's N 8 zone (Tsuchi, 1981). Ishizaki (1966) also reported ostracod faunas from the Moniwa Member and from the Hatatate Formation of the Sendai area. Recently the Moniwa Formation, once the Moniwa Member, was correlated with Blow's N 8 zone and the Hatatate Formation with the N 9 to N 16 zones (Text-figs. 1, 2). Hanai (1957) reported *Hemicytherura kajiyamai*



TEXT-FIG. 1—Localities of the Japanese Miocene ostracod samples.

from the Shukunohora Sandstone (Blow's N 8 zone) of Mizunami in the East Palaeo-Setouchi Province, and stated (1977) that "some species of living warm water ostracods, such as *Hemicythere kajiyamai, Aurila* sp. and *Schizocythere kishinouyei,* which settled in Japan in the Middle Miocene, have maintained *a status quo* in phenotype up to the present". By 1977, 47 species of 28 genera were reported from the Japanese Miocene. Among these, 13 species of 11 genera are extant.

While investigating Pleistocene shallow warm water ostracods, questions arose concerning their origin and their history. To clarify these, I studied Miocene ostracods from Shobara (lower sand of the Bihoku Group), Tsuyama (Yoshino Formation), Mizunami (Shukunohora Sandstone), Sekinohana (Togi Mud Formation), Sugota (Sugota Formation), and Kamikoani (Kamikoani Formation) (Text-figs. 1, 2).

EARLY MIDDLE MIOCENE-SOUTHWEST JAPAN

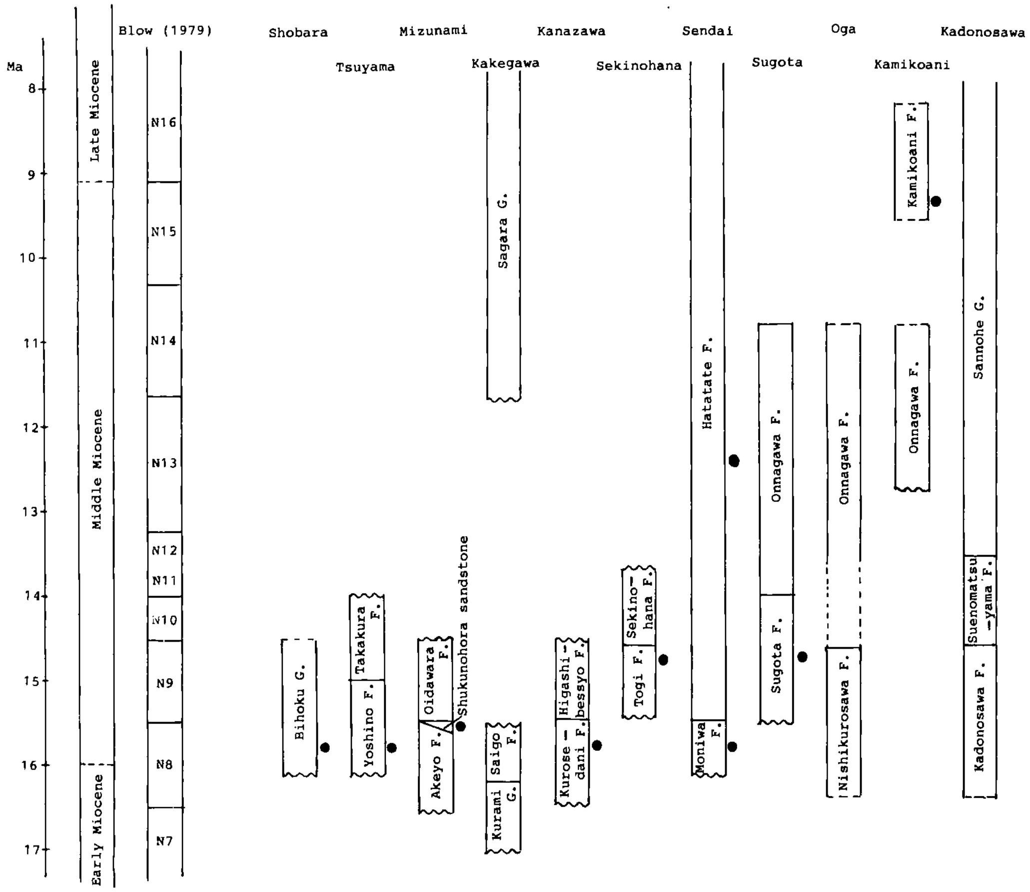
The Palaeo-Setouchi (Palaeo-Inland Sea) sediments are distributed in the Chugoku area. During the Early Middle Miocene, this area was covered by a shallow warm sea with many islands.

Shobara

In the Shobara Formation of the Bihoku Group, the only ostracods present are very rare *Cytherelloidea* sp.

Tsuyama

The Yoshino Formation at Tsuyama is about 15 m thick, light brown sand in the lower part,

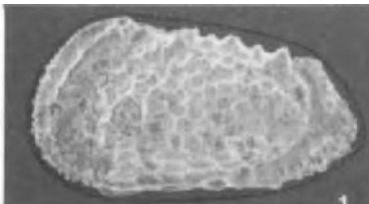


TEXT-FIG. 2—Stratigraphical correlation of ostracod-bearing Miocene sediments in the Japanese Islands. Solid circles show ostracod occurrences.

greenish mud in the middle part, and gravels and sand in the upper part, including many shallow warm-water molluscus.

Ostracods are rare in the Y2 and Y5 fossil horizons of Taguchi (personal communication) and very scarce in the Y3 and Y4 fossil horizons. The Y2 horizon is in the lower sand of the Yoshino Formation and includes the molluscan fossils *Phacosoma, Solidcorbula, Vasticardium, Crassostrea, Turbo,* and *Siratoria.* The Y5 horizon is a thin sand layer intercalated in the middle mud of the Formation and includes molluscan fossils such as *Phacosoma* and *Vasticardium.*

Ostracods are very rare in the Yoshino Formation (Table 1). Most specimens are articulated, but the carapaces are compressed laterally or dorso-ventrally. Among 14 species, *Trachyleberis* sp. and *Spinileberis?* sp. are common. Single valves of *Trachyleberis* sp. are very similar to Recent *Trachyleberis scabrocuneata,* but articulated valves differ a little in ornamentation from Recent ones. *Cletocythereis rastromarginata* is represented by only one valve. It is a tropical shallow water species. *Falsobuntonia taiwanica* is very rare. *Spinileberis quadriaculeata* is represented by only one broken valve. The ostracod assemblage is a shallow warm-water assemblage very similar to the Recent warm-water assemblages along the Pacific coast of Japan.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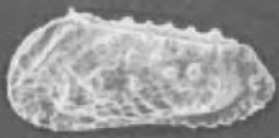
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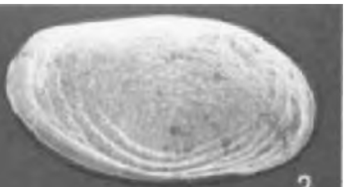
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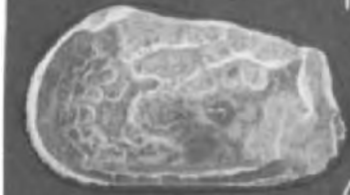
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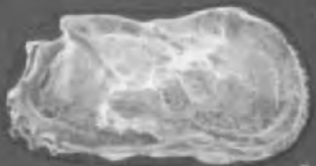
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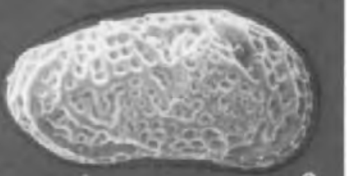
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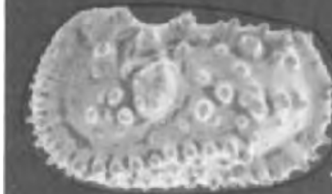
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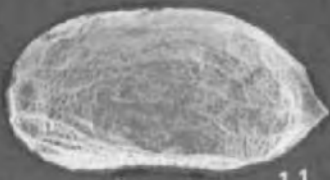
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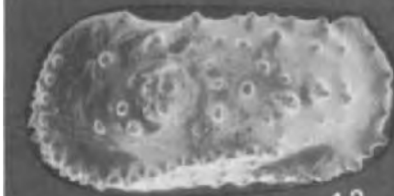
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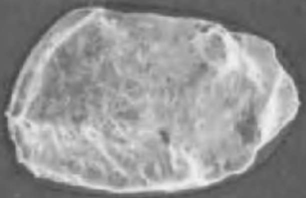
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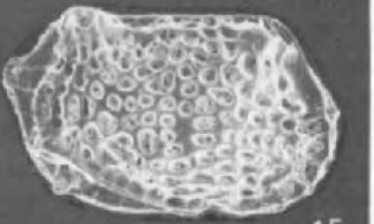
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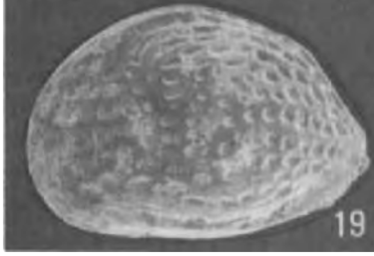
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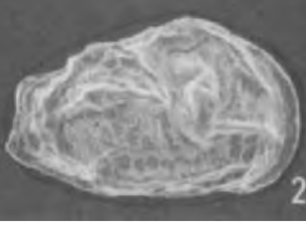
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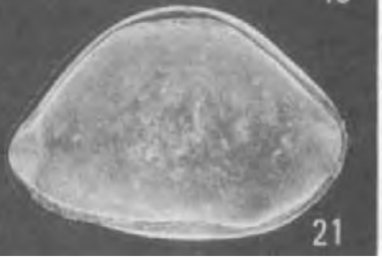
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Mizunami

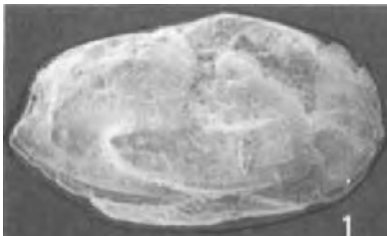
The Mizunami area is situated at the East end of the Palaeo-Setouchi Sea in Central Japan (Text-fig. 1). The transgression into the Palaeo-Setuouchi area occurred in three steps, and after the third, the seaway continued from the Japan Sea through the main part of the Palaeo-Setouchi area in the Chugoku area to east Setouchi (Itoigawa, 1981).

TABLE 1—LIST OF EARLY MIDDLE MIOCENE OSTRACOD SPECIES FROM THE TSUYAMA AREA.
Tsuyama (Yoshino Formation, Blow's N 8 zone)

Y-5 horizon	
Callistocythere sp.	R
* *Cythere omotenipponica* Hanai, 1959	R
Spinileberis? sp.	R
Trachyleberis sp.	C
Ambostracon ikeyai Yajima, 1978	R
* *Cletocythereis rastromarginata* (Brady, 1880)	R
Falsobuntonia taiwanica Malz, 1982	R
Aurila sp.	R
Cornucoquimba moniwensis (Ishizaki, 19660)	R
Semicytherura sp.	R
Loxoconcha sp.	R
Y-4 horizon	
Trachyleberis sp.	R
Y-3 horizon	
Trachyleberis sp.	R
Y-2 horizon (sample 1)	
* *Spinileberis quadriaculeata* (Brady, 1880)	R
S.? sp.	C
Trachyleberis sp.	C
"Buntonia" sp.	R
Ambostracon ikeyai Yajima, 1978	R
Loxoconcha sp.	R
Y–2 horizon (sample 2)	
Spinileberis? sp.	C
Trachyleberis sp.	C
* *Acanthocythereis munechikai* Ishizaki, 1972	R
Falsobuntonia taiwanica Malz, 1982	R

C=common; R=rare; *=extant species.

PLATE 1—Early Middle Miocene Ostracoda from Mizunami (Shukunohora Sandstone).
Fig. 1. *Trachylberis* sp. 1. Left valve, CA 17734. ×52. Figs. 2, 5. *Trachyleberis* sp. 2. Fig. 2. Left valve view of male carapace, CA 17735. ×52. Fig. 5. Right valve view of female carapace, CA 17736. ×52. Fig. 3. *Loxoconcha pulchra* Ishizaki, 1968. Right valve, CA 17737. ×62. Fig. 4. *Ambostracon ikeyai* Yajima, 1978. Female left valve, CA 17689. ×67. Fig. 6. *Cornucoquimba moniwensis* (Ishizaki, 1966). Right valve view of carapace, CA 17690. ×63. Fig. 7. *Falsobuntonia taiwanica* Malz, 1982. Left valve, CA 17691. × 68. Fig. 8. *Pontocythere subjaponica* (Hanai, 1959). Female left valve, CA 17692. ×68. Fig. 9. *Callistocythere* sp. Right valve view of carapace, CA 1769). ×89. Figs. 10, 13. *Hirsutocythere?* sp.—Fig. 10. Female left valve, CA 17694. ×42. Fig. 13. Male left valve, CA 17695. ×42. Fig. 11. *Semicytherura miurensis* Hanai, 1957. Left valve, CA 17696. ×107. Fig. 12. *Semicytherura henryhowei* Hanai and Iekya, 1977. Right valve view of carapace, CA 17697. ×107. Fig. 14. *Schizocythere kishinouyei* (Kajiyama, 1913). Left juvenile valve, CA 17698. ×82. Fig. 15. *Loxocorniculum* sp. Right valve, CA 17699. ×89. Fig. 16. *Loxoconcha* sp. Left valve, CA 17700. ×86. Fig. 17. *Kangarina* sp. Right valve, CA 17701. ×104. Fig. 18. *Hemicytherura cuneata* Hanai, 1957. Right valve, CA 17702. ×120. Fig. 19. *Aurila* sp. Left valve, CA 17703, ×62. Fig. 20. *Spinileberis quadriaculeata* (Brady, 1880). Right valve, CA 17704. ×62. Fig. 21. *Neonesidea* sp. Right valve view of carpace, CA 17705 ×40. (All illustrated specimens are deposited in the collection of the University Museum, University of Tokyo (UMUT). Specimen numbers are prefixed CA for Cenozoic Arthropoda).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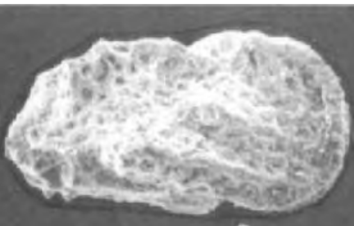
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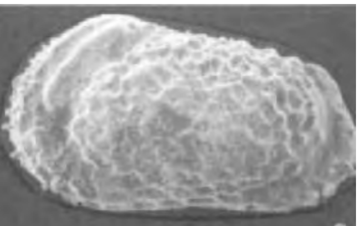
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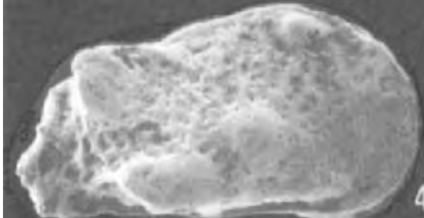
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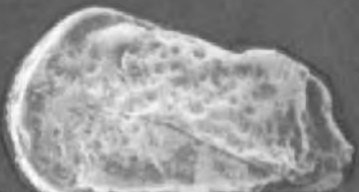
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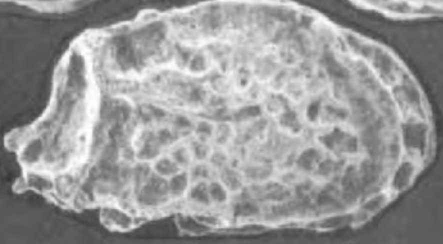
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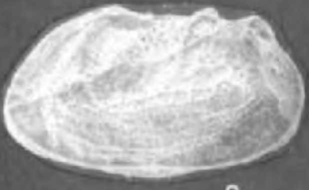
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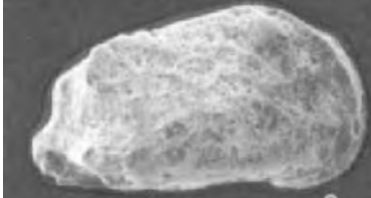
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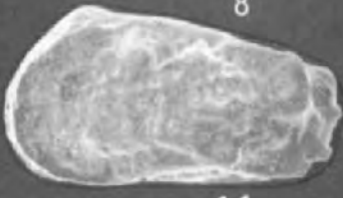
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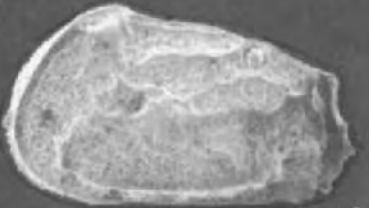
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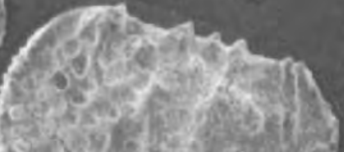
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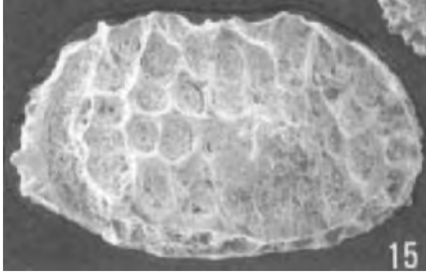
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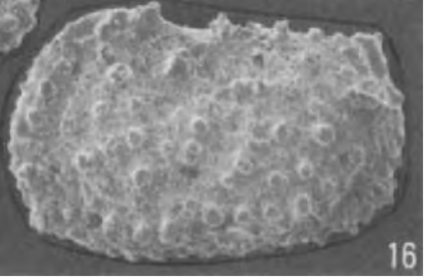
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TABLE 2—LIST OF EARLY MIDDLE MIOCENE OSTRACOD SPECIES FROM THE MIZUNAMI AREA.
Mizunami (Shukunohora Sandstone, Blow's N 8 zone)

Neonesidea sp.	A
Propontocypris sp.	R
**Pontocythere subjaponica* (Hanai, 1959)	R
P. sp.	R
**Parakrithella pseudadonta* Hanai, 1959	R
Munseyella sp.	R
Callistocythere sp.	C
**Cythere omotenipponica* Hanai, 1959	R
**Schizocythere kishinouyei* (Kajiyama, 1913)	C
**Spinileberis quadriaculeata* (Brady, 1880)	R
Trachyleberis sp. 1	C
T. sp. 2	R
Hirsutocythere? sp.	R
Falsobuntonia taiwanica Malz, 1982	R
Aurila sp.	A
Cornucoquimba moniwensis (Ishizaki, 1966)	C
Ambostracon ikeyai Yajima, 1978	C
**Hemicytherura cuneata* Hanai, 1957	C
Kangarina sp.	R
**Semicytherura henryhowei* Hanai and Ikeya, 1977	R
**S. miurensis* Hanai, 1957	R
S. wakamurasaki Yajima, 1982	R
Cytheropteron sp.	R
**Loxoconcha pulchra* Ishizaki, 1968	C
L. sp.	R
Loxocorniculum sp.	R
Xestoleberis sp.	R

A=abundant; C=common; R=rare; *, extant species.

The Shukunohora Sandstone of the Mizunami area is a thin (10 m), ill-sorted sandy silt with the foraminifer *Myogipsina kotoi* and many shallow warm-water molluscs.

The Shukunohora Sandstone contains abundant well-preserved ostracods (Table 2). Most of the ostracod valves are transparent and good for study of internal features. The sieve type pores of *Schizocythere kishinouyei* and *Spinileberis quadriaculeata* are well preserved.

The ostracod assemblage consists exclusively of shallow warm-water species (Plate 1). Among

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PLATE 2—Miocene Ostracoda from Tsuyama, Kamikoani, and Sekinohana.

Figs. 1–3. Tsuyama, Yoshino Formation, Early Middle Miocene (Blow's N 8 zone). Fig. 1. *Spinileberis*? sp., Right valve view of carapace, CA 17706 (Y-2 horizon), ×80. Fig. 2. *Cletocythereis rastromarginata* (Brady, 1880), Right valve view of carapace, CA 17707 (Y-5 horizon), ×82. Fig. 3. *Trachyleberis* sp., Left valve view of male carapace, CA 17708 (Y-5 horizon), ×58. Figs. 4–7. Kamikoani, Kamikoani Formation, Middle Miocene (Blow's N 15 zone). Fig. 4. *Finmarchinella japonica* (Ishizaki, 1966), Right valve, CA 17709. ×81; Fig. 5. *Finmarchinella japonica* (Ishizaki, 1966), Juvinile left valve, CA 17710, ×87. Fig. 6. *Hemicythere*? sp., Right valve, CA 17711, ×80. Fig. 7. *Hemicytherura cuneata* Hanai, 1957, Right valve, CA 17712, ×130. Figs. 8–16. Sekinohana, Togi Formation, Middle Miocene (Blow's N 9 zone). Fig. 8. *Palmenella limicola* (Norman, 1865), Left valve view of juvenile carapace, CA 17713, ×82. Fig. 9. *Finmarchinella hanaii* Okada, 1979, Right valve, CA 17714 (sample Togi D), ×81. Fig. 10. *Finmarchinella hanaii* Okada, 1979. Left valve, CA 17715 (sample Togi D), ×80. Fig. 11. *Munseyella* sp., Left valve, CA 17716 (sample Togi C), ×82. Fig. 12. *Cornucoquimba saitoi* (Ishizaki, 1963), Right valve, CA 17717 (sample Togi D), ×79. Fig. 13. *Ambostracon ikeyai* Yajima, 1978, Female left valve, CA 17718 (sample Togi D), ×81. Fig. 14. *Acanthocythereis*? *munechikai* Ishizaki, 1982, Left valve, CA 17719 (sample Togi D), ×58. Fig. 15. *Bradleya* sp., Right valve, CA 17720 (sample Togi D), ×58. Fig. 16. *Hirsutocythere*? *nozokiensis* (Ishizaki, 1963), Left valve, CA 17721 (sample Togi D), ×58.

27 species of 21 genera, 9 species are extant. *Neonesidea* sp. which is very similar to the Recent *Neonesidea oligodentata,* and *Aurila* sp. which is very similar to the Recent *Aurila punctata* are abundant. *Callistocythere* sp., *Schizocythere kishinouyei, Trachyleberis* sp., *Cornucoquimba moniwensis, Ambostracon ikeyai, Hemicytherura cuneata* and *Loxoconcha pulchra* are common. *Pontocythere subjaponica, Parakrithella pseudadonta, Cythere omotenipponica, Spinileberis quadriaculeata, Semicytherura henryhowei,* and *S. miurensis* are rare but identical to the species presently living along the Pacific coast of Japan. Tropical species of *Kangarina* sp., *Falsobuntonia taiwanica* and *Loxocorniculum* sp. are rare.

EARLY MIDDLE MIOCENE-NORTHEAST JAPAN

Kanazawa

Ishizaki studied Miocene ostracods from the Sunakosaka Member (Blow's N 8 zone) in 1963. The ostracod assemblage is very small but resembles that from the Tsuyama area because *Trachyleberis* is abundant.

Sendai

Miocene ostracods from the Moniwa Formation (Blow's N 8 zone), Sendai, were reported by Ishizaki (1966). Ostracods are very rare. Abundance of *Neonesidea oligodentata, Trachyleberis scabrocuneata, Cornucoquimba saitoi,* and *Schizocythere kishinouyei* shows that the assemblage is similar to the Mizunami and Tsuyama faunas.

MIDDLE MIOCENE-NORTHEAST JAPAN

Seikinohana

The Sekinohana area is situated on the Noto Peninsula, near Kanazawa along the Japan Sea. The Togi Mud Formation in Sekinohana is a very thin (2 m), greenish, massive, silty mudstone containing abundant foraminifers, and rare radiolarians, diatoms, and ostracods. Suda and Ishigaki (1984) reported the presence of *Groborotalia peripheroronda* and correlated the sediments with Blow's N 7 to N 9 zones, a little later than the earliest Middle Miocene transgression.

Ostracods are rare (Table 3). The fauna is dominated by *Neonesidea* sp., *Hirsutocythere? nozokiensis,* and *Acanthocythereis? munechikai* (Plate 2). Only one immature carapace of *Palmenella limicola* is present. This is a typical arctic species. *Finmarchinella hanaii,* which is common in shallow Pleistocene sediments along the Japan Sea coast, is common. Rarely found *Bradleya* sp. is very similar to the Recent deep sea species of *Bradleya albatrossia.* The extant species *Pontocythere subjaponica, Hanaiborchella miurensis,* and *Semicytherura henryhowei* are rare. Occurrences of other species are hitherto confined to Miocene sediments.

Sugota

The Sugota Formation is a 180 m thick, fine argillaceous sandstone found around Sugota near Akita, in Northeast Japan. The basal part of the Sugota Formation is dark greenish, poorly sorted medium to coarse sandstone with abundant fragments of barnacles, molluscs, and benthonic foraminifers. Molluscs show that the sediments were deposited in temperate water, and planktonic foraminifers present correlate with Blow's N 9 zone or higher. Ostracods are very rare. Only one broken valve of *Hemicythere* was found. The Middle part of the Formation is dark grey to dark

TABLE 3—LIST OF MIDDLE MIOCENE OSTRACOD SPECIES FROM THE SEKINOHANA AREA.
Sekinohana (Togi Mud Formation, Blow's N7–9 zones)

Togi C	
Munseyella sp.	R
Schizocythere sp.	R
**Palmenella limicola* (Norman, 1865)	R
Finmarchinella hanaii Okada, 1979	C
Cornucoquimba moniwensis (Ishizaki, 1966)	C
C. saitoi (Ishizaki, 1963)	R
**Hirsutocythere? nozokiensis* (Ishizaki, 1963)	A
**Acanthocythereis munechikai* Ishizaki, 1972	A
Bradleya sp.	R
Cytheropteron sawanense Hanai, 1957	C
Paracytheridea neolongicaudata Ishizaki, 1966	R
Togi D	
Neonesidea sp.	C
**Pontocythere subjaponica* (Hanai, 1959)	R
**Hanaiborchella miurensis* (Hanai, 1970)	R
**Palmenella limicola* (Norman, 1865)	R
Finmarchinella hanaii Okada, 1979	C
Ambostracon ikeyai Yajima, 1978	R
Caudites? posterocostatus (Ishizaki, 1966)	C
Cornucoquimba saitoi (Ishizaki, 1963)	R
Hirsutocythere? nozokiensis (Ishizaki, 1963)	C
**Acanthocythereis munechikai* Ishizaki, 1972	C
Bradleya sp.	R
Eucytherura neoalae (Ishizaki, 1966)	R
**Semicytherura henryhowei* Hanai and Ikeya, 1977	R
Loxocorniculum kotoraformum Ishizaki, 1966	R

A=abundant; C=common; R=rare; *=extent species.

brownish-grey, fine argillaceous sandstone with autochthonous cold water molluscs and foraminifers. Ostracods are very rare, only a few specimens of *Callistocythere* were found.

Kamikoani

The Kamikoani Formation in the Kamikoani area is a calcareous fine sand. It is considered to have been deposited 10 to 8 Ma., based on its stratigraphical position. Ostracods are very abundant and well-preserved (Table 4). *Schizocythere kishinouyei, Aurila* sp. 1, *Finmarchinella japonica, Hemicytherura cuneata,* and *Cytheroteron sawanense* are abundant. *Palmenella limicola,* a typical arctic species, is rare. Among ostracods found in this formation, *Munseyella hokkaidoana, Finmarchinella japonica, F. nealei, Howeina neoleptocytheroidea,* and *Cytheropteron sawanense* are species common in the Pleistocene sediments and Recent shallow water fauna along the Japan Sea coast. A specimen which probably belongs to the genus *Hemicythere,* a cold water genus, is also present. Many species such as *Cornucoquimba moniwensis, Hirsutocythere? nozokiensis, Paracytheridea neolongicaudata, Loxoconcha nozokiensis,* and *Loxocorniculum kotoraformum,* are confined to the Miocene.

Sendai

Ishizaki's report (1966) also included the ostracod fauna from the Hatatate Formation. This formation is correlated with Blow's N 9 to N 15 zones, and the formation is considered to have been deposited under the influence of cold currents on the basis of the molluscan fossils. Ishizaki

TABLE 4—LIST OF MIDDLE MIOCENE OSTRACOD SPECIES FROM THE KAMIKOANI AREA..
Kamikoani (Kamikoani Formation, 10–8 Ma).

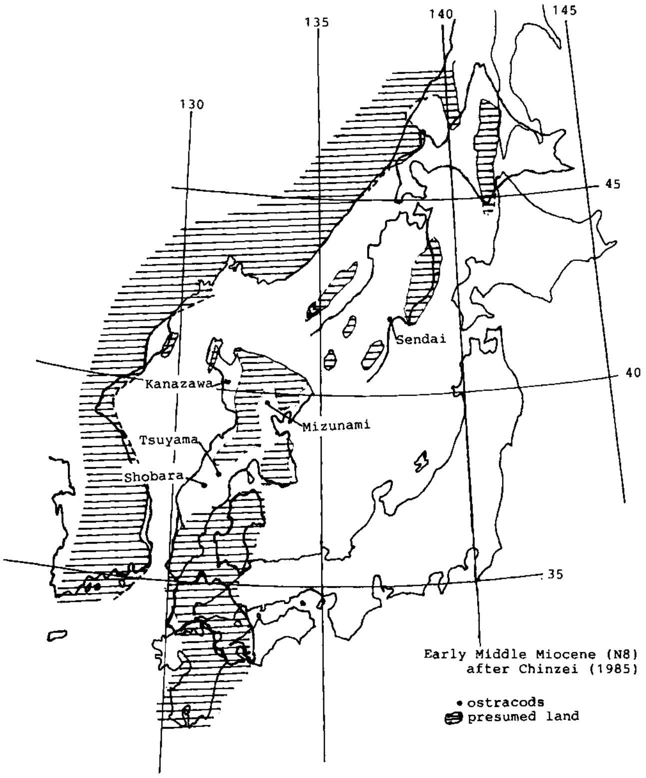
Munsyella hokkaidoana (Hanai, 1959)	R
**Callistocythere japonica* Hanai, 1957	R
**C. ruogsoforma* Hanai, 1957	R
**Cythere uranipponica* Hanai, 1959	R
Schizocythere sp.	C
**Palmenella limicola* (Norman, 1865)	R
Aurila sp. 1	A
A. sp. 2	R
Finmarchinella japonica (Ishizaki, 1966)	C
**F. nealei* Okada, 1979	R
Hemicythere? sp.	R
Caudites? posterocostatus (Ishizaki, 1966)	R
Cornucoquimba moniwensis (Ishizaki, 1966)	R
**C. tosaensis* (Ishizaki, 1968)	R
Trachyleberis sp.	R
Hirsutocythere? nozokiensis (Ishizaki, 1963)	C
Eucytherura sp.	R
**Hemicytherura cuneata* Hanai, 1957	A
**Semicytherura henryhowei* Hanai and Ikeya, 1977	R
**Howeina neoleptocytheroidea* Hanai, 1957	R
H. sp.	R
Cytheropteron sawanense Hanai, 1957	A
Paracytheridea neolongicaudata Ishizaki, 1966	C
P. sp.	R
Loxoconcha nozokiensis Ishizaki, 1963	R
Loxocorniculum kotoraformum Ishizaki, 1966	C

A=abundant; C=common; R=rare; *=extant species

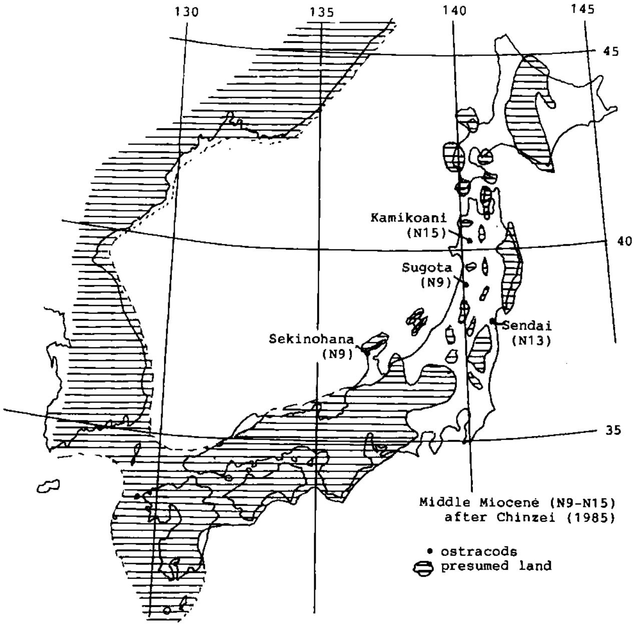
pointed out that the ostracod fauna of "the Hatatate Formation is not essentially different from that of the Moniwa Member, although it is more or less different in productivity" (1966, p. 135). I think that the occurrence of *Palmenella limicola* and *Finmarchinella japonica* in the Hatatate Formation demonstrate cold water influence.

FAUNAL CONSIDERATIONS

Palaeogeographical maps (Chinzei, 1986) of the Japanese Islands during the Early Middle Miocene (Blow's N 8 zone) and Middle Miocene (Blow's N 9 to N 15 zones) are shown in Text-figs. 3 and 4. Recent palaeomagnetic studies show that in the Early Middle Miocene the Japanese Islands were situated closer to the Asian continent and the Japanese Island arc was convex toward the northwest, opposite to the trend of the present arc. The Tsushima Strait between the Korean Peninsula and Kyushu Island opened and tropical water flowed into the Palaeo-Inland Sea and the Japan Sea up to Northeast Japan. Cold water influence was very weak and only extended into the Hokkaido area. Ostracods from Shobara, Tsuyama, Mizunami, Kanazawa, and Sendai, during the age of Blow's N 8 zone are shallow, tropical water species, similar to the warm-water ostracods presently living along the Pacific coast of Southwest Japan. Ostracods from the Shukunohora Sandstone are very similar to Recent ones. The Shukunohora Sandstone was probably deposited a little after the deposition of the main part of the Palaeo-Inland Sea sediments. Among the Early Middle Miocene ostracod faunas, the one from the Shukunohora Sandstone may have persisted up until Recent times.



TEXT-FIG. 3—Palaeogeographical map of the Japanese Islands during the age of Blow's N 8 zone, Early Middle Miocene. (after Chinzei, 1986).



TEXT-FIG. 4—Palaeogeographical map of the Japanese Islands during the age of Blow's N9-15 zones, Middle Miocene. (after Chinzei, 1986).

During the Middle Miocene (Blow's N 9 to N 15 zones), Southeast Japan was emergent except for a few localities along the Pacific coast. The Japanese Islands moved to nearly the same position as they occupy today. The Tsushima Strait closed, and the influence of warm water ceased, while Northeast Japan came under cold water influence. Ostracods from Sekinohana, Sendai, Sugota, and Kamikoani show cold water influence and are very similar to Pleistocene and Recent ostracod faunas distributed along the Japan Sea and Pacific coast of Northeast Japan.

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DISCUSSION

Cronin: Are the Miocene species of *Finmarchinella* and *Cornucoquimba* still extant?

Yajima: Three cold water species of *Finmarchinella* and one warm water species of *Cornucoquimba* are extant. Two species of *Cornucoquimba* are confined to the Miocene as far as we know at present.

Hazel: I noticed that you had *Ambostracon ikeyai* as old as N7 or N8 in the Miocene. This seems to be a long range for a hemicytherid. Would you care to comment?

Yajima: Morphologically, *Ambostracon ikeyai* from Mizunami (Shukunohora sandstone, N8 zone) is the same as that from Chiba (Kioroshi Formation, 143,000 yr BP). I think that many species not only of *Ambostracon*, but also of other hemicytherids from the Miocene are still extant.

Neale: I congratulate the author on an excellent and most interesting paper. I missed the reference noted by an earlier speaker to *Finmarchinella* and would be interested to hear how she interprets the ecology of the species in terms of temperature. Does she regard this as indicative of colder waters when this genus appears? Are there other associated genera which can also be interpreted in terms of a colder environment?

Yajima: From the molluscan assemblage I think that the ostracod assemblage from the N9 to N15 zones was of cold water species. *Finmarchinella* came down from a cold stock and then stayed, even in temperate waters. The ostracod assemblage also includes *Palmenella limicola.*

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Marine Ostracods of the Upper Miocene of the Well Ashtart 1 (Gulf of Gabès, Southeastern Tunisia)

GIOACCHINO BONADUCE,[1] HECTOR BISMUTH,[2] GIULIANO RUGGIERI,[3]
ANTONIO RUSSO[4] AND PATRIZIA MASCELLARO[1]
Zoological Station of Naples, Italy; [1] *SEREPT, P.O.B. 145, 1002 Tunis-Belvédère Tunisia;*[2]
University of Palermo, Italy;[3] *and University of Modena, Italy.*[4]

ABSTRACT

We studied the ostracod fauna from a Late Miocene–Early Pliocene interval 600 m thick, in Ashtart 1, an offshore well in the Gulf of Gabès, southeastern Tunisia. Most of the 131 samples analyzed contained rich and much diversified populations of marine ostracods. In fact, 212 species have been found, belonging to 70 genera. Among them, eight genera, 122 species and subspecies, considered as new, will be described elsewhere.

In spite of contamination, usual in oil wells due to caving from higher levels previously drilled, some stratigraphical and palaeoenvironmental features have been established.

The last occurrence datum of a selected group of species has been defined with accuracy, and some assemblages have been tentatively recognized.

The Tortonian–Messinian boundary did not show any important biostratigraphic event for the species taken into consideration. In fact, the Tortonian "Sands of Somaâ", a mollassic formation, are practically azoic; the apparently rich ostracod assemblages found in the samples of this unit are only contaminations from the overlying beds.

Three abundance maxima have been noticed within the "Melqart limestones" formation, a lithostratigraphic unit considered of Early Messinian age.

The Upper Messinian, with the gypsiferous clays of the "Oued bel Khedim" formation, showed the rather abrupt extinction of most of the marine species, the survival of some euryhaline taxa and the development of a brackish environment colonised by *Cyprideis*. The environment becoming too hostile, all forms of life disappeared and the upper 70 metres of the formation are azoic.

Thus, in this area of the Tunisian shelf, the Messinian sediments perfectly registered the progressive deterioration of the environment, certainly related to the "salinity crisis" which affected the whole Mediterranean Sea at the same time.

The first Early Pliocene sediments are characterised by the re-establishment of a normal marine environment, thus showing a sharp contrast with the underlying Upper Miocene series.

During the Lower Messinian, the palaeobathymetry, as deduced by the ostracod genera represented, seemed to be rather constant, with weak oscillations between 70 and 100 metres. This palaeoenvironmental interpretation suggests a subsidence phenomenon of more than 300 m during the Late Miocene.

INTRODUCTION

The Miocene ostracod assemblages of the southern Mediterranean Basin and surrounding areas are poorly known. As far as we know, the contributions dealing with this subject are the monographic works of Bossio *et al.* (1976), Ducasse and Cirac (1981) for Morocco, Sissingh (1972), Guardia *et al.*, (1974), Guernet *et al.* (1984) for Algeria, and Van Hinte *et al.* (1980) for Libya. Very interesting information on the Messinian ostracod faunas are given in the thesis by Carbonel (1971) for Morocco.

In Tunisia, Bismuth (1984b) could mention only five papers making rather short references to Upper Miocene ostracods. They are from Benson (1976a, 1976b), Bizon *et al.* (1980) and Demarcq *et al.* (1976). The indication of marine species is only found in Fournié (1978); this author, describing the new "Melqart carbonates" formation from the Upper Miocene of MELQART 1, another borehole drilled in the Gulf of Gabès, cites the presence of *Hemicythere deformis* and of the genus *Parakrithe.*

The scarce information on Upper Miocene Tunisian ostracods is certainly not related to their paucity in the sediments, at least in most of the offshore drillings of Eastern Tunisia. The abundance and diversity of the ostracod assemblages was previously pointed out (Bismuth, 1976) in the Upper Miocene of the Gulf of Gabès, associated with abundant bryozoans, corals and exclusively benthic foraminifers (including the remarkable presence of *Borelis*).

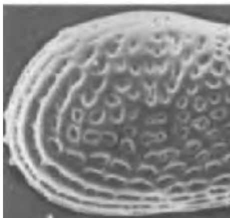
On the basis of previous studies, we believe there is an urgent need for detailed work on the systematics of these rich ostracod populations and on their stratigraphical, palaeoecologic and palaeobiogeographical significance. The present paper deals with only a part of this project and with a selected number of 51 species, most of which are partially illustrated (pls. 1 and 2). All the systematics will be the object of a subsequent monographic paper.

GENERAL DATA

The offshore Well Ashtart 1 was drilled in 1971 by SEREPT for the Aquitaine Tunisie–ETAP association. It is located on the Tunisian shelf about 80 km SE of Sfax (Text-fig. 1). The water depth at the drilling site was 217 feet (66 m). The rotary table, which is the basis of all depth measurements was 37 feet (11 m) above sea level and, consequently 254 feet (77 m) above the sea bottom. The drilling was conducted vertically.

The section studied is comprised, *grosso modo,* between 800 and 2900 feet (245 to 870 m) and includes all the terminal Miocene (Messinian) and part of the Pliocene and Tortonian sediments which embrace it.

PLATE 1—Fig. 1. *Cytheridea* n. sp. 1. LV of complete carapace (×71). Fig. 2. *Cytheridea* n. sp. 2. LV (×68). Fig. 3. *Peteraurila* n. sp. 1. LV (×59). Fig. 4. *Paijenborchella* n. sp. 1 LV of complete carapace (×84). Fig. 5. *Paijenborchella laskarevi* Krstic and Pietrzeniuk. LV (×90). Fig. 6. *Graptocythere* n. sp. 1. LV of complete carapace (×68). Fig. 7. Hemicytherid n. sp. 4. LV (×60). Fig. 8. Hemicytherid n. sp. 1. LV (×74). Fig. 9. Hemicytherid n. sp. 3. LV (×68). Fig. 10. *Chrysocythere paradisus* Doruk-LV (×65). Fig. 11. *Chrysocythere* n. sp. 1. LV (×68). Fig. 12. *Chrysocythere* n. sp. 2. LV of complete carapace (×65). Fig. 13. Hemicytherid n. sp. 2. LV (×81). Fig. 14. Trachyleberid n. sp. 1. LV of complete carapace (×62). Fig. 15. *Cytherelloidea petrosa* Doruk. LV of complete carapace (×68). Fig. 16. *Occlusacytheris* n. sp. 1. LV (×84). Fig. 17. *Pterygocythere* sp. LV (×54). Fig. 18. *Cytherella* n. sp. 1. LV of complete carapace (×71). Fig. 19. *Loxoconcha* n. sp. 1. LV (× 96). Fig. 20. *Loxoconcha gibbosofoveolata* (Seguenza) LV (×81). Fig. 21. *Trachyleberis* n. sp. 1. LV (×59).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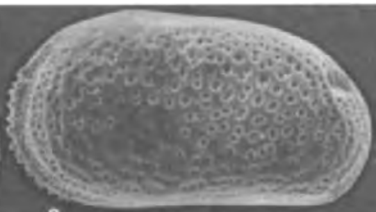
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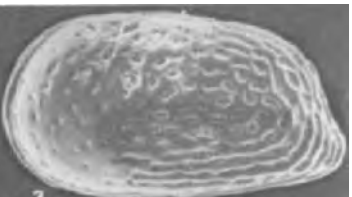
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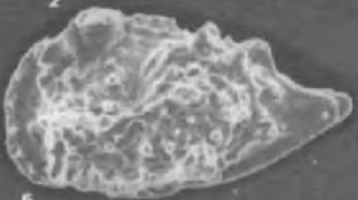
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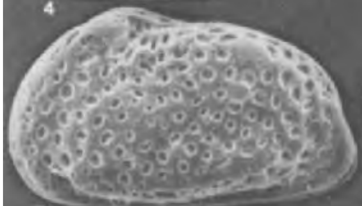
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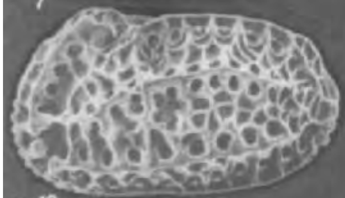
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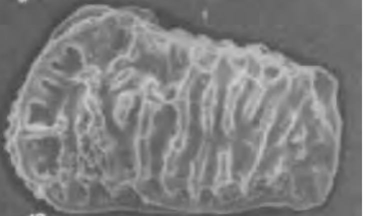
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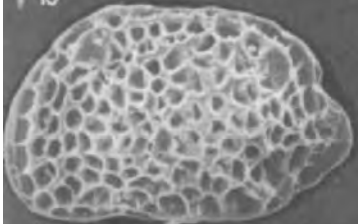
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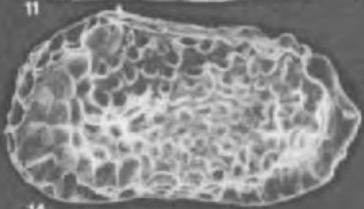
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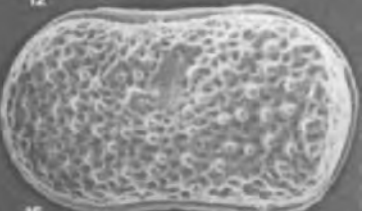
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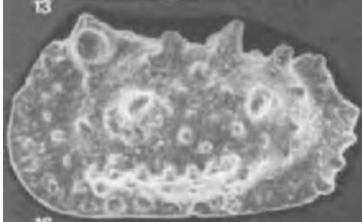
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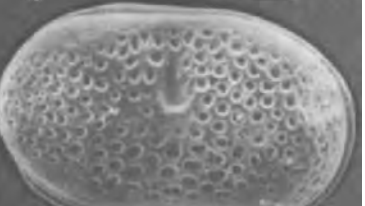
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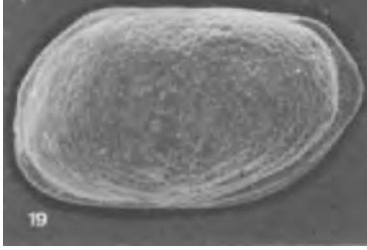
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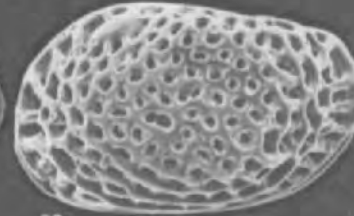
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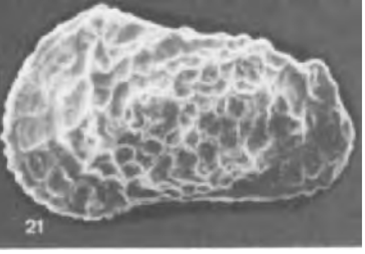
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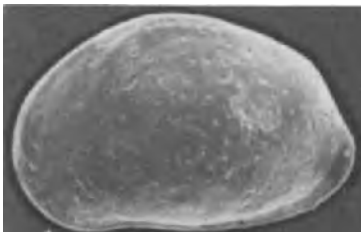
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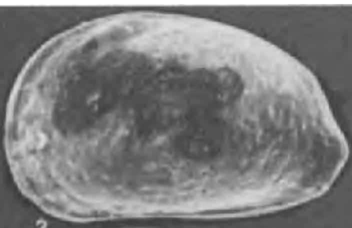
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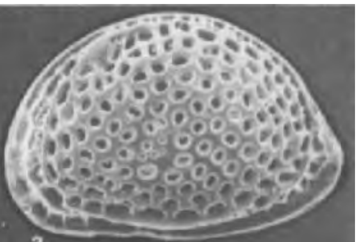
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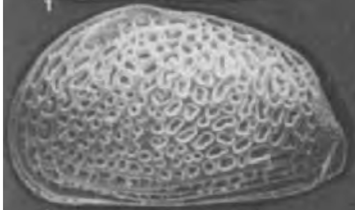
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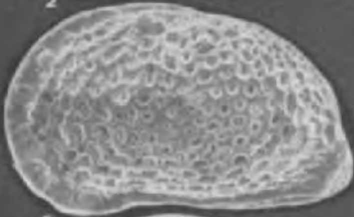
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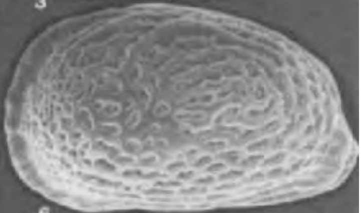
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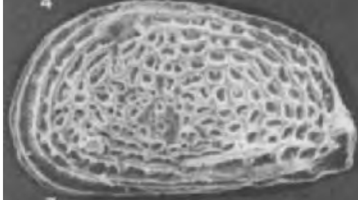
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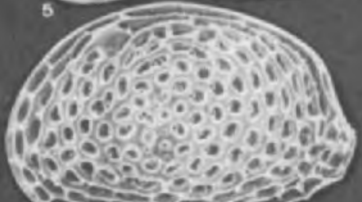
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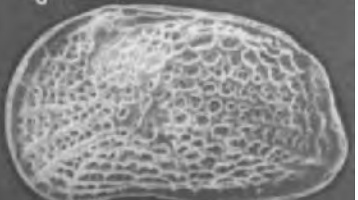
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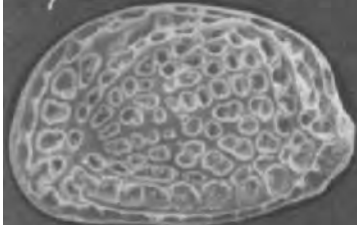
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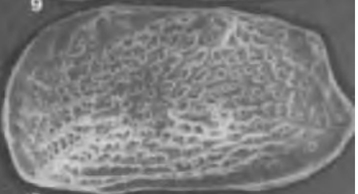
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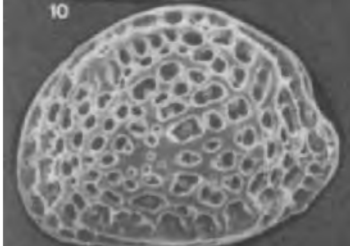
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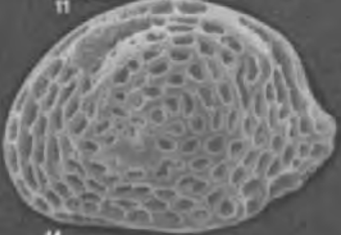
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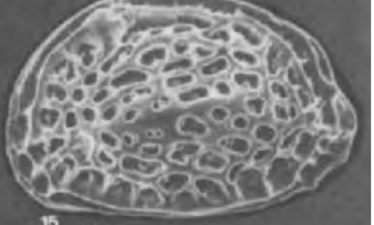
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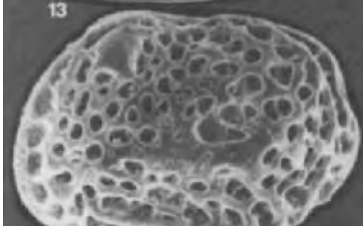
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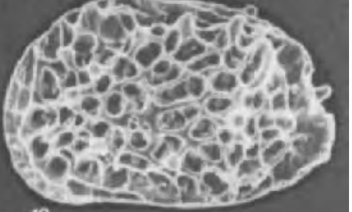
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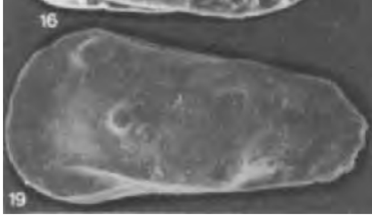
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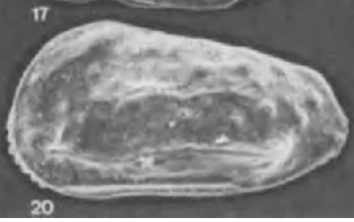
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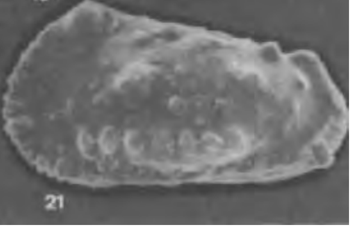
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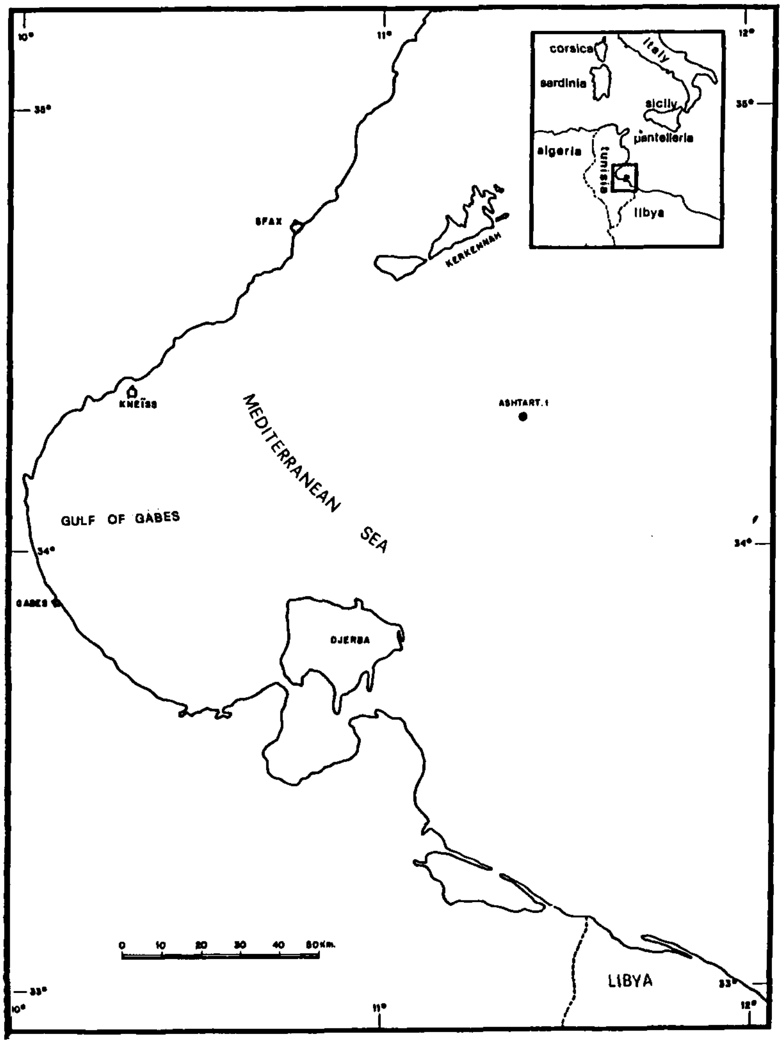


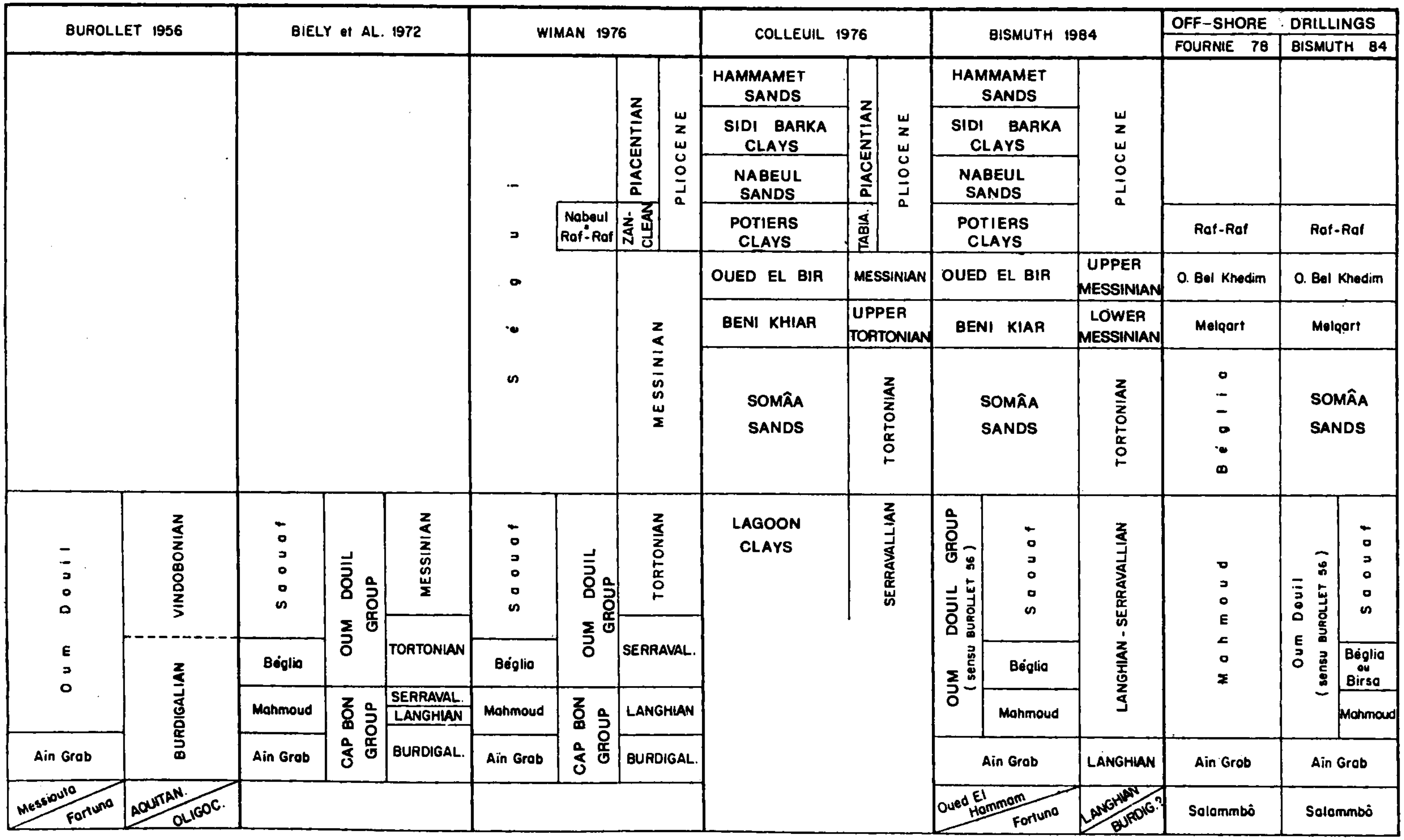
TEXT-FIG. 1—Location of the Well Ashtart-1 in the Gulf of Gabès.

Because of the drilling technique, the vertical distribution of the taxa extends artificially downward. As a result, it is almost impossible to establish with certainty the first appearance of a certain taxon, whereas we are able to define precisely its extinction.

PLATE 2—Fig. 1. *Aurila* n. sp. 3. LV (×48). Fig. 2. *Aurila* n. sp. 4. LV (×52). Fig. 3. *Aurila* n. sp. 5. LV (×68). Fig. 4. *Aurila freudenthali* Sissingh-LV of complete carapace (×59). Fig. 5. *Aurila* n. sp. 6. LV of complete carpace (×65). Fig. 6. *Aurila* n. sp. 7. LV of complete carapace (×62). Fig. 7. *Aurila* n. sp. 1. LV (×62). Fig. 8. *Aurila bradleyana* Ruggieri-LV (×59). Fig. 9. Hemicytherid n. sp. 5. LV of complete carapace (× 57). Fig. 10. *Cimbaurila* n. sp. 2. LV (×74). Fig. 11. *Aurila* n. sp. 8. LV of complete carapace (×74). Fig. 12. Hemicytherid n. sp. 6. LV of complete carapace (×57). Fig. 13. *Cimbaurila* n. sp. 1. LV (×84). Fig. 14. *Cimbaurila diecii* (Sissingh). LV of complete carapace (×71). Fig. 15. *Cimbaurila cimbaeformis* (Seguenza). LV (×81). Fig. 16. Hemicytherid n. sp. 7. LV of complete carapace (×84). Fig. 17. Hemicytherid n. sp. 8. LV (×68). Fig. 18. Hemicytherid n. sp. 9. LV of complete carapace (×81). Fig. 19. *Ruggieria* n. sp. 2. LV of complete carapace (×77). Fig. 20. *Ruggieria* n. sp. 1. LV of complete carapace (×81). Fig. 21. *Actinocythereis* n. sp. 1. LV of complete carapace (×84).

TABLE 1—LITHO-AND CHRONOSTRATIGRAPHY OF THE WELL ASHTART 1.

Litho-biostratigraphy	Depth feet m	Thickness(m)	Age		Formations
Depth datum level rotary table	0'- 0				
Sea bottom	254'- 77				
	404'- 123	46	Quatern.	Holocene	
1st sample collected	813'- 248	125	(266 m)	Not observed	
Appearance marine microfauna	1125'- 343	95		Villafranchian	
Top frequent planktonic microfauna	1420'- 433	90	Pliocene	Piacentian	
Diagraphic boundary	1519'- 463	30	(120 m)	Tabianian	Raf-Raf
Top of gypsum	1540'- 469	127		Upper	Oued bel Khedim
Appearance marine microfauna	1780'- 542			Messinian	
Diagraphic boundary	1935'- 590		Upper		
Appearance *Borelis*	1980'- 603	253	Miocene		
			(636m)	Lower	Melqart
Diagraphic boundary	2765'- 843			Messinian	
Diagraphic boundary	3604'-1099	256		Tortonian	Somaâ
Diagraphic boundary	4240'-1292	356	Middle	Serravallian	
Top frequent planktonic microfauna	4340'-1323		Miocene	to	Oum Douil
Diagraphic boundary	4773'-1455		(462m)		
		6		Langhian	Mahmoud
					Ain Grab
Diagraphic boundary	4795'-1461				
		120	Middle	Langhian	Salammbō
Diagraphic boundary	5186'-1581		Miocene	basal	
Appearance *Amphistegina*	5220'-1591		(basal)	Burdigal.	
Appearance *Heterostegina*	5240'-1597		to	Aquitan.	
			Lower		
Appearance *Miogypsina*	5500'-1676		Miocene		Ketatna
Appear. *Eulepidina & Spiroclypeus*	5580'-1701		(240m)		
Appear. *Miogypsinoides* cf. *complanata*	5730'-1746	360	Basal	Aquitanian	
			Miocene	Chattian	
Appear. *Pararotalia viennoti /mexicana*	6000'-1829		and	Upper Stampian	
			Oligocene		
Diagraphic boundary	6345'-1934		(233 m)		
			Lower		
Appearance *Nummulites*	6360'-1938		Oligocene	Lower	
Diagraphic boundary	6368'-1941		(7 m)	Stampian	"vascus"
Appear. *Loculicytheretta cavernosa*	6900'-2103	162		Priabonian	
Diagraphic boundary	7548'-2300	241		Upper	Cherahil
			Eocene	Lutetian	"B"
Appear. *Loculicytheretta minuta*	7690'-2344				
					Reinèche
Diagraphic boundary	7771'-2368			Lower	
Diagraphic boundary	9126'-2781	536		Lutetian	Cherahil
Top oil-field with *Nummulites*	9448'-2880		(1076,50)		"A"
Base oil-field	9704'-2958	78			El Guerria
Diagraphic boundary	9777'-2980			Ypresian	
Diagraphic boundary	9787'-2983	59,50			Chouabine
Final depth reached	9900'-3017				



TEXT-FIG. 2—Miocene lithostratigraphical units of East Tunisia (Bismuth, 1984).

LITHO-AND BIOSTRATIGRAPHY

In Table 1 the bio-, litho-, and chronostratigraphical frame of the complete Well Ashtart 1 is presented.

The Upper Miocene of Ashtart 1, which this paper is particularly concerned with, is 636 m thick and can be subdivided into three formations. Text-figure. 2 shows the correlations between the Miocene lithostratigraphical units of eastern Tunisia used by different authors. From the bottom upward, the three formations identified in Ashtart 1 are, successively:

The Somâa Sands Formation

Encountered between 2765 feet (843 m) and 3604 feet (1099 m) this unit essentially consists of detrital argillaceous and siliceous material the continental origin of which is obvious. This mollassic series contains only reworked microfossils from older strata (*Globotruncana, Heterohelix,* etc.). The geological position and lithological characters of this unit fully agree with the definition given by Colleuil (1976) of the Somâa Sands formation which he attributed to the Tortonian. Only the upper levels of this formation have been studied at Ashtart 1, about thirty metres below its top, just to check that there were no occurrences of taxa which had not been seen before in the overlying beds. Indeed, the assemblages found in the samples of that interval were very similar to those observed higher up and, because of the clastic lithology, are considered to be a result of caving.

The Melqart Carbonates Formation

This unit, mainly composed of bioclastic and sometimes oolitic limestones (often vacuolar due to the dissolution of the clasts and oolites) interbedded with very fossiliferous clays, also includes strata of nearly reef environment such as biosparitic boundstones built by corals (*Porites*). This undoubtedly marine formation is 253 m thick here and extends from 1935 feet (590 m) down to 2765 feet (843 m). Its top more or less coincides with the last occurrence of *Borelis melo.* In this formation, planktonic foraminifers do not occur, but only benthonic forms such as *Borelis, Dendritina,* Miliolids, *Ammonia* gr. *beccarii, A. tepida, Elphidium crispum, E.* spp., *Cellanthus* cf. *craticatulus, Elphidiella* sp., *Glabratella* spp., *Schakoinella* sp., *Pararotalia* aff. *audouini* and *Discorbis* sp. Fournié (1978), who was the first to describe the Melqart formation, thought it was of Tortonian age and a lateral equivalent of the Oum Douil formation well known in the outcrops of northeastern Tunisia. Recently, Bismuth (1984a) moved the Melqart formation to a higher stratigraphical level, proposing for it a Lower Messinian age, because of the great similarity between its facies and faunas and those also attributed to the Lower Messinian in outcrops in Sicily and the Italian peninsula, as well as those in Morocco and western Algeria.

The "Oued bel Khedim" Formation

The upper part of the last Upper Miocene series, the "Oued bel Khedim" formation, 127 metres thick and extending from 1519 feet (463 m) down to 1935 feet (590 m), is mostly composed of brackish or evaporitic sediments with gypsiferous marls, gypsum layers and soft, fine gypsiferous sandstones. From its lower part and upwards, one can observe the successive disappearance of all the marine species inherited from the underlying Melqart limestones and the colonisation by an association of benthonic foraminifers and ostracods much more tolerant in respect to the wide variations in environmental salinity and, following this temporary adaptation to high stress conditions, the extinction of all kinds of life. The last 70 metres of the formation seem to be azoic.

As in the whole Gulf of Gabès, the Messinian sediments in Well Ashtart 1, represented by the Melqart and Oued bel Khedim formations, appear as the last megasequence of sedimentation in the Miocene. It is regressive as it undoubtedly begins with marine facies and ends with nearly emersive thick evaporitic layers. It is also a post-tectonic sedimentary sequence as testified by the underlying "Somâa sands" formation which is mollassic facies contingent on intense orogenic activity.

The Messinian sediments of Ashtart 1 perfectly registered the fast deterioration of the palaeoenvironment that happened in the Mediterranean Sea during the Upper Miocene "salinity crisis".

The "Raf-Raf" Clays Formation

At a depth of 1519 feet (463 m) a most important unconformity underlines the boundary between the last evaporitic upper Miocene sediments and those open marine sediments beginning the Pliocene sedimentary cycle. Indeed, the clays of the Raf-Raf formation, which here are Tabianian (Lower Pliocene) in age due to the presence of very scarce *Globorotalia margaritae*, which contrast sharply in their lithology as well in their planktonic foraminiferal content with the azoic gypsum layers of the Oued bel Khedim formation. They testify to the restoration of normal marine environmental conditions, perhaps for a shallow water connection to the deep sea.

THE OSTRACOD ASSEMBLAGES AND THEIR SIGNIFICANCE

Text-figure 3 shows the stratigraphical and quantitative distribution of 51 selected ostracod species.

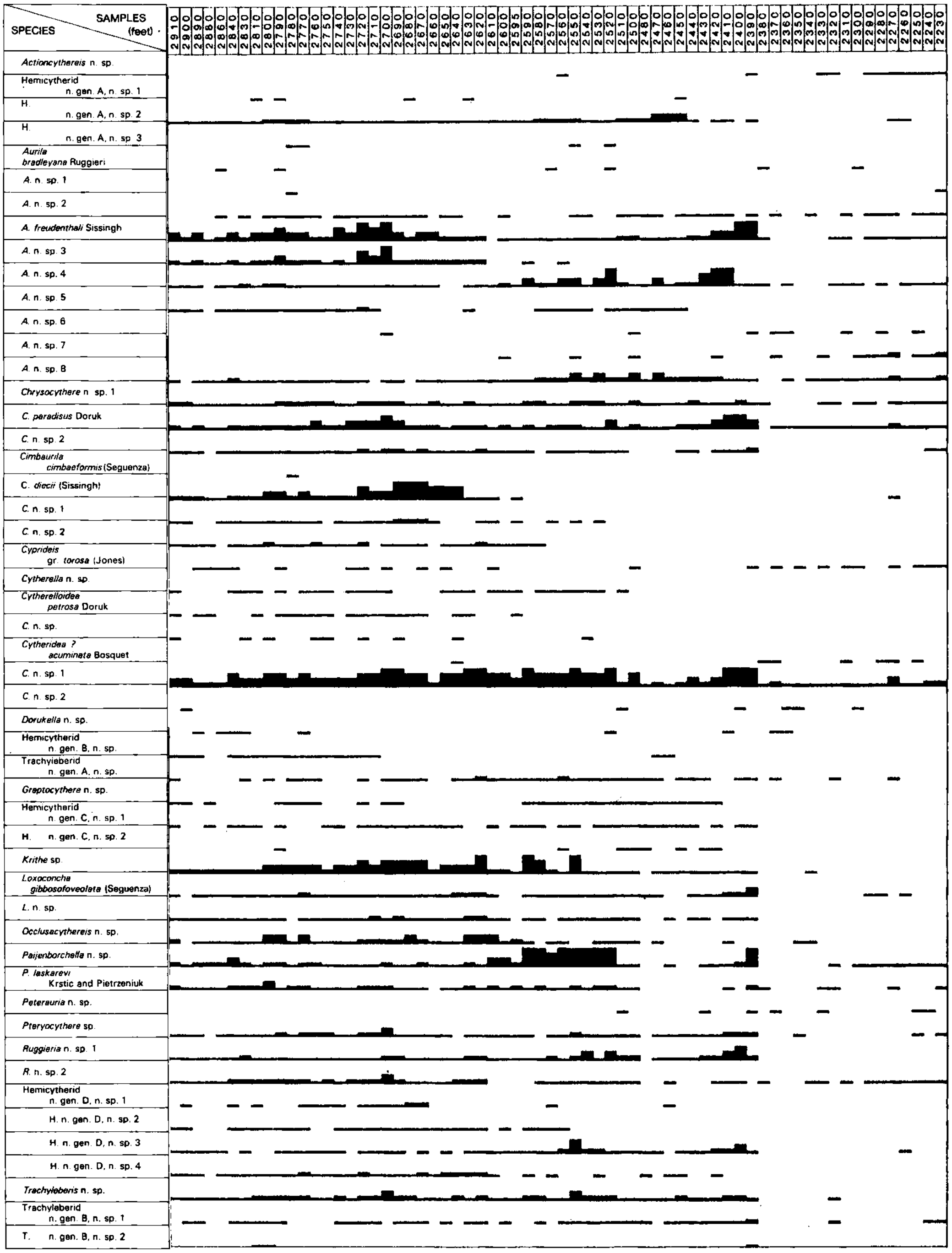
On the basis of our data on the vertical evolution of the ostracod assemblages, we have been able to reach the following preliminary conclusions:

1) The number of species and specimens was generally very high during the Lower Messinian, with three abundance maxima corresponding to the following levels: A) just above the Tortonian-Lower Messinian boundary (± sample 2700 feet); B) at about the median part of the Lower Messinian (± sample 2390 feet); and C) just before the Lower-Upper Messinian boundary (± 2040 feet).

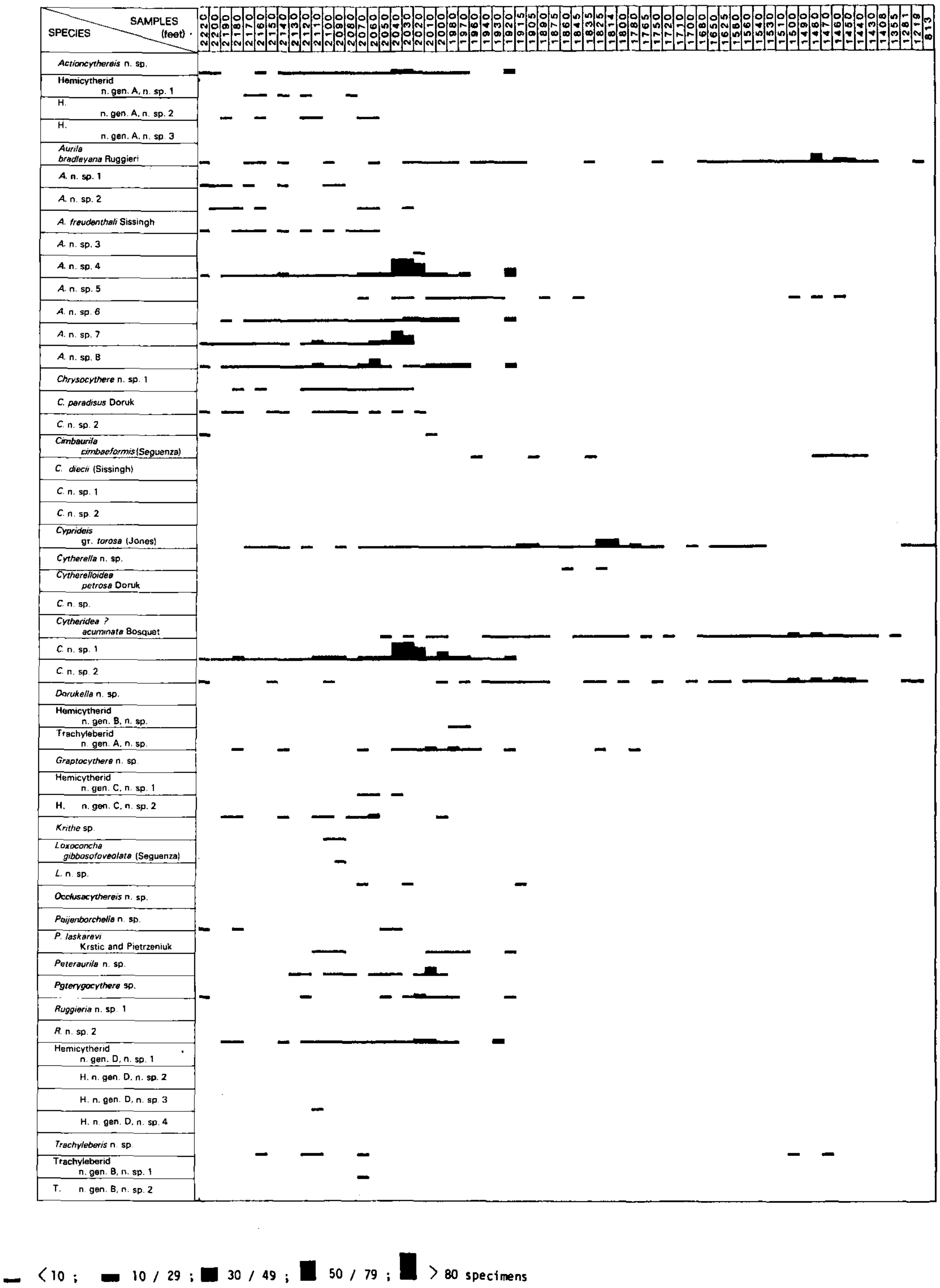
The Tortonian-Messinian boundary did not show any apparent important biostratigraphical event for the species taken into consideration. In fact, the assemblages found in the Tortonian detrital sediments are all considered as contaminations from the above Messinian.

2) During the Lower Messinian, mainly corresponding to peak B, we noted the last occurrence of the following 12 species which seemed to characterise the sediments of the older part of the Lower Messinian : *Aurila* n. sp. 3, *Cimbaurila* n. sp. 1, *Cimbaurila* n. sp. 2, *Cytherella* n. sp. 1, *Cytherelloidea petrosa Doruk*, *Cytherelloidea* n. sp. 1, *Graptocythere* n. sp. 1, *Occlusacythereis* n. sp. 1, *Ruggieria* n. sp. 1, Hemicytherid n. sp. 1, Hemicytherid n. sp. 2 and Hemicytherid n. sp. 4.

3) The part of the Lower Messinian between samples at 2380 feet and 2080 feet (a thickness of about 100 m) showed an abrupt decrease in the abundance of specimens, whereas the number of species (in spite of the disapperarance of the previously cited 12 species) remains constant. This interval was followed in the upper part of the Lower Messinian by a new abundance maximum for the following selected species found in the levels 1970 feet to 2070 feet : *Aurila* n. sp. 4, *Aurila* n. sp. 8, Trachyleberid n. sp. 3, *Cytheridea* n. sp. 1, and *Pterygocythere* sp. We also noted that some species such as *Aurila* n. sp. 6, *Aurila* n. sp. 7, and *Actinocythereis* n. sp. 1 reached their maximum abundance at the end of the Lower Messinian, being represented by only a few specimens in the older sediments.



TEXT–FIG. 3—Stratigraphical distribution and abundance of some ostracod species in the Well Ashtart-1 sequence.


SPECIES
SAMPLES (feet)
2220
2200
2190
2180
2170
2160
2150
2140
2130
2120
2110
2100
2090
2080
2070
2060
2050
2040
2030
2020
2010
2000
1980
1970
1960
1940
1930
1920
1915
1905
1890
1875
1860
1845
1835
1825
1814
1800
1780
1765
1750
1720
1710
1700
1680
1650
1625
1580
1560
1540
1530
1510
1500
1490
1480
1470
1460
1450
1440
1430
1408
1355
1281
1219
813
Actinocythereis n. sp.
Hemicytherid n. gen. A, n. sp. 1
H. n. gen. A, n. sp. 2
H. n. gen. A, n. sp. 3
Aurila bradleyana Ruggieri
A. n. sp. 1
A. n. sp. 2
A. freudenthali Sissingh
A. n. sp. 3
A. n. sp. 4
A. n. sp. 5
A. n. sp. 6
A. n. sp. 7
A. n. sp. 8
Chrysocythere n. sp. 1
C. paradisus Doruk
C. n. sp. 2
Cimbaurila cimbaeformis (Seguenza)
C. diecii (Sissingh)
C. n. sp. 1
C. n. sp. 2
Cyprideis gr. torosa (Jones)
Cytherella n. sp.
Cytherelloidea petrosa Doruk
C. n. sp.
Cytheridea ? acuminata Bosquet
C. n. sp. 1
C. n. sp. 2
Dorukella n. sp.
Hemicytherid n. gen. B, n. sp.
Trachyleberid n. gen. A, n. sp.
Graptocythere n. sp.
Hemicytherid n. gen. C, n. sp. 1
H. n. gen. C, n. sp. 2
Krithe sp.
Loxoconcha gibbosofoveolata (Seguenza)
L. n. sp.
Occlusacythereis n. sp.
Paijenborchella n. sp.
P. laskarevi Krstic and Pietrzeniuk
Peteraurila n. sp.
Pterygocythere sp.
Ruggieria n. sp. 1
R. n. sp. 2
Hemicytherid n. gen. D, n. sp. 1
H. n. gen. D, n. sp. 2
H. n. gen. D, n. sp. 3
H. n. gen. D, n. sp. 4
Trachyleberis n. sp.
Trachyleberid n. gen. B, n. sp. 1
T. n. gen. B, n. sp. 2
< 10 ; 10 / 29 ; 30 / 49 ; 50 / 79 ; > 80 specimens

4) The end of the Lower Messinian and the subsequent Upper Messinian, samples 1960 feet to 1530 feet characterised by gypsiferous clays, showed the abrupt extinction of most of the marine species and the survival of euryhaline species such as *Cytheridea*? *acuminata* Bosquet, *Cytheridea* n. sp. 2, and an increase in the brackish species *Cyprideis* gr. *torosa* (Jones).

5) The Upper Messinian, the top part of which is completely azoic, corresponds to the well known "salinity crisis" and was followed by Pliocene sediments which showed the re-establishment of normal marine conditions, even if the ostracod fauna taken into consideration appeared rather scarce and poorly diversified. It was represented by *Aurila bradleyana* Ruggieri, *Aurila* n. sp. 5, *Cimbaurila cimbaeformis* (Seguenza) and *Cytheridea* n. sp. 2.

6) The bathymetry of the studied sequence after the Tortonian up to the base of the Upper Messinian was clearly included within the depth of the continental shelf. The presence of numerous species of *Aurila, Cimbaurila, Peteraurila, Loxoconcha,* Hemicytherids, *Xestoleberis, Cytheretta, Callistocythere, Tenedocythere, Urocythereis* and *Sagmatocythere* seems to indicate a general bathymetry not exceeding 70 m. But in addition to these genera, we frequently noted the presence of species of *Chrysocythere, Trachyleberis, Acanthocythereis, Ruggieria, Costa, Pterygocythereis, Semicytherura, Krithe* and *Polycope,* the known habitat of which is at depths exceeding 80 m. Moreover, we observed the constant occurrence of very near-shore and euryhaline genera such as *Cytheridea, Paijenborchella, Miocyprideis* and *Caudites.* The evaluation of the those assemblages suggests that the palaeobathymetry during the Lower Messinian was about 80 to 100 m, in the proximity of a coral-reef environment and with strong influence from a shallower environment. It also suggests the periodic inlet of seasonal brackish-water elements, possibly from sebkhas bordering the coast.

During the Lower Messinian, we observed the disappearence of some species characteristic of the deeper environment and belonging to the genera *Krithe, Ruggieria, Trachyleberis* and *Occlusacythereis,* suggesting a regression phenomenon.

Just before the end of the Lower Messinian, at the time underlined by Peak C, normal marine conditions were temporarily re-established, but only some of the species taken into consideration were able to recolonise the environment and reach their previous quantitative levels.

7) The Upper Messinian was characterised by the catastrophic event known as the "Mediterranean salinity crisis" which caused the complete destruction of the marine ostracod fauna and the development of a brackish environment as demonstrated by the colonisation by *Cyprideis torosa* and the survival of some euryhaline species of *Cytheridea* before all kinds of life became extinct.

8) Above the sample at 1530 feet, and corresponding to the first Lower Pliocene sediments, the marine environment is re-established. The ostracod fauna however, is very reduced in number of species, among them : *Aurila bradleyana, Aurila* n. sp. 5, *Cimbaurila cimbaeformis, Cytheridea*? *acuminata, Cytheridea* n. sp. 2 and *Trachyleberis* n. sp. 1. Some of these show a certain quantitative abundance (*Aurila bradleyana* and *Cytheridea* n. sp. 2).

9) As previously mentioned, the Messinian sedimentary sequence is 380 m thick. On the basis of the previous palaeobathymetrical interpretation, it appears evident that during the marine Lower Messinian (250 m thick) the bathymetry was more or less constant. This means that during this interval a subsidence of at least 250 m occurred.

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DISCUSSION

Peypouquet: Do you have any evidence of tectonic events in this Dullmy well?

Bonaduce: Tectonic events may have happened duing the higher part of the lower Messinian during which most of the deeper species disappear but all, the area is connected with the historical evolution of the Mediterranean which was certainly controlled to some extent by tectonic events.

Peypouquet: Most of the Messinian ostracode fauna is no longer present in the Pliocene and just a relatively few species have been able to cross the "sálinity crisis" barrier.

Depositional Paleoecology of Miocene Ostracodes in the Monterey Formation, Laguna Hills, Southern California, U.S.A.

Kenneth L. Finger
Chevron Oil Field Research Company, California, U.S.A.

Abstract

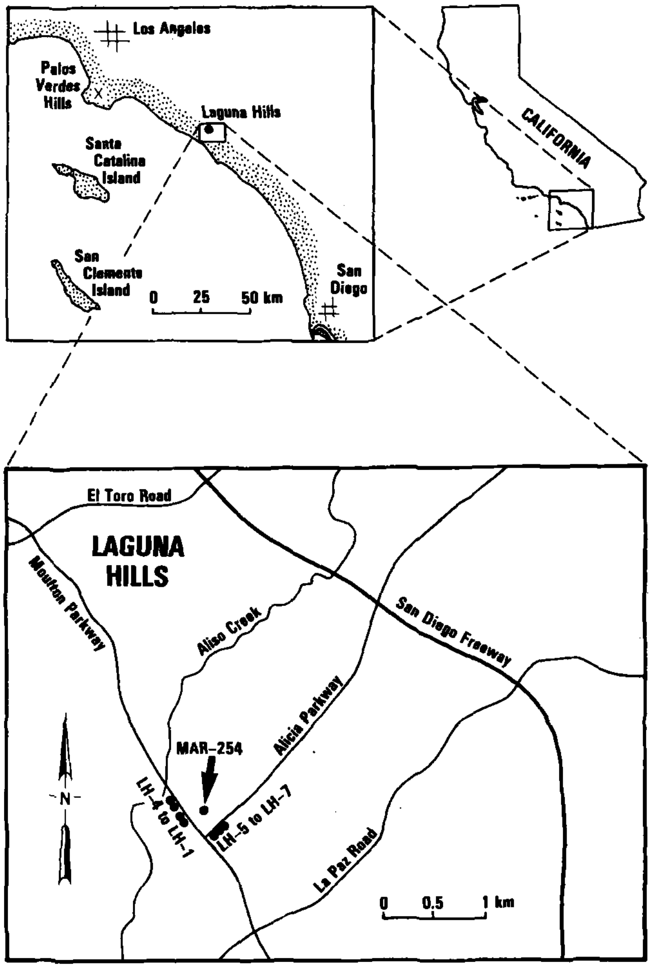
Outcrop sections of the lower Monterey Formation in Laguna Hills, southern California, contain an unusual early middle Miocene (Luisian Stage) subtropical marine fauna of macroinvertebrates and microfossils. The basal exposures consist of patch reefs constructed by serpulids, oysters, and bryozoans interbedded with sands, silts, and muds dominated by bivalves. In the overlying section, turbidite sands yield abundant ostracodes. The purpose of this study is to analyze this ostracode assemblage in relation to the paleoenvironment of deposition.

Ten genera and 14 new species comprise the ostracode assemblage recovered at one of the localities where the turbidites had been exposed: *Microcytherura* sp. (33%), *Aurila* sp. A (27%), *Aurila* sp. B (11%), *Aurila* sp. C (7%), "*Cytheretta*" sp. (5%), *Loxoconcha* (*Loxoconcha*) sp. (4%), *Ambostracon* sp. (3%), *Loxoconcha* (*Palmoconcha*) cf. *L.* (*P.*) *polugari* Finger (3%), *Paracosta* cf. *P. huddlestoni* Finger (3%), *Hamanella* cf. *H. implexa* Finger (2%), *Neonesidea* sp.? (<1%), *Cytherelloidea* sp. (<1%), "*Microcytherura*" sp. (<1%), and *Xestoleberis* sp. (<1%). The species of *Loxoconcha* (*Palmoconcha*), *Paracosta*, and *Hamanella* may be descendants of those previously described from the Oligo-Miocene Rincon Formation of central California. Rare specimens of other neritic taxa were obtained from nearby outcrops of this discontinuous unit.

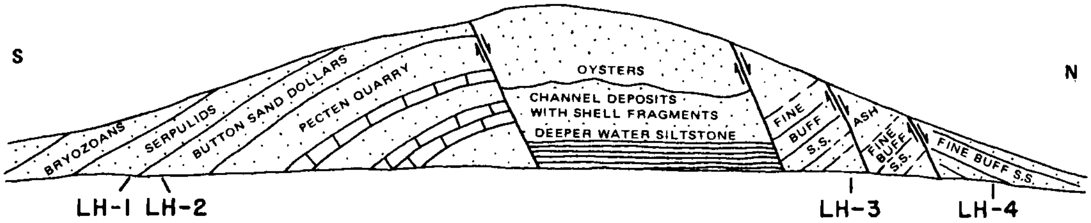
The ostracodes appear to be a mixed neritic assemblage, and most are preserved as complete carapaces, suggesting that they had been rapidly displaced and buried downslope. This mode of deposition is also evident in the associated foraminifers, which constitute a mixed assemblage of inner-neritic to upper middle-bathyal taxa. Mudstones within the superjacent section are barren of ostracodes but richer in bathyal foraminifers, suggesting that the embayment continued to get wider and deeper during the early middle Miocene.

Rapid basin subsidence is a tectonic phenomenon prevalent throughout the early and middle Miocene of California. Further study of basal sedimentary units along the California borderland could uncover additional ostracode assemblages that can be useful in determining the geologic, ecologic, and paleontologic history of the East Pacific Rim.

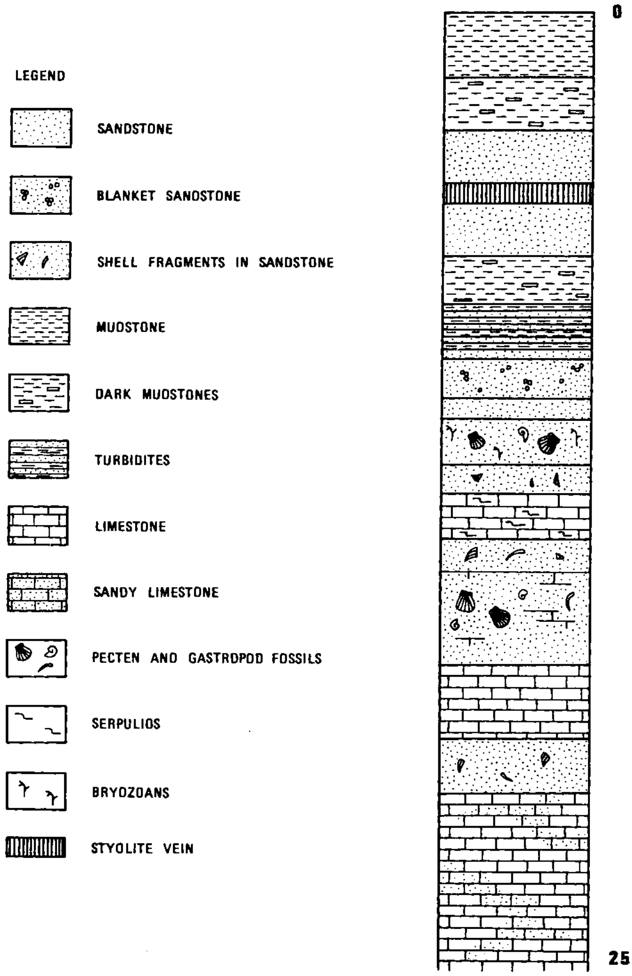
The Monterey Formation is one of the most geographically and geochronologically extensive lithostratigraphic units in the California Neogene. It has been the focal point of intensive study by academia, government, and industry because "it represents the confluence of tectonic, climatic, and oceanographic events which resulted in Miocene basin development coincident with intensified upwelling systems and high organic productivity" (Garrison and Douglas, 1981), and it is both a major source of, and reservoir for, hydrocarbons. Many fossil groups are documented in the literature on the Monterey Formation, including foraminifers, calcareous nannoplankton, siliceous microfossils, macroinvertebrates, fishes, and marine mammals, but not ostracodes. This may be attributed to the rarity of ostracodes in the predominantly low-oxygen bathyal deposits which characterize the Monterey Formation. If significant concentrations of marine ostracodes were to be encountered in this formation, they would most likely be found in those basal units which were deposited when the basins first subsided and incorporated displaced neritic sediments. This is often seen in the stratigraphic succession as a rapid and conformable transition from inner-neritic sands to deep-water mudstones. The occurrence of ostracodes in the Oligo-Miocene lower Rincon Formation of coastal central California (Finger, 1983a, b) exemplifies this phenomenon. A somewhat analogous situation encountered in the middle Miocene Monterey Formation of southern California is the subject of the present investigation. The purpose of this report is to determine the depositional paleoecology of these ostracodes.



Text-fig. 1—Location of Laguna Hills sample localities referred to in this study.



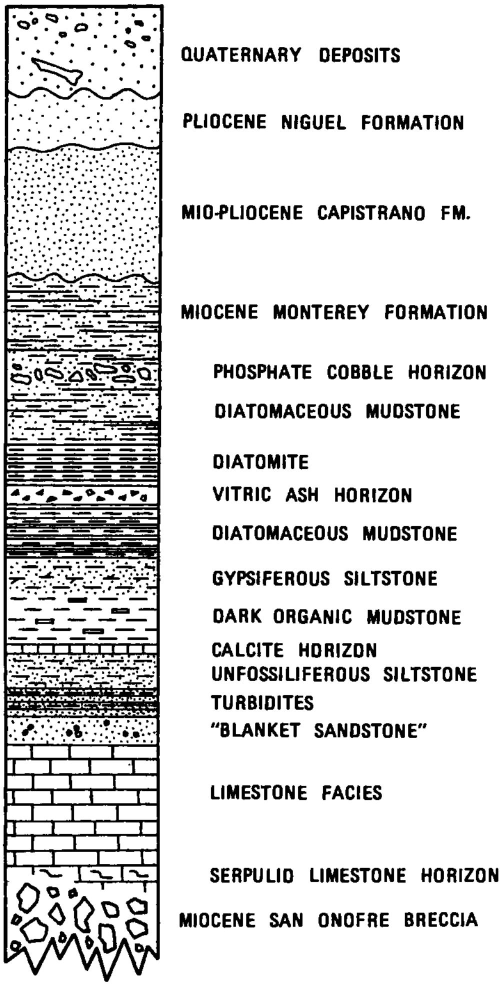
TEXT-FIG. 2—CSA81R bluff section along Moulton Parkway (Stadum, 1982), with demarcation of LH-1 to -4 samples analyzed in this study.



TEXT-FIG. 3—CSA81P columnar section of the Monterey Formation as previously exposed in sewer trenches near sample locality MAR-254 (Stadum, 1982).

MATERIALS

The ostracodes were collected in Laguna Hills, Orange County, in the Saddleback Valley region of southern California (Text-fig. 1). They occur in a basal sequence of the Monterey Formation which includes an unusual limestone deposit referred to as the "Pecten Reef" by local residents because it contains dinner-plate sized scallops; this limestone is actually a discontinuous series of small patch reefs interfingering with and covered by clastic sediments bearing abundant serpulids, oysters, bryozoans, button sand dollars, and pectens (Stadum, 1982, 1984; see Text-figs. 2–4). Because the area was targeted for extensive housing development, paleonotologists from the Los Angeles County Museum of Natural History and salvage teams from the Natural History Museum of Orange County acquired extensive collections of fossils from this region during the 1972–1982 interval. As is so often the case with California fossil localities, the majority of collecting sites have since been obliterated by suburban sprawl.



TEXT-FIG. 4—Generalized stratigraphic columnar section (Stadum, 1982) for Laguna Hills.

One of the lithologic units in the Laguna Hills area is a series of greenish-grey mudstone and unconsolidated calcareous sand turbidites. Stadum (1984, p. 87) noted that the sand is extremely rich in foraminifers, ostracodes, shell fragments, shark teeth, and fish bones and otoliths. Mr. Mark A. Roeder, one of the consultants involved in the collections, salvaged an entire lens of this sand (approximately 4 m^3) and some of the surrounding greenish-grey mudstone exposed on the surface of a graded area in the property immediately north of the intersection of Moulton and Alicia Parkways (Text-fig. 1; MAR-254). This material is equivalent to Stadum's (1982, 1984) locality CSA81N. After processing these sediments for fish teeth and otoliths, Mr. Roeder kindly presented me with a washed residue that was extremely rich in foraminifers and ostracodes, and an ample supply of unprocessed material from both lithologies. On a subsequent visit to the area in December, 1983, G. L. Armstrong and I collected seven samples (LH-1 to -7) from two nearby exposures (see Text-fig. 1) to supplement this study. Four sandstone samples (LH-1 to -4) were obtained from what remained of Stadum's (1982) CSA81R section along Moulton Parkway (Text-fig 2), even though there was no evidence in the field to suggest the presence of calcareous microfossils. The other three samples are slightly younger mudstones (LH-5 to -7) collected from six stratigraphic metres of section that had been exposed along the southeastern side of Alicia Parkway prior to grading. Abundant foraminifers were visible without magnification in two of these mudstones.

FAUNAL RECOVERY

Although abundant foraminifers were retrieved from four of the sandstones and two of the mudstones, only the siltstones and sandstones of MAR-254, LH-1, LH-3, and LH-4 yielded ostracodes. All of these ostracode-bearing sediments are from the turbidite unit stratigraphically positioned above the reef complex (Text-fig. 4).

The silty sand of MAR-254 contains approximately 8000 foraminifers and 900 ostracode valves per kg. Neither of these microfossils were recovered from the surrounding mudstone. Processing of both MAR-254 lithologies for siliceous microfossils and calcareous nannofossils yielded negative results.

Most of the ostracodes in MAR-254 are preserved as complete carapaces which have undergone slight dissolution. Preservation of complete carapaces has been enhanced by cementation of their internal margins with secondary calcite. Although the carapaces are not infilled, attempts to disarticulate them inevitably fragment the valves. Examination of marginal pore canals and muscle scars has been hindered by these preservational features. Further study and documentation of the microfauna is planned for a forthcoming publication.

The MAR-254 ostracode assemblage consists of 10 genera and 14 new species: *Microcytherura* sp. (33%), *Aurila* sp. A (27%), *Aurila* sp. B (11%), *Aurila* sp. C (7%), "*Cytheretta*" sp. (5%), *Loxoconcha* (*Loxoconcha*) sp. (4%), *Ambostracon* sp. (3%), *Loxoconcha* (*Palmoconcha*) cf. *L.* (*P.*) *polugari* Finger (3%), *Paracosta* cf. P. *huddlestoni* Finger (3%), *Hamanella* cf. *H. implexa* Finger (2%), *Neonesidea* sp.? (< 1%), *Cytherelloidea* sp. (< 1%), "*Microcytherura*" sp. (< 1%), and *Xestoleberis* sp. (< 1%).

Calcite cement made it particularly difficult to isolate clean and unbroken ostracodes from the sandstones along Moulton Parkway. One specimen of *Cytherella* was obtained from LH-1, and a few early instars of *Aurila* were retrieved from LH-3. LH-4 yielded a substantially richer assemblage which includes *Aurila, Hermanites, Loxoconcha, Loxocorniculum, Neonesidea*?, "*Paijenborchella*", and *Paracytheridea,* but most of the specimens are juveniles and/or too poorly preserved to warrant further study.

Most of the ostracode species recovered from Laguna Hills are illustrated as scanning electron micrographs in Plates 1 and 2.

BIOSTRATIGRAPHY

There are remarkable similarities between the Laguna Hills species of *Loxoconcha (Palmoconcha), Hamanella, Paracosta,* and "*Paijenborchella*", and those described from the Oligo-Miocene lower Rincon Formation approximately 250 km to the northwest (Finger, 1983a). The Laguna Hills species of *Paracosta* is morphologically and chronostratigraphically intermediate between *P. huddlestoni* Finger from the lower Rincon Formation and *P. simiensis* (LeRoy) from the upper Pliocene part of the Fernando Formation and the lower Pleistocene Santa Barbara Formation (see LeRoy, 1943; Cronin *et al.,* 1983).

Precise age-dating of the Laguna Hills section relies on other fossil groups which have been more extensively studied and correlated in the California Neogene. Stadum (1982) employed several consultants to analyze the local micropaleontology: H. Haga for palynomorphs, E. D. Milow for calcareous nannoplankton and siliceous microfossils, and A. D. Warren for foraminifers. Recovery of microfossils from the limestone was practically nil, whereas the sandstone and mudstone yielded significant associations of dinocysts, gymnosperm and angiosperm pollen, calcareous nannofossils, diatoms, silicoflagellates, ebridians, and foraminifers. The most diagnostic assemblages are those of the calcareous nannofossils, diatoms, and benthic foraminifers, each of which is characteristic of the early middle Miocene, 14–16 Mya. The same age is implied by the Luisian Stage benthic foraminiferal assemblages isolated from the neritic sands and bathyal mudstones analyzed in the present study.

PALEOECOLOGY

A subtropical to warm-temperate biota inhabited coastal California during the early middle Miocene. Stadum (1982, 1984) has determined the geologic and ecologic history of the Laguna Hills section in considerable detail; the following is a slightly modified version of her interpretation:

The depositional environment of the limestone reef was a submerging northward trending strait with a steep escarpment to the west and a semi-arid low-relief plain to the east across which a river meandered through a marsh or swamp. Submarine toes of debris fans extending from the schistose highland to the west formed a substrate on which finer sediments accumulated and serpulid worms flourished. Eventually, the limey tubes of these animals formed a series of welded frameworks, or patch reefs. Oysters added to the growth of these reefs in the fluviomarine areas subject to fluctuating salinities and turbid waters. Cheilostome bryozoans replaced this community wherever normal marine salinities and clear waters prevailed, as warm marine currents

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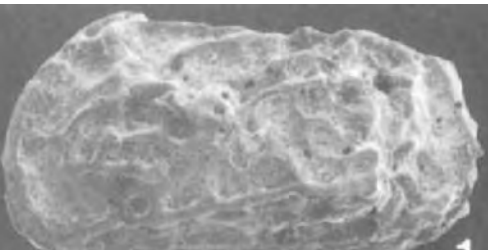
PLATE 1—Fig. 1. *Ambostracon* sp., left lateral view of female carapace, sample no. MAR-254, ×75. Fig. 2. *Microcytherura* sp., right lateral view of female carapace, sample no. MAR-254, ×73. Fig. 3. *Cytherelloidea* sp., left valve of male carapace, sample no. MAR-254, ×60. Fig. 4. *Hamanella* cf. *H. implexa* Finger, right lateral view of female carapace, sample no. MAR-254, ×68. Fig. 5. "*Microcytherura*" sp., left lateral view of female carapace, sample no. MAR-254, ×77. Fig. 6. "*Cytheretta*" sp., left lateral view of male carapace, sample no. MAR-254, ×81. Fig. 7. *Neonesidea* sp.?, right lateral view of female? carapace, sample no. MAR-254, ×37. Fig. 8. *Paracosta* cf. *P. huddlestoni* Finger, left lateral view of female carapace, sample no. MAR-254, ×69. Fig. 9. *Loxoconcha (Loxoconcha)* sp., right lateral view of male? carapace, sample no. MAR-254, ×80. Fig. 10. *Loxoconcha (Palmoconcha)* cf. *L. (P.) polugari* Finger, left lateral view of female carapace, sample no. MAR-254, ×111.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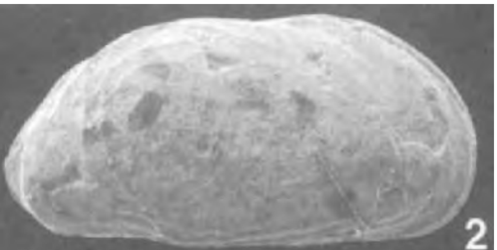
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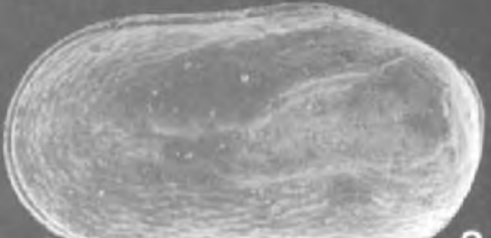
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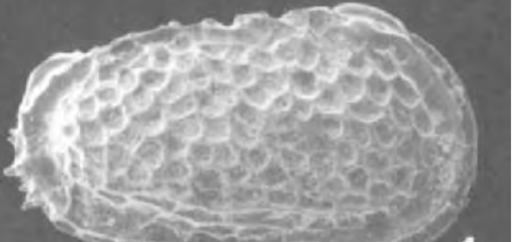
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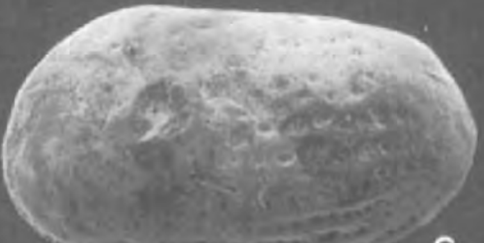
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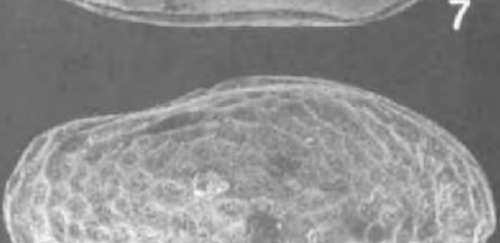
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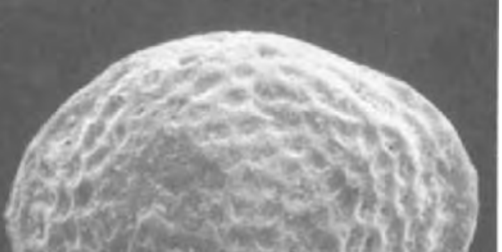
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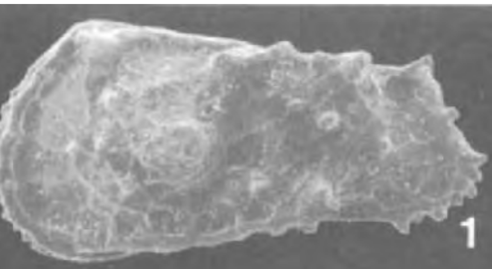
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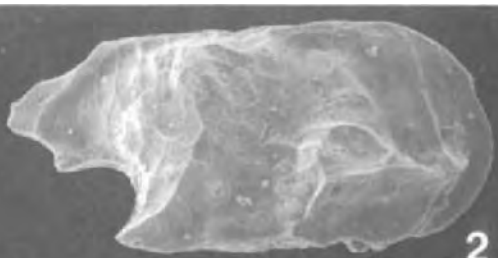
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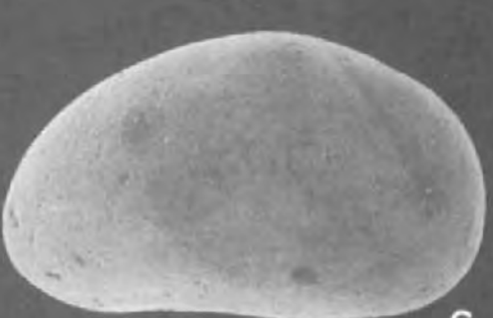
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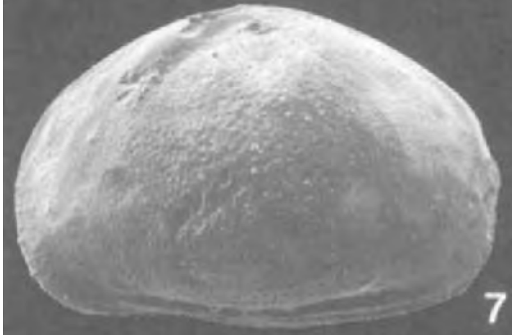
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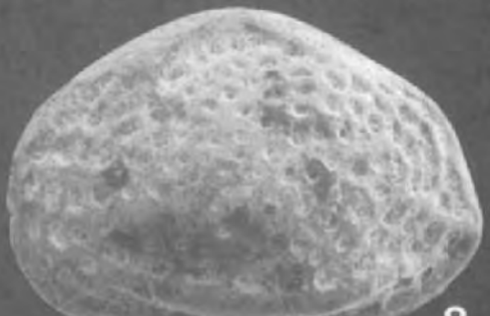
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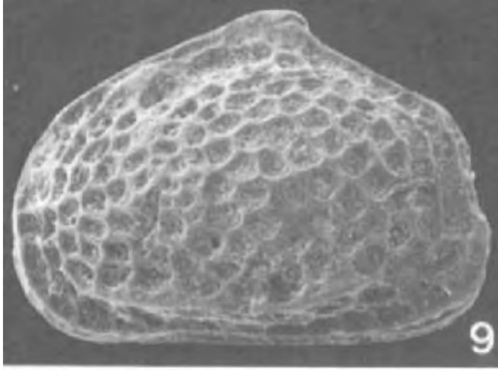
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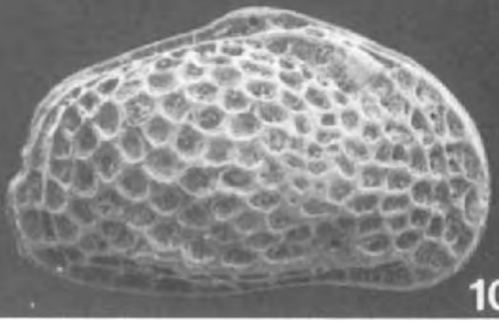
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from the south circulated through the embayment. Other benthic invertebrates patchily distributed among the reefs included echinoids, barnacles, bivalves, gastropods, limpets, and boring sponges. As the embayment began to subside, nearshore sands and shell fragments blanketed the reefs. Rapid subsidence of the basin to bathyal depths resulted in turbidity currents which spilled out a series of silty sands and muds on the basin floor. The turbidite sands incorporated rich assemblages of inner-neritic (0–50 m) to upper middle-bathyal (500–1500 m) benthic foraminifers, with a predominance of neritic species, as determined from the upper-depth limits of benthic foraminifers designated and subsequently modified by Ingle (1980; 1985, unpubl. data). Downslope displacement of sediments was rapid enough to bury alive ostracodes derived from the neritic zone, as evidenced by the predominance of complete carapaces in their assemblage (see Oertli, 1971; Finger, 1983a, b). These sands also incorporated calcareous nannoplankton and planktic foraminifers which were being transported into the bay from the open ocean.

The mudstones higher in the section contain assemblages of foraminifers, palynomorphs, and siliceous microfossils, as well as some of the earlier macrofauna. Benthic foraminiferal species indicate that the basin floor was still within upper middle-bathyal (500–1500 m) depths, but bathyal species now predominate in the assemblage. Significant downslope displacement is evidenced by the inclusion of inner-neritic to upper bathyal foraminifers, terrestrial palynomorphs, and remnants of the reef macrofauna. Planktic assemblages of foraminifers, diatoms, silicoflagellates, and ebridians precipitated into these muds from overlying oceanic currents. Ostracodes are not present in these bathyal sediments. The contrast between the sandstone and mudstone facies, which may represent proximal and distal turbidites, respectively, suggests that the embayment continued to subside and widen during this interval of time. Subsequent deposition of diatomites resulted from increased upwelling during the middle to late Miocene cooling trend and preceded gradual emergence of the area from the Pliocene to the Recent.

It is somewhat difficult to explain why ostracodes and foraminifers are more abundant in the turbidite sands than in the earlier reef deposits. Perhaps this is a preservational factor, as many of the earlier units are well-indurated with calcite cement.

PALEOGEOGRAPHY

In addition to those found in the Laguna Hills area, significant limestone beds in the Monterey Formation have been recorded from Palos Verdes Hills (Bramlette, 1946), west of Santa Barbara near Naples (Bramlette, 1946), San Clemente Island (Susuki and Stadum, 1978; Vedder and Howell, 1976; Vedder and Moore, 1976), and Santa Catalina Island (Vedder and Howell, 1976; Vedder and Moore, 1976). Most of these occurrences are unrelated. On San Clemente Island, however, Susuki and Stadum (1978) collected an ostracode-bearing loosely consolidated orange sandstone (sample locality 6317) in a sequence similar to that of Laguna Hills. T. Susuki presented me with some washed residue from this sample, which contains a shallow-marine ostracode assemblage

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PLATE 2—Fig. 1. *Hermanites* sp., external view of left valve, sample no. LH-4, ×110. Fig. 2. *Paracytheridea* sp., external view of right valve, sample no. LH-4, ×150. Fig. 3. *Cytherella* sp., external view of right valve, sample no. LH-1, ×90. Fig. 4. "*Paijenborchella*" aff. "*P.*" sp. Finger (1983a), external view of left valve, sample no. LH-4, ×120. Fig. 5. *Loxocorniculum* sp., external view of left valve, sample no. LH-4, ×130. Fig. 6. *Xestoleberis* sp., left lateral view of female carapace, sample no. MAR-254, ×110. Fig. 7. *Aurila* sp. B, left lateral view of female carapace, sample no. MAR-254, ×72. Fig. 8. *Aurila* sp. C, left lateral view of female carapace, sample no. MAR-254, ×79. Fig. 9. *Aurila* sp. A, left lateral view of female carapace, sample no. MAR-254, ×74 (the pronounced anterior cardinal angle of the left valve is a variation seen in both sexes of this species). Fig. 10. *Aurila* sp. A, right lateral view of male carapace, sample no. MAR-254, ×74.

dominated by species of *Aurila* and *Ambostracon,* and includes some of the same species recognized in Laguna Hills. There can be little doubt that these assemblages are part of the same fauna.

CONCLUSIONS

The neritic ostracode assemblage recovered from Laguna Hills occurs in a turbidite sequence which was deposited in an embayment as it subsided to upper middle-bathyal depths during the early middle Miocene. Predominance of complete carapaces supports other evidence for this mode of deposition. The turbidite unit is stratigraphically above a nearshore patch-reef complex and below upper middle-bathyal mudstones. These superjacent mudstones, dominated by bathyal foraminifers and devoid of ostracodes, are more typical of the lower Monterey Formation elsewhere.

In a previous study, paleontologic and lithostratigraphic analyses of the lower Rincon Formation reveal much about the development of the Santa Barbara Embayment (Finger, 1983a, b). Similarly, interpretation of the lower Monterey Formation in Laguna Hills provides a geologic record of the early Santa Ana Embayment. Ostracodes complement other data useful in determining the depositional histories of these basins. Further study of the basal Monterey Formation and equivalent units could uncover additional ostracode assemblages of similar value in reconstructing the evolution of the California Continental Borderland. Knowledge of such assemblages is critical to our understanding of the ecology, phylogeny, and evolution of the East Pacific fauna. Another piece in this very incomplete puzzle is anticipated from a more detailed documentation of the calcareous microfauna recovered from Laguna Hills and San Clemente Island.

ACKNOWLEDGEMENTS

I would like to thank a number of colleagues who have assisted me in this study: M. A. Roeder brought the Laguna Hills ostracodes to my attention and provided the ostracode-rich sample; G. L. Armstrong aided in fieldwork, sample picking, scanning electron microscopy, and drafting of the figures; C. J. Ford processed the samples; E. M. Brouwers and R. C. Whatley reviewed my generic assignments. Much of the information conveyed in this report was extracted from C. L. Stadum's excellent thesis on the subject area, and I appreciate the time she spent discussing it with me and reviewing this manuscript. Chevron Oil Field Research Company and Chevron U.S.A., Inc. (Western Division) kindly granted publication permission. T. M. Cronin was most gracious in presenting this study for me at the Ninth International Symposium on Ostracoda.

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Middle Miocene Ostracoda from Northern Iraq

SALEH K. KHALAF
Mosul University, Mosul-Iraq.

ABSTRACT

Four new ostracod species are described and figured from the lower Fars Formation (M. Miocene) of Northern Iraq. These ostracods show strong affinities with those of the adjacent areas.

INTRODUCTION

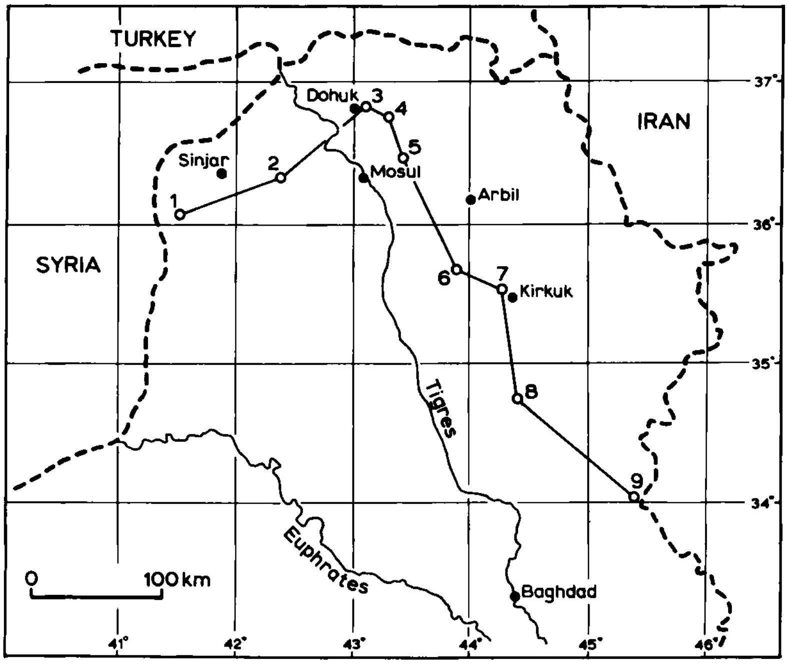
In Iraq, ostracods have received little attention from micropalaeontologists. As far as the author is aware there is no published work on Tertiary Ostracoda from Iraq. The present paper is part of a comprehensive study of the Middle Miocene Ostracoda from Northern Iraq in which nine sections of the Lower Fars Formation have been studied in detail (Text-fig. 1).

The Miocene in Iraq is characterised by a quiet tectonic regime, slight subsidence and wide transgression with the development of a relatively broad shallow basin which is in-filled with sediments that can be divided into a lower and an upper cycle. The transgression started in the lower Miocene with the deposition of the lagoonal Euphrates limestone. Deposition during the Lower Miocene is in accordance with movements which caused the deposition of the Dhiban anhydrite during which the basin became partially or wholly enclosed. After a break in sedimentations the Middle Miocene cycle started with the deposition of a shallow lagoonal limestone (Jeribe) and ended with a regression caused by the movements indicated by the basal Fars conglomerate. The following transgression led to the deposition of the Lower Fars Formation, which represents the most widespread and stratigraphically important part of the Fars group in Iraq. Lithologically, the formation consists of alternations of gypsum, anhydrite, limestone, clay, marl and siltstone. In the Kirkuk area, according to Kitchen (1927), the formation can be subdivided into a number of informal units. He recognized and designated within each unit a number of limestone markers. From bottom to top these units are as follows:

a. Transition Beds,
b. Saliferous Beds,
c. Seepage Beds,
d. Upper Red Beds.

According to Al-Mubark (1978), in the Sinjar area, the Lower Fars Formation may be divided into two members.

Lower member: This member is mainly composed of thick, massive gypsum with interbedded thin horizons of limestone, occasionally with yellowish-green marl below, or alternating with, the limestone.



1. Tel-Hajer well 1.
2. Shek Ibrahim section
3. Dohuk section
4. Shaikhan section
5. Bashiqa section
6. Bai Hassan well 33.
7. Kirkuk well 208.
8. Hamrin well 2.
9. Naft Khana well 34.

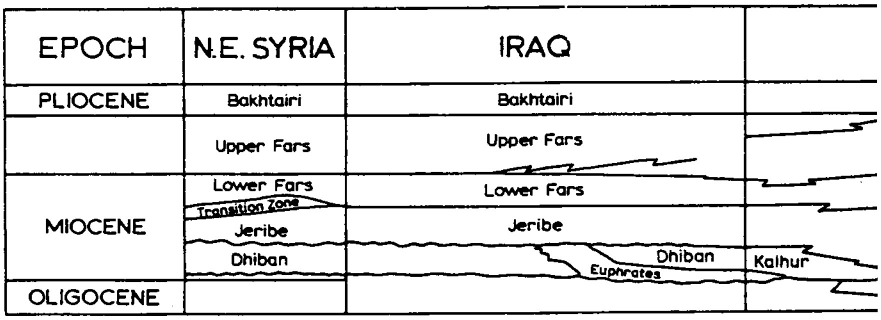
TEXT-FIG. 1—Showing locations of the studied sections.

Upper member: This is represented by claystone, marl, limestone and gypsum in regular sequence.

The distribution of the Lower Fars is affected by the structure of the surrounding area, *i.e.* it is affected by the tectonics. In Iraq the formation is limited in its distribution by the Arabian shield to the southwest and the Zagros range to the northeast, which was already rising at the time of the Lower Fars deposition.

The Lower Fars Formation is not differentiated in Turkey, although Altinli (1966) has described molasse which included facies equivalents of the Lower Fars Formation. In Syria, on the other hand, the formation concerned is widely distributed in the Al-Jezira area and extends towards the Syrian-Turkish border. In Saudia Arabia, the formation has as its equivalent the Dam Formation which has a marine fauna identical with that of the lower Fars Formation (Power *et al.*, 1967) (Text-fig. 2).

Repository.—All figured specimens are deposited in the Tertiary collection of the Geology Dept.,



TEXT-FIG. 2—Correlation between the Miocene in N.E. Syria, Iraq, Iran, Kuwait and Saudi Arabia. Modified (after

Hull University, England.

SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA G.W. Müller, 1894
Family CYTHERIDEINAE Sars, 1925
Genus MIOCYPRIDEIS Kollmann, 1960

Type species.—*Miocyprideis janoscheki* Kollmann, 1960

MIOCYPRIDEIS OVALIS n. sp.
(Pl. 1, figs. 6–12)

Derivation of name.—In reference to its oval outline.

Holotype.—A male carapace HU. 277 T. 13.

Paratypes.—Six specimens HU. 277 T. 14, 1–6.

Type horizon.—M. Miocene, L. Fars Formation, Bed no. 20, sample SH. II.

Type locality.—Sheikhan anticline, southern limb, 27 km, N. E. of Mosul City.

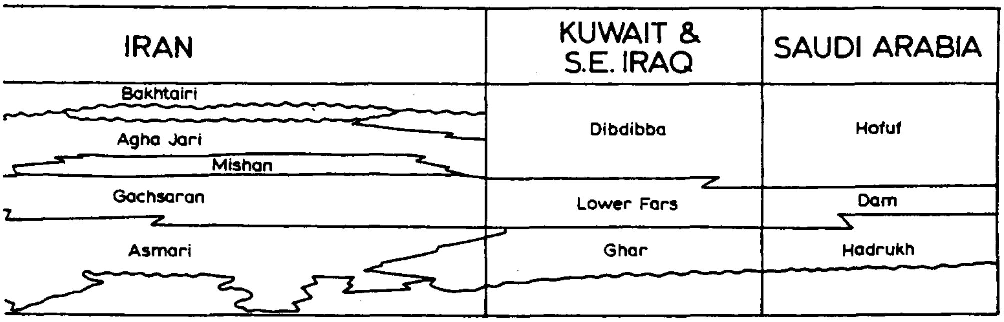
Material.—Two hundred specimens.

Diagnosis.—A species of *Miocyprideis* with wide, flat anterior margin, lower than the rest of the valve and forming a distinct furrow. Surface strongly pitted. The flat ventral margin is horizontal in the right and convex in the left valve.

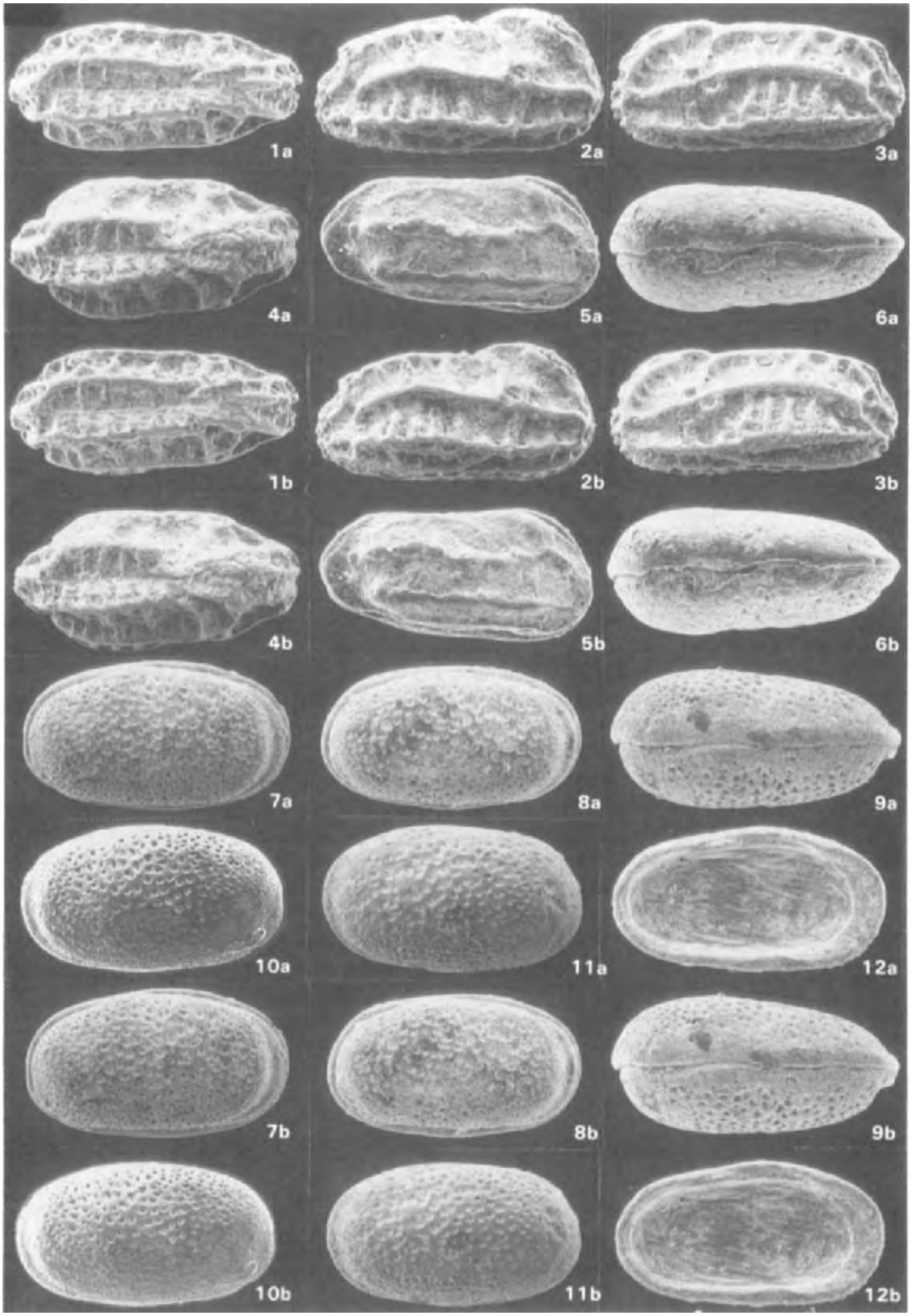
Description.—Carapace elongate, ovate in lateral view, greatest height anterior to the middle, greatest length at the mid-height.

Anterior margin broadly, obliquely rounded, lower than the rest of the carapace and very distinct. Some specimens show a trace of marginal denticulation. Posterior margin obliquely truncated in the right valve, evenly rounded in the left.

Dorsal margin slightly convex with rounded anterior and posterior corners, ventral margin flat and horizontal in the right valve, sinuate in the left valve. Carapace inflated posteriorly and anteriorly, slightly lower at the middle. Lateral surface coarsely pitted, coarse and dense pits centrally, becoming finer and tending to arrange themselves in parallel rows along the ventral margin. Left valve larger than the right, overlapping along the entire margin, except just behind the mid-dorsal margin where the two valves coincide. Sexual dimorphism pronounced, the presumed males narrower and more elongate than the presumed females. Sexual dimorphism is more distinct in dorsal view. In dorsal view carapace pear-shaped, swollen and rounded posteriorly, narrower anteriorly; maximum thickness and width in the posterior half, the male slightly slimmer in dorsal



G. A. James and J. G. Wynd, 1965).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view than the female. Internally, line of concrescence and inner margin coincide and run parallel to the outer margin; marginal pore canals simple, moderate in number. A distinctive flange and selvage run subperipherally. Muscle scars and hinge as for the genus; normal pore canals not numerous, scattered over the surface.

Dimensions of figured specimens.—

Holotype: ♂carapace HU. 277 T. 13, Pl. 1, figs. 7, 10; L = 740 μm, H = 440 μm.
Paratype: ♂carapace HU. 277 T. 14.1, Pl. 1, figs. 8, 11; L = 730 μm, H = 420 μm.
Paratype: ♂carapace HU. 277 T. 14.2, Pl. 1, fig. 6; L = 745 μm, H = 440 μm, W = 340 μm.
Paratype: ♀caraapce HU. 277 T. 14.3, Pl. 1, fig. 9; L = 710 μm, H = 430 μm, W = 380 μm.
Paratype: LVI HU. 277 T. 14.4, Pl. 1, fig. 12; L = 680 μm, H = 370 μm.

Affinities and Differences.—This species has some resmeblance to *Miocyprideis iranica* Krstic, 1979, but the latter differs in being higher and having more rounded anterior and posterior ends and a covenx dorsal margin. From *Miocyprideis fortisensis* Keij, 1955, the present species differs in the absence of the small rounded depression and group of vertical furrows beneath the anterior cardinal angle. *M. ovalis* sp. nov. shows some similarities to *Miocyprideis* cf. *spinulosa* Brady in Gramann (1971), but the latter differs in having narrower anterior and posterior ends, being less high and having slightly coarser pits covering the lateral surface. *Miocyprideis* sp. Bold, 1976 differs in having dense pits and in being narrower posteriorly and less high.

Distribution.—The present species was found at the Sheikh Ibrahim, Dohuk, Sheikhan, Bashiqa, Bai-Hassan, Krikuk and Naft-Khana, localities in Northern Iraq.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948
Tribe COSTAINI Hartmann and Puri, 1974
Genus CHRYSOCYTHERE Ruggieri, 1961

Type species.—*Chrysocythere cataphracta* Ruggieri, 1961

CHRYSOCYTHERE NAQIBI Khalaf, 1982
(Pl. 1, figs. 1–4)

Chrysocythere naqibi KHALAF, 1982, 55–58.

Figured specimens.—Holotype, ♀carapace HU. 275 T. 13, paratype, ♂carapace HU. 275 T. 14.

Horizon.—M. Miocene.

Locality.—Sheikh Ibrahim anticline, southern limb, N. W. Iraq, 45 km west of Mosul City, L. Fars Formation, Bed no. 50; M. Miocene: lat. 36° 18′ N, long. 42° 39′ E.

Material.—Two specimens.

Description.—Carapace subrectangular in lateral view, greatest height at the anterior cardinal angle, greatest length passing through mid-height.

Anterior margin obliquely rounded, decorated with marginal denticulations and marginal ridge, commencing at the anterodorsal corner and continuing along the anterior margin to join the ventral

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PLATE 1—Figs. 1–4. *Chrysocythere naqibi* Khalaf, 1982. Fig. 1. Paratype, male carapace, dorsal view, HU. 275. T. 14. ×46. Fig. 2. Holotype, female carapace from right, HU. 275. T. 13. ×51. Fig. 3. Paratype, male carapace from left, HU. 275. T. 14. ×47. Fig. 4. Holotype, female carapace dorsal view, HU. 275. T. 13. ×51. Fig. 5. *Ruggieria* (*Ruggieria*) *nova* n. sp. Fig. 5. Holotype female carapace from right, HU. 278. T. 35. ×56. Figs. 6–12. *Miocyprideis ovalis* n. sp. Fig. 6. Paratype, male carapace dorsal view, HU. 277. T. 14.2. ×63. Fig. 7. Holotype, male carapace from right, HU. 277. T. 13. ×58. Fig. 8. Paratype, male carapace from right, HU. 277. T. 14.1. ×58. Fig. 9. Paratype female carapace dorsal view, HU. 277. T. 14.3. ×66. Fig. 10. Holotype, male carapace from left, HU. 277. T. 13. ×57. Fig. 11. Paratype, male carapace from left, HU. 277. T. 14.1. ×58. Fig. 12. Paratype, left valve internal view, HU. 277. T. 14.4. × 65.

ridge at the anteroventral corner. Posterior margin truncate, narrowly rounded ventrally, slightly concave in the upper part.

Dorsal margin modified by the dorsal ridge, anterior and posterior cardinal angles marked. Ventral margin straight. Lateral surface ornamented with three longitudinal ridges. The dorsal and median are connected by a short curved transverse ridge at about one-third the length from the anterior end, the dorsal one projecting over the dorsal margin, curving down to terminate anterior to the posterior margin.

The median ridge runs in an elegantly curved, convex upward arc from the middle of the anterior margin towards the middle of the posterior end. The ventral ridge starts from the anteroventral corner and runs longitudinally above the ventral margin to join the median ridge at its posterior end, the rest of the surface is characterised by a typical ornamentation of thick transverse ridges which connect the median and ventral ridges forming distinctive reticula; two rounded reticula alternate in the anterior part of the median ridge; a distinctive additional longitudinal ridge is developed below the ventral ridge which is joined to the latter and follows a curved path in the posterior two-thirds of the shell.

Eye tubercle pronounced, with a shallow furrow behind. Left valve larger than the right, but overlapping is conspicuous.

Sexual dimorphism is very marked, the presumed male being longer and narrower than the female.

In dorsal view the carapace is biconvex, slightly tumid posteriorly in the female, slimmer in the male, anterior margin rounded, posterior end narrowly rounded, slightly pointed at the middle, maximum width and thickness posteriorly.

Dimensions of figured specimens.—

Holotype: ♀carapace, HU. 275 T. 13, Pl. 1, figs. 2, 4; L = 904 μm, H = 480 μm.

Paratype: ♂carapace, HU. 275 T. 14, Pl. 1, figs. 1, 3; L = 992 μm, H = 470 μm.

Affinities and Differences.—The present species differs from *Chrysocythere paradisus* Doruk, 1973, which is more elongate and differs in details of reticulum. *C. naqibi* is more elongate than *C. cataphracta* Ruggieri, 1962, and differs in details of the reticulation.

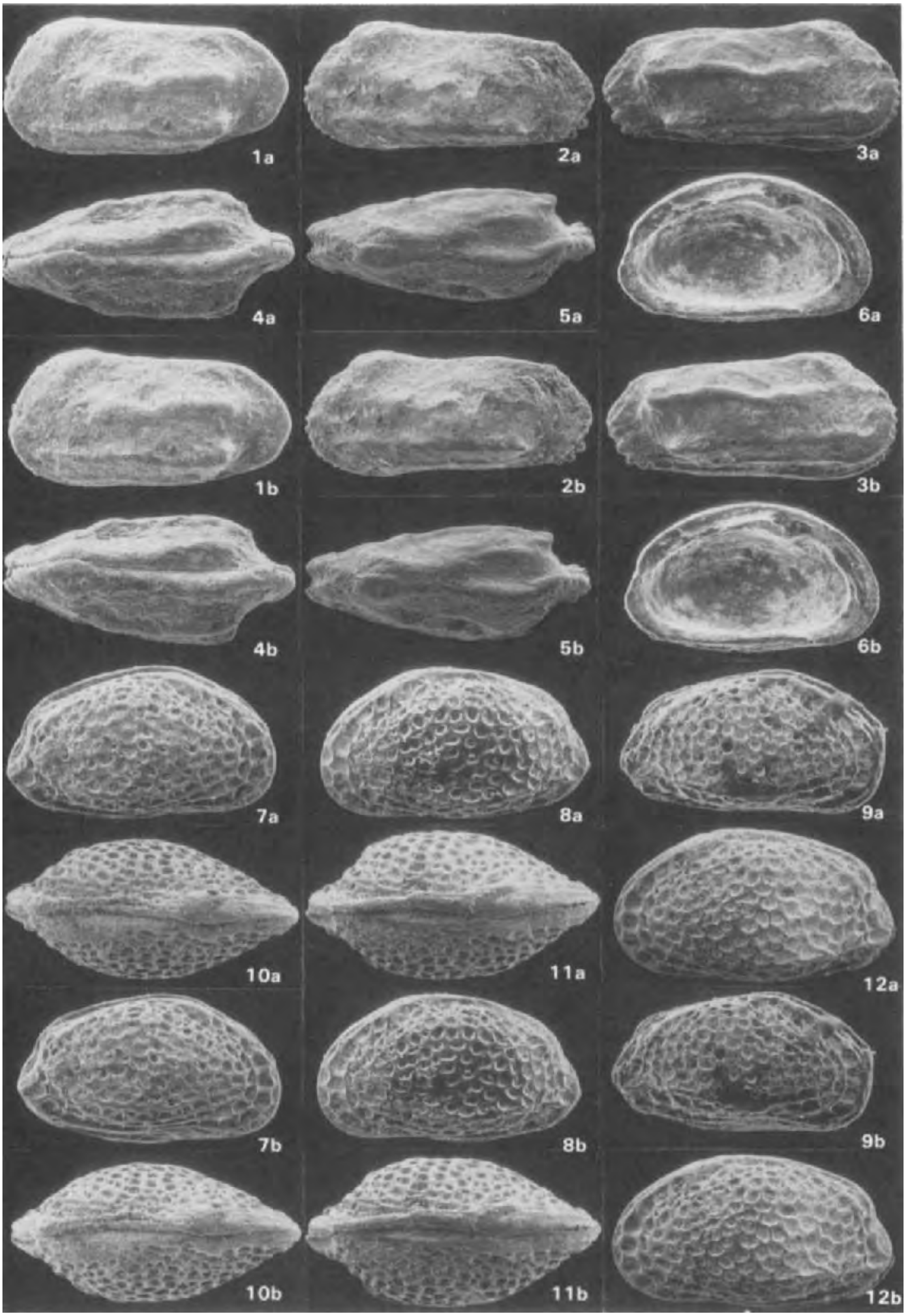
The new subspecies of *C. cataphracta* described from the M. Miocene of Mersin of Turkey by Bassiouni (1979) shows some similarity in ornamentation but the present species differs in the development of an additional ridge below the ventral ridge which is joined to the latter and follows a curved path in the posterior two-thirds of the shell.

Distribution.—*C. naqibi* occurs in the Middle Miocene sections of the Sheikh Ibrahim anticline, N.W. Iraq.

Subfamily BUNTONINAE Apostolescu, 1961
Tribe LEGUMINOCYTHERINI Howe, 1963
Genus RUGGIERIA Keij, 1957
Subgenus RUGGIERIA Keij, 1957

Type species.—*Cythere michelinia* Bosquet, 1852

PLATE 2—Figs. 1–5. *Ruggieria (Ruggieria) nova* n. sp. Fig. 1. Holotype, female carapace from left, HU. 278. T. 35. ×58. Fig. 2. Paratype, male carapace from left, HU. 278. T. 36.1. ×65. Fig. 3. Paratype, male carapace from right, HU. 278. T. 36.1. ×67. Fig. 4. Holotype, female carapace dorsal view, HU. 278. T. 35. ×59. Fig. 5. Paratype, male carapace dorsal view, HU. 278. T. 36.1. ×65. Figs. 6–12. *Mutilus fortireticulata* n. sp. Fig. 6. Paratype, female left valve internal view, HU. 279. T. 2.3. ×54. Fig. 7. Holotype, female carapace from right, HU. 279. T.1. ×51. Fig. 8. Holotype, female carapace from left, HU. 279. T.1. × 51. Fig. 9. Paratype, male carapace from right, HU. 279. T.2.1. ×52. Fig. 10. Paratype, female carapace dorsal view, HU. 279. T. 2.2. ×59. Fig. 11. Paratype, male carapace dorsal view, HU. 279. T.2.1. ×57. Fig. 12. Paratype, male carapace from left, HU. 279. T.2.4. ×52.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RUGGIERIA (RUGGIERIA) NOVA n. sp.

(Pl. 1, figs. 5a; Pl. 2, figs. 1–4, 11)

Derivation of name.—L. novus-new.

Holotype.—A female carapace, HU. 278 T. 35.

Paratypes.—Three specimens HU. 278 T. 36. 1-3.

Type locality.—Bashiqa anticline, S. limb, 28 km, N. E. of Mosul City.

Type horizon.—M. Miocene, L. Fars Formation, Bed no. 1, sample no. BA. 1.

Material.—Twenty specimens.

Diagnosis.—A species of the subgenus *Ruggieria* characterised by three longitudinal ridges and slightly compressed posterior end, lower than the anterior end.

Description.—Carapace elongate, subovate in lateral view, greatest height anteriorly, maximum length at below mid-height.

Anterior margin gently sloping in the upper part, broadly, obliquely rounded in the lower part and with a marginal row of 12–15 fine denticles; posterior end slightly compressed and lower than the anterior, sub-triangular shape, slightly concave in the upper part, gently convex in the posterior half, joining the posterior end with an obtuse angle; anterior cardinal angle high and smoothly curved, ventral margin nearly straight, smoothly joining the anterior and posterior ends.

The lateral surface has three longitudinal ridges, the ill-defined dorsal one forms the thick dorsal margin in some specimens and in others bends down posteriorly; the median ridge starts at the posterior end of the subcentral tubercle and runs backwards to end at two-thirds of the length with a slight ala in some specimens; a strongly developed ventral ridge starts from the ventral third of the anterior end and runs posteriorly, overhanging the ventral margin, forming an ala at the posterior end above the posteroventral corner. Between the ventral ridge and the ventral margin, there is a weak ventrolateral rib which ends posteriorly below the posterior end of the ventral ridge; the anterior continuation dies out in the weakly developed submarginal anterior ridge. The rest of the surface is smooth.

Eye tubercle present but not prominent, overreached by the anterior cardinal angle; subcentral tubercle marked and forms the anterior end of the median ridge. Left valve larger than the right, overreaching the latter along the posterior and antero-dorsal margins. Sexes easily distinguished, presumed males more elongated and narrower than the presumed females.

The material consists predominantly of closed carpaces. Only one fragile valve was obtained, and it is very difficult to see all the internal features, but the available ones conform with the diagnostic features of the subgenus.

In dorsal view the carapace is sagittate or arrow-head shaped, with rounded anterior end and pointed posterior end, the lateral alae are very prominent; maximum width and thickness in the posterior half.

Dimensions of figured specimens.—

Holotype: ♀carapace, HU. 278 T. 35 Pl. 1, fig. 5a; Pl. 2, figs. 1, 4; L = 800 μm, H = 390 μm

Paratype: ♂carapace, HU. 278 T. 36.1 Pl. 2, figs. 2, 3, 11; Pl. 2, fig. 5; L = 720 μm, H = 380 μm

Affinities and Differences.—*Ruggieria* (*Ruggieria*) *nova* n. sp. is fairly similar to *Ruggieria tetraptera tetraptera* (Sequenza, 1879) as figured by Bassiouni (1979) from the Neogene of Turkey, but the Iraqi species differs in being higher with comparatively broad anterior and posterior margins, whilst the median ridge swells slightly anteriorly to form the subcentral tubercle which is not seen in the Turkish material.

In addition, *R.* (*R.*) *tetraptera tetraptera* has a distinctive concave posteroventral corner. The present species shows some similarities to *Ruggieria dictyon* Bold (1966), but the latter differs in its subrectangular shape and strong reticulation with deep rectangular, square and hexagonal pits.

Distribution.—This species was found at the Bashiqa and Dohuk localities in Northern Iraq.

Family HEMICYTHEREIDAE Puri, 1953
Subfamily HEMICYTHERINAE Puri, 1953
Tribe AURILINI Puri, 1973
Genus MUTILUS Neviani, 1928

Type species.—Mutilus retiformis (Terquem), RUGGIERI and SYLVESTER-BRADLEY (1973).

MUTILUS FORTIRETICULATA n. sp.
(Pl. 2, figs. 5–12)

Derivation of name.—In reference to its strong reticulation.

Holotype.—A female carapace HU. 279, T. 1.

Paratypes.—Four specimens HU. 279, T. 2. 1–4.

Type locality.—Sheikh Ibrahim anticline, S. limb, 45 km N.W. of Mosul City.

Type horizon.—M. Miocene, L. Fars Formation, Bed no. 75, sample no. SHI. 40.

Material.—Eleven specimens.

Diagnosis.—A species of the genus *Mutilus* characterised by a massive carapace with four concentric ridges in the anterior third of which the last two project over the ventro-lateral inflation.

Description.—A strongly calcified carapace with semicircular outline in side view with the greatest height just behind the eye tubercle; carapace inflated ventrally with ventro-lateral prolongation.

Anterior margin forms a subcircular arc and joins the dorsal margin in a rounded angle; posterior margin narrower, concave in the upper part and ending posteroventrally in a short truncate caudal process.

Dorsal margin in the left valve slightly convex when seen from outside and nearly straight when seen from inside; in the right valve, dorsal margin slightly convex in the anterior half and gently sloping backwards in the posterior half; anterior and posterior cardinal angles present, more prominent in the right valve.

Surface ornamentation consists of thick muri, some of which are fairly pitted, enclosing relatively deep rounded fossae which are arranged concentrically at the middle; along the anterior third there are four concentric ridges originating from the eye tubercle area, running parallel to the anterior margin and forming parallel rows of rectangular or polygonal meshes anteriorly and along the ventral margin.

The first ridge dies out in the ventral margin at the anteroventral corner, the second and third are connected together above the mid-ventral margin whilst the fourth one forms the lateral prolongation of the ventrolateral inflation and ends with slight alar extension in front of the caudal process; a weak prolongation is developed in some specimens at the posterodorsal margin.

Eye tubercle small, glassy and rounded. Left valve larger than the right, overreaching more conspicuously along the dorsal, posterodorsal and anterodorsal margins.

Duplicature moderately wide. The line of concrescence and the inner margin coincide throughout, selvage well developed and parallel to the outer margin. The marginal pore canals are straight, mostly simple, closely spaced anteriorly, less so in the posterior area. The hinge is holamphidont, in the left valve the relatively deep anterior socket is bounded ventrally by the continuation of the postero-median bar which joins the reniform posterior socket; there is a well developed knob-like antero-median tooth. Central muscle scar consists of three frontal scars and four adductor scars, some of which are divided.

In dorsal view the carapace has regularly convex sides with slightly pointed anterior and postrior ends; maximum width and thickness at the middle. Sexual dimorphism marked, the presumed females a little higher and wider posteriorly than the presumed males.

Dimensions of figured specimens.—

Holotype: ♀carapace, HU. 279, T. 1, Pl. 2, figs. 5, 6; L = 860 μm, H = 520 μm. Holotype Ornamentation, Pl. 1, fig. 56.

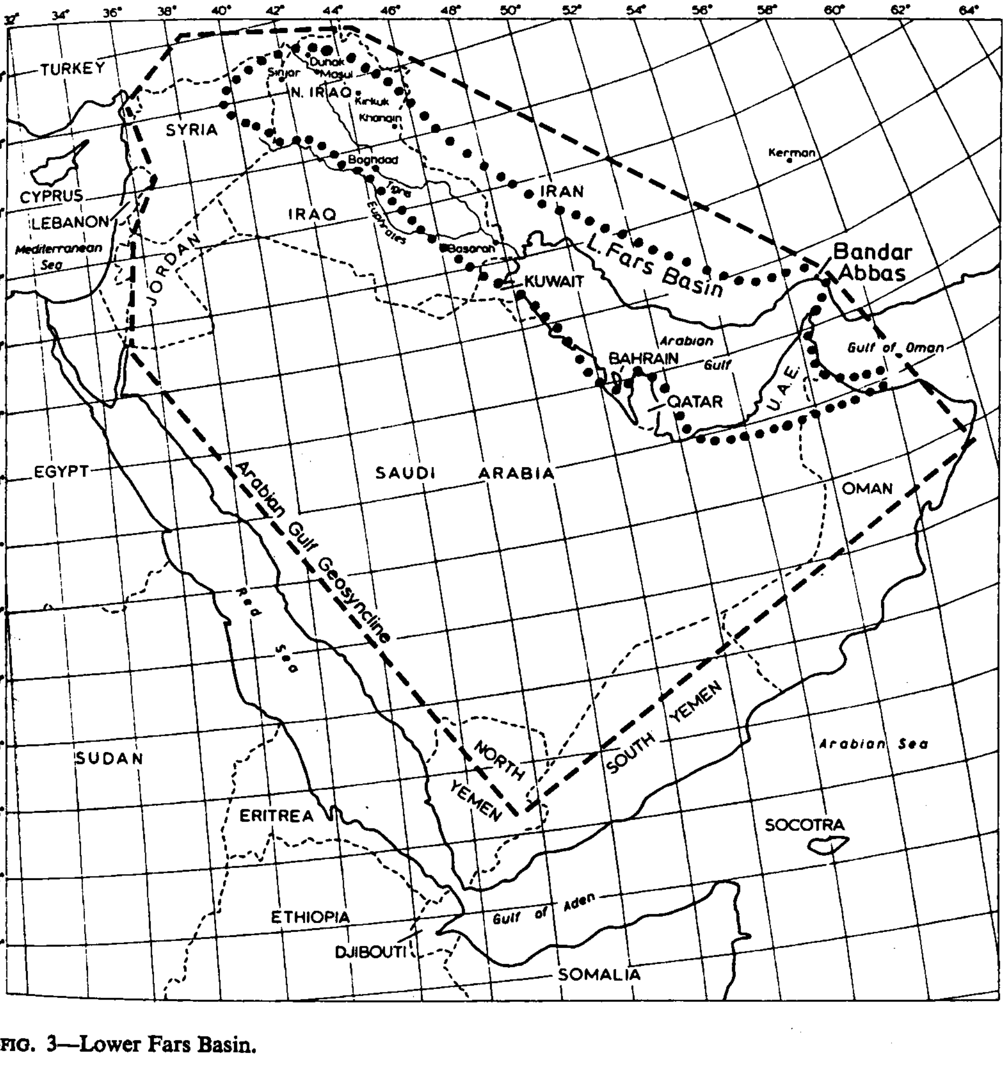
Paratype: ♂carapace, HU. 279, T. 2.1, Pl. 2, fig. 9; L = 830 μm, H = 505 μm.

Paratype: ♀carapace, HU. 279, T. 2.2, Pl. 2, fig. 8; L = 810 μm, H = 510 μm, W = 460 μm.

Paratype: ♀LV, HU. 279, T. 2.3, Pl. 2, fig. 7; L = 760 μm, H = 480 μm.

Paratype: ♂carapace, HU. 279, T. 2.4, Pl.2, fig. 12; L = 870 μm, H = 490 μm, W = 455 μm.

Affinities and Differences.—Mutilus freudenthali described originally as *Aurila freudenthali* by Sissingh, 1972 then transferred to *Mutilus* by N. Doruk (1973) resembles *Mutilus fortireticulata* sp. nov. in some respects, but differs in being larger in size, having a convex dorsal margin in both valves and a short, nearly straight posterior margin. The Iraqi species is characterised by relatively coarser fossae separated by thick pitted muri which form three concentric rows of rectangular or pentagonal shaped pits in the anterior third and above the ventral margin, while Sissingh's species is ornamented with fossae which are variable in shape with excavate muri and with rows of angular



TEXT-FIG. 3—Lower Fars Basin.

pits along the margin. The Iraqi species also has a prominent ventrolateral ridge which forms the ventrolateral prolongation.

Aurila pigadiana Sissingh, 1972 has some similarities to the present species, but the latter differs in having a strongly ornamented surface, in being more elongate with a concave ventral margin in the anterior third and a comparatively broader anterior margin. Sissingh's species may belong to *Mutilus* rather than *Aurila*, but it needs further examination.

Mutilus keiji Ruggieri, 1962 differs in having coarser, deep fossae and a narrower and pointed posterior end ventrally.

Distribution.—This species was found at the Dohuk, Bashiqa and Shikh Ibrahim localities in Northern Iraq.

CONCLUSIONS

These ostracod species from N. Iraq show affinities with the Mediterranean area and the fauna is closely related in its similar generic composition. Some species are very close to those described from the Antakya, Adana and Mersin regions of southeast Turkey. For example, the Turkish species *Chrysocythere paradisus* Doruk, 1973, *Chrysocythere cataphracta* Bassiouni, 1979, *Mutilus albicans* Ruggeri, 1973 and *Ruggieria tetraptera tetraptera* (Sequenza) are similar to the Iraqi species *Ruggieria nova* n. sp., *Chrysocythere naqibi* Khalaf, 1982 and *Mutilus fortireticulata* n. sp.

Other species are fairly similar and related to species described from Sicily, Italy and Crete.

The above faunal relationships of Miocene Ostracoda from N. Iraq lead to the conclusion that the Lower Fars basin in N. Iraq was part of a broad, shallow trough developed in front of the Zagros chain striking NW-SE and extending from Bandar Abbas in the extreme south east more than 2,000 km to connect with the extreme eastern extension of the Mediterranean trough possibly in Syria or Turkey (Text-fig. 3).

However, the presence of *Miocyprideis* in Turkey, Iraq, Iran and further east in India indicate (as suggested by McKenzie, 1967) that the genus arrived in India before the disruption of Tethys. This leads to the conclusion that the lower Fars basin in Iran, Iraq and Syria may represent the final remnant of western Tethys.

ACKNOWLEDGEMENTS

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DISCUSSION

Keen: I would just like to comment that this is an important contribution to our knowledge of Miocene ostracods, filling in the vital gap between the Mediterranean and Indian region. The species described show obvious Mediterranean affinities and must be amongst the last migrants from the west before the separation of eastern and western Tethys.

Upper Oligocene–Lower Miocene Ostracods from the YPF. SCA. ECa. X-1 (El Campamento) Borehole, Austral Basin, Argentina

ANA A. KIELBOWICZ
Yacimientos Petrolíferos Fiscales, Florencio Varela, Argentina

ABSTRACT

Ostracods recovered from cuttings-samples of the upper member of the Magallanes Formation are described and illustrated. The samples are from the YPF. SCA. ECa. X-1 (El Campamento) borehole, drilled in the southwestern region of the Austral basin in the Santa Cruz province. Fourteen genera and nineteen species were recognized. Most of the studied forms are strongly ornamented and a few of them are smooth or delicately punctated. Of the nineteen recorded species three are described as new and eight are designated as *nomina aperta.* According to the biostratigra phical and paleoecological evidence, the ostracod assemblage is considered to be of upper Oligocene-lower Miocene age and to represent a shallow-shelf environment of normal salinity and temperate-cold waters.

INTRODUCTION

An ostracod fauna recovered from cuttings of the YPF. SCA. ECa. X–I (El Campamento) borehole is described and illustrated.

The borehole, drilled in the southwestern area of the Austral basin in the Santa Cruz province (Text-fig. 1), runs through the Santa Cruz, Magallanes, Palermo Aike and Springhill Formations and reaches a few metres of the economic basement.

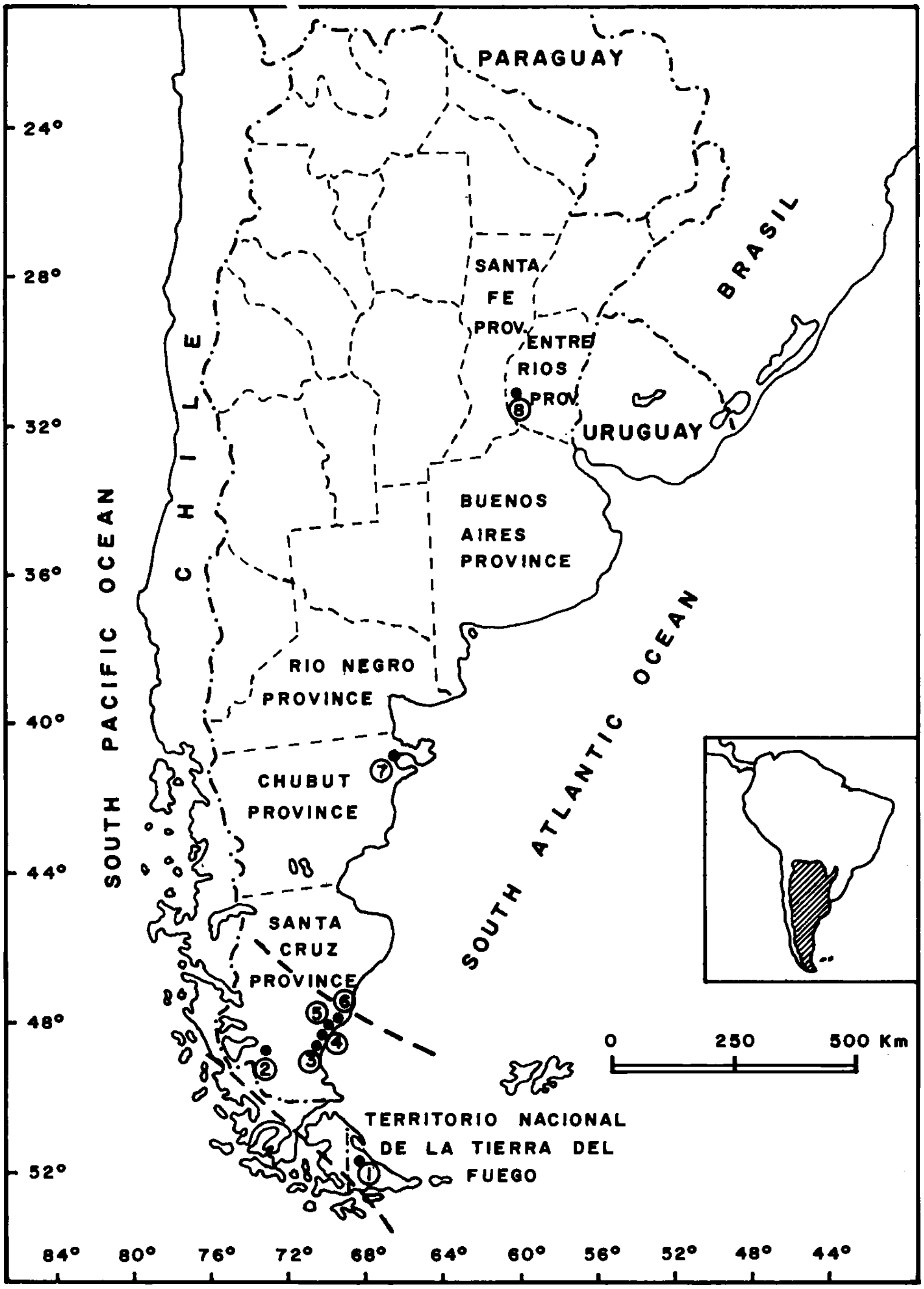
The biostratigraphic zonation of the sedimentary column is characterized by typical foraminiferal assemblages and lower Cretaceous to upper Tertiary ages were recognized.

The afore mentioned ostracods were found in the upper member of the Magallanes Formation and they are a part of a typical microfaunal assemblage, widely distributed in outcrops and subsurface late Oligocene - early Miocene strata of the Austral basin.

PREVIOUS STUDIES

Tertiary marine ostracods from the Austral basin have not been well documented, possibly because they are scarcer than foraminifers and because the hydrocarbon search essentially focuses on Cretaceous strata.

For the Argentine part of the basin, Becker (1964) studied Miocene genera from Las Cuevas and Monte Entrance localities (Text-fig. 1) in the Santa Cruz province. Bertels (1975), in her study on



Text-fig. 1—Location map of the Argentine areas referred to in this study. ①, Carmen silva; ②, YPF. ECa. X-1 borehole; ③, Las Cuevas; ④, Monte León; ⑤, Monte Entrance; ⑥, Gran Bajo de San Julián; ⑦, Puerto Pirámides; ⑧, Victoria; — —, Limits of the Austral basin.

ostracod ecology of the upper Cretaceous and Cenozoic of Argentina, referred to and illustrated Becker's genera and assigned the assemblage to the "Patagonian Stage *s. l.*" (Text-fig. 2).

Later, Echevarría (1982) studied an early Miocene ostracod fauna from the type locality of the Carmen Silva Formation in the Tierra del Fuego Island.

Finally, Eocene to Miocene species of the genus *Argenticytheretta* Rossi de García, 1969 were described by Rose (1975, 1979) for the Chilean part of the basin, from outcropping and subsurface strata of the Magallanes province and the Tierra del Fuego island.

GEOLOGY

The Austral basin extends through the southwestern part of the Santa Cruz province and through the National Territory of Tierra del Fuego. It lengthens to the Republic of Chile to the west and into the Atlantic Ocean to the east.

The area of sedimentation is limited by the "Nesocratón del Deseado" and its atlantic prolongation and by the Andean ranges.

The economic basement is represented by the "Complejo Porfídico". After this vulcanic event, sedimentation began in the upper Jurassic-lower Cretaceous with terrigenous deposits. The first marine ingression started in the lower Cretaceous and continued with brief interruptions up to the end of the Mesozoic. Marine sedimentation was mainly clastic with some carbonates in the eastern shelf. Towards the borders of the basin terrigenous and pyroclastic deposits are gradually replacing marine sediments.

For the Tertiary period, atlantic ingressions with minor pulsations are known and three sedimentary cycles: Paleocene – Oligocene, late Oligocene – early Miocene and Miocene were recognized (Russo *et al.*, 1980).

The upper part of the subsurface Magallanes Formation represents the late Oligocene – early Miocene cycle. Its outcropping marine equivalent is known as Monte León Formation (Bertels, 1970) or as Patagonia Formation (Russo *et al.*, 1980) and integrates the deposits of the "Patagonian stage *s. l.*". This deposits have a wide areal distribution. They crop out in the Santa Cruz province, where the stratotypes of the stage are located and in the Chubut province (Bertels, 1975b). According to electrical-log correlations (Russo *et al.*, 1980) and micropaleontological studies, the late Oligocene – early Miocene sediments are present in almost all the subsurface of the Santa Cruz province.

OSTRACOD FAUNA

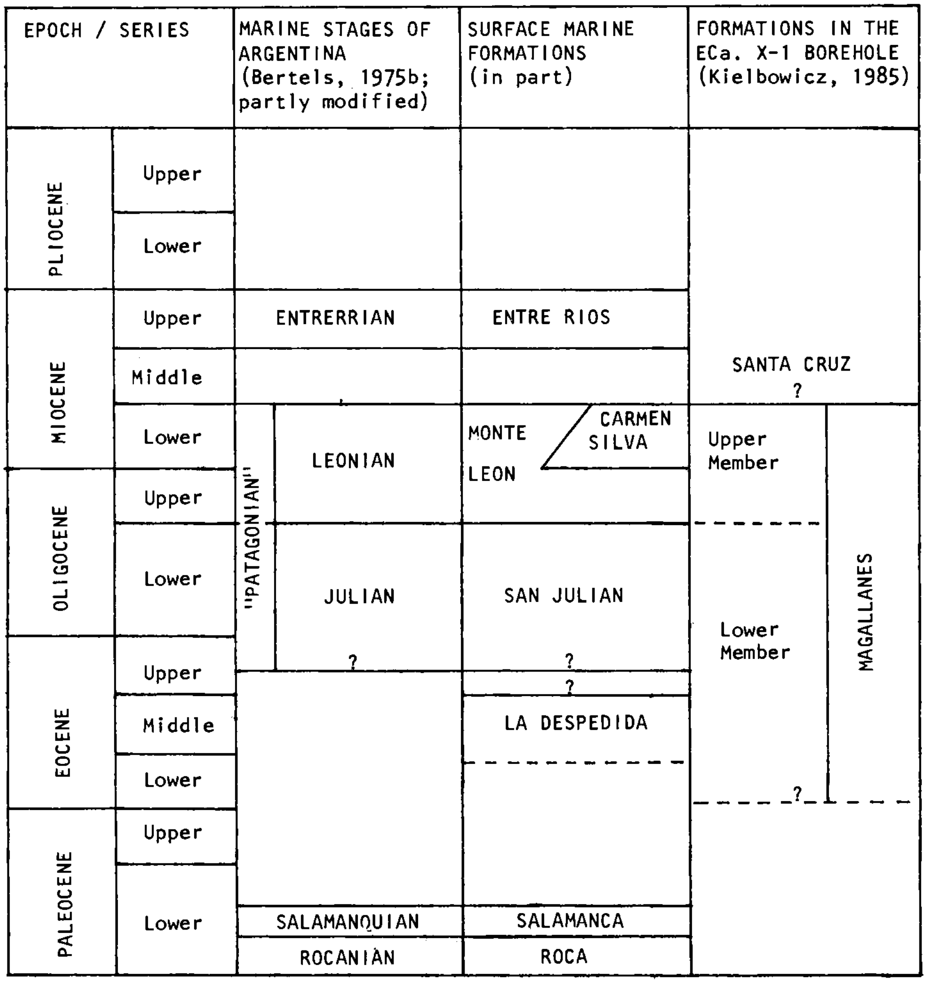
One hudred and thirteen moderately-well preserved carapaces were recovered from cuttings-samples of the upper member of the Magallanes Formation in the YPF. SCA. ECa. X-1 (El Campamento) borehole and fourteen genera and nineteen species were recognized.

Most of the studied forms are strongly ornamented and a few of them are smooth or delicately punctated.

Of the nineteen recorded species, three are described as new and eight are designated as *nomina aperta*.

The ostracod assemblage is composed as follows:

Aurila cf. *convexa* (Baird, 1850)
Aurila magallanica n. sp.
Australicythere sp. 1 (Becker, 1964)
Bairdia sp.



EPOCH / SERIES		MARINE STAGES OF ARGENTINA (Bertels, 1975b; partly modified)		SURFACE MARINE FORMATIONS (in part)	FORMATIONS IN THE ECa. X-1 BOREHOLE (Kielbowicz, 1985)	
PLIOCENE	Upper				SANTA CRUZ ?	
	Lower					
MIOCENE	Upper	ENTRERRIAN		ENTRE RIOS		
	Middle					
	Lower	"PATAGONIAN"	LEONIAN	MONTE LEON CARMEN SILVA	Upper Member	MAGALLANES
OLIGOCENE	Upper					
	Lower		JULIAN	SAN JULIAN	Lower Member	
EOCENE	Upper		?	? ?		
	Middle			LA DESPEDIDA		
	Lower				?	
PALEOCENE	Upper					
	Lower	SALAMANQUIAN ROCANIAN		SALAMANCA ROCA		

TEXT-FIG. 2—Correlation chart.

Bensonia cf. *miocenica* (Rossi de García, 1969)
?*Bensonia leoniana* Bertels, 1975a
Bensonia sp.
Callistocythere litoralensis (Rossi de García, 1966)
Copytus sp.
Cytherella aff. *C. (Platella) fragilis* (Rossi de García, 1966)
Henryhowella aff. *evax* (Ulrich and Bassler, 1904)
Henryhowella cuevense Bertels, 1975a
Munseyella santacrucensis n. sp.
Munseyella sp.
Paracypris? sp.
Quadracythere sp.
Soudanella sp.
Urocythereis bertelsae n. sp.
Wichmanella deliae Bertels, 1975a

Frequency of genera and species is graphically represented in Text-fig. 3.

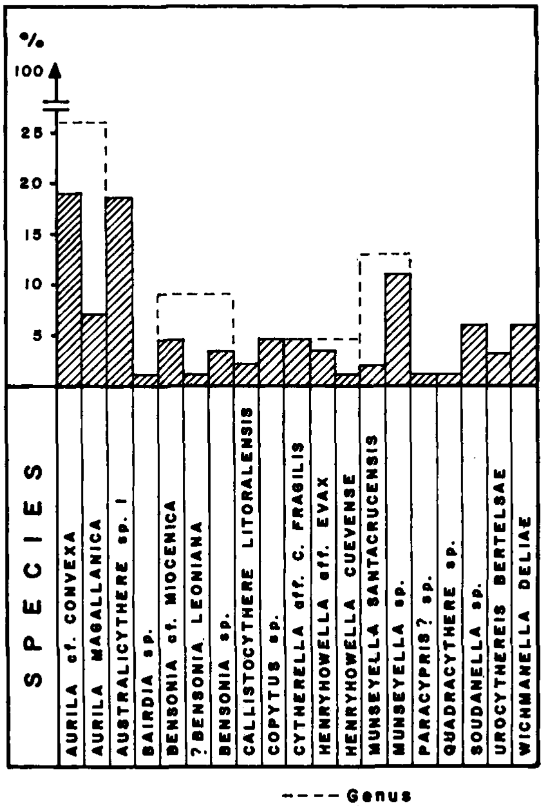
STRATIGRAPHY

Most of the ostracods described herein are known in Argentina from the Leonian Stage deposits and some of them from the Entrerrian Stage.

The Leonian Stage integrates the "Patagonian Stage *s. l.*" (Text-fig. 2) whose deposits have a wide areal distribution. They crop out in the Austral basin and in the Chubut province and equivalent subsurface sections are known in the Santa Cruz and Buenos Aires provinces (Malumián, 1969, 1970).

The Leonian Stage is represented by the Monte León Formation (which at the same time is the stratotype of the Stage) and its equivalents. The zones of *Globigerina anguliofficinalis, Globigerina ciperoensis* and *Globigerina angulisuturalis* were proposed by Bertels (1975c) for the Monte León Formation and related with the upper Rupelian and Chattian Stages of Europe. According to Malumián and Palma (1984) the presence of *Cassigerinella chipolensis* (Cushman and Ponton) in sediments of the type area of the Leonian Stage, indicates an Oligocene – lower Miocene age and the faunal similarity partially correlates with the Carmen Silva Formation (lower Miocene), which crops out in the Tierra del Fuego Island.

Correlation is also possible with subsurface strata of the northern region of the Austral basin, which were referred to the Patagonia Formation and considered of upper Oligocene – lower Mio-



TEXT-FIG. 3—Frequency of genera and species.

cene age (Masiuk and Ronchi, 1981) and in which *Australicythere* sp. 1 (Becker, 1964), *Copytus* sp., *Munseyella* sp., *Cytherella* aff. *C.* (*Platella*) *fragilis* (Rossi de García, 1966) have been found together with the planktonic foraminifer *Globigerina* (*G.*) *ciperoensis ciperoensis* and with representatives of the benthic "*Cribrorotalia hornibrooki* assemblage". Representatives of the genus *Cribrorotalia* are very frequent in Tertiary deposits of southern Argentina and they are useful for stratigraphic control, specially for those facies in which planktonic foraminifera are not common. The "*Cribrorotalia hornibrooki* assemblage" is widely distributed from the Andean region to the Atlantic coast and it seems to be restricted to the "Patagonian" desposits (Malumián, 1970).

With regard to the foraminiferal evidence in the ECa. X-1 borehole, *Cribrorotalia hornibrooki* f. *planoconvexa* Malumián and Masiuk, 1971 is the most significant species. It characterizes the upper part of the "Patagonian" deposits and is not known from posterior marine ingressions.

PALEOECOLOGY

The most frequent species of the ostracod assemblage: *Aurila* cf. *convexa* (Baird) and *Australicythere* sp. 1 (Becker) have been described by Becker (1964) in her study of the ostracods found in Miocene strata in the southern coast of Argentina, together with species of foraminifera which inhabit the South American shelf today and are limited in depth to littoral and shallow waters. Taking into account the Recent distribution of these foraminifera, the presence of typical epineritic genera of ostracods and the regressive facies of the deposits, Bertels (1975b) concluded that the ostracods described by Becker (1964) respond to a shallow water (no deeper than the inner shelf) environment, normal salinity, normal pH and temperate climate (similar to Recent latitudes 30° – 40° S) and that they can inhabit lower latitudes today.

Representatives of the genus *Australicythere* are actually present in the cold and shallow waters of the Antarctic region (Benson, 1964). As fossils they are known in Argentina (besides the assemblage described by Becker) from Eocene levels of the La Despedida Formation, in the Tierra del Fuego Island (Echevarría, 1985, pers. comm.) and from the upper Oligocene – lower Miocene strata of the northern region of the Austral basin. The desposits of the La Despedida Formation have been referred by Codignotto and Malumián (1981) to a restricted marginal marine environment of low energy. The subsurface strata of the northern region of the Austral basin have been related, on the basis of its foraminiferal fauna, to a shallow shelf environment (depth up to 80 m) of normal salinity (Masiuk and Ronchi, 1981). Furthermore, *Australicythere* is also known in the Miocene strata of the Pelotas basin, in southern Brazil (Sanguinetti, 1979). This evidence suggests some amplitude of latitudinal distribution, at least during the Tertiary period, in shallow-water environments.

Munseyella is another well-represented genus in the ECa. X-1 borehole ostracod assemblage. *Munseyella* sp., the most frequent representative of the genus in the borehole, is known from the afore mentioned upper Oligocene – lower Miocene shallow-shelf sediments of the nothern area of the Austral basin and from lower Miocene deposits of the Carmen Silva Formation in the Tierra del Fuego island (Echevarría, 1985, pers. comm.).

With regard to the *Bensonia* group, Argentine species such as *Bensonia leoniana* Bertels (1975a) and *Bensonia miocenica* (Rossi de García, 1966) are typical of shallow marine deposits.

Representatives of *Copytus*, a qualitatively signicative genus of the assemblage, inhabit in the Southern Hemisphere today, the shallow and cold waters of the Antarctic region (Benson, 1964). According to Rose (1979), its high frequency in the lower Miocene of southern Chile suggests cool, rather shallow marine conditions. In Argentina, it was found in the Carmen Silva Formation (Echevarría, 1982) together with species of foraminifera which are characteristic of marginal environments and cold waters and it is also known from the shelf deposits of the northern area of the basin.

With regard to the foraminiferal evidence, *Cribrorotalia meridionalis* (Cushman and Kellet) and *Cribrorotalia hornibrooki* f. *planoconvexa* Malumián and Masiuk are the most typical species in the ECa. X-1 borehole and *Buccella* is the most frequent genus. Murray (1973) has related the abundance of *Buccella* to temperate-cold waters and, according to Boltovskoy (1976), *Cribrorotalia meridionalis* today replaces the *Elphidium* species in the littoral area of the septentrional Chilean coast, probably in the same marmer as in the "Patagonian" deposits.

CONCLUSIONS

According to the afore mentioned evidence, the ostracod assemblage recovered from the upper member of the Magallanes Formation is considered to be of upper Oligocene – lower Miocene age and to represent a shallow shelf environment of normal salinity and temperate-cold waters.

SYSTEMATIC DESCRIPTIONS

The classification adopted in the present work is that proposed in the Treatise of Invertebrate Paleontology (Moore, R. C., ed., 1961), except for the genera *Australicythere, Bensonia, Soudanella* and *Wichmanella* for which Benson (1964), Rossi de García (1969), Apostolescu (1961) and Bertels (1969) have been followed respectively.

The micrographs were obtained with a LEITZ-AMR 1200 scanning microscope, after coating the specimens with a gold-palladium alloy.

The material described is kept in the collection of the Laboratory of Geology of Yacimientos Petrolíferos Fiscales, Buenos Aires under the numbers 352–370.

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily BAIRDIACEA Sars, 1888
Family BAIRDIIDAE Sars, 1888
Genus BAIRDIA McCoy, 1844

Type species.—Bairdia curtus McCoy, 1844.

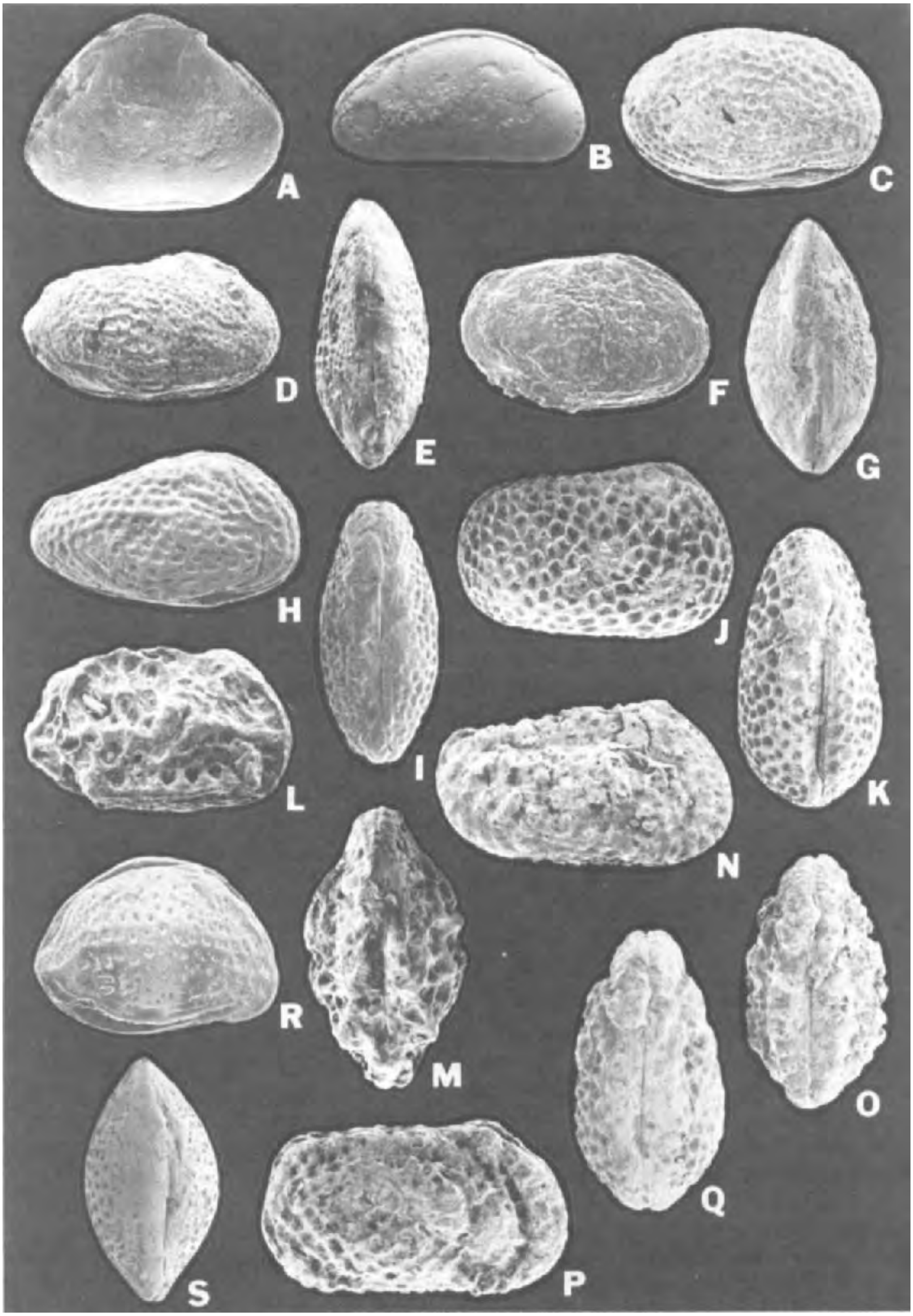
BAIRDIA sp.
(Plate 1, fig. A)

Material.—1 carapace.

Description.—Carapace triangular in lateral view, highest in the middle. Anterior and posterior ends obliquely rounded. Dorsal margin strongly convex; ventral margin straight to gently convex in the left valve and slightly concave in the middle of the right valve. Left valve overlapping the right one along dorsal and ventral margins, with greatest overlap dorsally and mid-ventrally. Surface regularly covered with small and shallow punctations. Other features not observed.

Dimensions.—length: 1.02 mm; height: 0.72 mm; width: 0.5 mm.

Remarks.—Bairdia sp. presents marked similarities to the Recent species *Bairdia fusca* Brady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(1866), but differs in the more arched dorsal margin. It also shows similarities to *Bairdia formosa* Brady (1869) known from the Recent of Turkey, but lacks the anterior and posterior denticles of that species. *Bairdia croskeiana* Brady (1866) is a similar finely punctated species, but its greatest height is at the anterior third of the carapace and the posterior end is more acute than in *Bairdia* sp. *Bairdia dimorpha* Van den Bold (1963), from the upper Miocene of Trinidad differs in the outline and shows stronger surface punctations. Finally, *Bairdia anachoreta* Bertels (1968), a Danian species of Argentina, is smaller than *Bairdia* sp. and lacks surface ornamentation.

Repository.—YPF. Lab. Geol. N° 352.

Superfamily CYPRIDACEA Baird, 1845
Family PARACYPRIDIDAE Sars, 1923
Genus PARACYPRIS Sars, 1866

Type species.—*Paracypris polita* Sars, 1866.

PARACYPRIS? sp.
(Plate 1, fig. B)

Material.—1 carapace.

Description.—Carapace elongate-subtriangular in lateral view. Maximum height somewhat in front of the middle. Dorsal margin convex; ventral margin straight; anterior end rounded; posterior end subrounded. Left valve larger than the right, overlapping it at the periphery. Surface smooth. Carapace elliptical in dorsal view; maximum width at the middle. Internal features not observed.

Dimensions.—length: 0.95 mm; height: 0.52 mm; width: 0.43 mm.

Remarks.—*Paracypris*? sp. differs from the typical representatives of the genus in the low length/height ratio (1.8). It shows marked similarities to *Paracypris*? sp. Bertels (1973), described from lower Danian (Rocanian Stage) strata of Argentina, but the ventral and anterior overlap is not as strong as in Bertels' species. It differs from *Paracypris* sp. (Zabert, 1978), known from upper Miocene subsurface sediments of the Santa Fe province (Text-fig. 1) in being larger, less elongated in side view and in the position of the maximum height, which is of middle-length in Zabert's species. *Paracypris* sp. (Echevarría, 1982), described from the Carmen Silva Formation (lower Miocene) of the Tierra del Fuego island, is smaller, more pointed posteriorly and its lenght/height ratio is 2.15.

Repository.—YPF. Lab. Geol. N° 353.

Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDAE Baird, 1850
Genus BENSONIA Rossi de García, 1969

Type species.—*Cytheretta argentinensis* Rossi de García, 1966.

PLATE 1—Fig. A. *Bairdia* sp., RV lateral view, ×40. Fig. B. *Paracypris*? sp., RV lateral view, ×50. Fig. C. ?*Bensonia leoniana*, RV lateral view, ×60. Figs. D, E. *Bensonia* cf. *B. miocenica* (Rossi de García); D, female, RV lateral view, ×60; E, female, dorsal view, ×60. Figs. F, G. *Bensonia* sp. F, female, RV lateral view, ×60; G, female, dorsal view, ×60. Figs. H, I. *Soudanella* sp.; H, female, RV lateral view, ×60; I, female, dorsal view, ×60. Figs. J, K. *Wichmanella deliae* Bertels. J, female, RV lateral view, ×60; K, female, dorsal view, ×60. Figs. L, M. *Quadracythere* sp.; L, RV lateral view, ×65; M, dorsal view, ×65. Figs. N, O. *Henryhowella* aff. *evax* (Ulrich and Bassler). N, female, RV lalateral view, ×60; O, female, dorsal view, ×60. Figs. P, Q. *Henryhowella cuevense* Bertels; P, female, RV lateral view, ×50; Q, female, dorsal view, ×50. Figs. R, S. *Aurila* cf. *convexa* (Baird); R, female, RV lateral view, ×60; S, female, dorsal view, ×60.

Remarks.—The genus *Bensonia* appears in the Leonian Stage (Oligocene) in the ostracod evolutionary lineages of Argentinian species and is thought to be a *Togoina* Apostolescu (1961) descendant (Bertels, 1976). It is common in Oligocene-Miocene strata.

?BENSONIA LEONIANA Bertels, 1975a
(Plate 1, fig. C)

Leguminocythereis 1 BECKER, 1964, p. 335, Pl. 4, fig. 5.
Bensonia leoniana BERTELS, 1975a, p. 265, Pl. 2, figs. 6–9.

Material.—1 deformed and broken carapace.

Remarks.—*Bensonia leoniana* Bertels (1975a) was originally described from the Leonian Stage strata of La Cuevas, Santa Cruz province. The specific assignation of the specimen of the ECa. X-1 borehole cannot be proved certain because the carapace is deformed and broken posterodorsally. Nevertheless, the ornamentation of pits arranged in rows which follow the outline of the carapace resembles Bertels' species.

Repository.—YPF. Lab. Geol. N° 354.

BENSONIA cf. B. MIOCENICA (Rossi de García, 1969)
(Plate 1, figs. D, E)

Argenticytheretta miocenica ROSSE DE GARCIA, 1969, p. 221, Pl. 1, fig. 2, Pl. 2, figs. 2a, b.

Material.—5 carapaces.

Description.—Carapace elongated, ovate to sub-rectangular in lateral view. Dorsal margin straight to gently convex with well-marked cardinal angles; ventral margin convex; anterior end rounded; posterior end somewhat pointed. Eye-tubercle not conspicuous. Maximum height at the anterior cardinal angle. Left valve larger than the right, overlapping it at the cardinal angles and at the posterior and ventral margins. The ornamentation consists of pits which are larger in the central portion of the valves and which diminish in size toward the anterior and posterior margins. They are randomly disposed in the central and dorsal surface of the valves, but ventrolaterally the pits are arranged in longitudinal rows and fine ribs are developed between them. In dorsal view, carapace sub-elliptical with slightly compressed extremities. Greatest width posterior to the middle. Sexual dimorphism present, the males being more elongated than females. Internal features not observed.

Dimensions.—(female): length: 0.67 mm; height: 0.37 mm; width: 0.30 mm.

Remarks.—Studied specimens resemble Rossi de García (1969) *Argenticytheretta miocenica,* which was described from Miocene strata of northeastern Argentina. Although they show more randomly disposed pits in the central portion of the valves, they have a less convex dorsal margin with well-marked cardinal angles and a more pointed posterior end. Pitted *Argenticytheretta* representatives: *Argenticytheretta* (*A.*) *patagoniensis* and *Argenticytheretta* (*A.*) *gonzalezi* described by Rose (1975) from Tertiary strata of southern Chile, differ mainly in the more inflated carapace.

Bensonia miocenica is also known for the Entrerrian Stage, in the Puerto Pirámides area (Bertels, 1976) and from Miocene strata of the Tierra del Fuego Island (Echevarría, 1985, pers. comm.). It is thought to have evolved in a direct lineage from *Bensonia leoniana* (Bertels, 1976).

Repository.—YPF. Lab. Geol. N° 355.

BENSONIA sp.
(Plate 1, figs. F, G)

Material.—4 carapaces.

Description.—Carapace ovate in lateral view. Dorsal margin straight with well-marked cardinal angles; ventral margin gently convex; anterior end broadly rounded; posterior end rounded. Maximum height at the anterior cardinal angle. Left valve larger than the right, overlapping it at the cardinal angles and at the anterior and ventral margins. Lateral surface ornamented with small and randomly arranged punctations, which are stronger in the central and central-dorsal portions of the valves. Fine longitudinal striae are developed ventrolaterally. Eye-tubercle not conspicuous. Carapace ovoid in dorsal view, with compressed ends. Greatest width posterior to the middle. Other features not observed.

Dimensions.—(female): length: 0.68 mm; height: 0.37 mm; width: 0.30 mm.

Remarks.—*Bensonia* sp. shows finer and more regularly distributed surface ornamentation and a less pointed posterior end than *Bensonia* cf. *miocenica* (Rossi de García, 1969). It presents some similarities to *Bensonia tenuipunctata* Bertels (1975a), a randomly punctated species described from the Entrerrian Stage, but differs in being smaller, lower at the anterior cardinal angle, in the presence of ventrolateral striae and in the less conspicuous ventrolateral overlap.

Bensonia minipunctata Sanguinetti (1979), a Miocene species of the Pelotas basin (Brazil), shows a different outline, stronger surface punctations and better developed ventrolateral striae. *Argenticytheretta carmensilvaensis* Echevarría (1982), described from lower Miocene strata of Tierra del Fuego Island, differs in the more inflated carapace and in surface ornamentation, which consists of weak punctations separated by delicate longitudinal striae.

Repository.—YPF. Lab. Geol. N° 356.

Genus SOUDANELLA Apostolescu, 1961

Type species.—*Soudanella laciniosa* subsp. *laciniosa* Apostolescu, 1961

Remarks.—The genus *Soudanella* appears in Argentina in the lower Danian (Rocanian Stage) and developed throughout the Paleogene and Neogene. The evolutionary tendency is represented by the acquisition of a stronger and more aligned reticular pattern (Bertels, 1976).

SOUDANELLA sp.
(Plate 1, figs. H, I)

Material.—7 carapaces.

Description.—Carapace sub-triangular in lateral view. Dorsal margin straight; ventral margin sinuous in the right valve and convex in the left one; anterior end broadly rounded from eye-tubercle to venter; posterior end triangular; posterior and anterior margins finely denticulated. Maximum height at the anterior cardinal angle. Left valve larger than the right, overlapping it at the cardinal angles and at the ventral margin. Eye-tubercle conspicuous; sub-central tubercle well-marked. The surface of the valves is ornamented with a strong reticle which is longitudinal to the anterior, posterior, dorsal and ventral margins, and nearly sigmoid in the central portion of the valves. One of the ridges of the reticular pattern is stronger than the others and extends along the median from the sub-central tubercle to the posterior end. Another ridge insinuates ventrolaterally and converges toward the posterior end. A third ridge elevates the dorsal margin and curves from the eye-tubercle toward the median ridge. Carapace sub-elliptical in dorsal view. Greatest width in the middle. Sexual dimorphism present, males being longer and narrower than females. Other features not observed.

Dimensions.—(female): length: 0.72 mm; height: 0.40 mm; width: 0.30 mm.

Remarks.—*Soudanella* sp. shows some similarities to *Soudanella cleopatrae* Bertels (1975a), originally described for the Leonian Stage, but differs in the straighter dorsal margin, in the more pointed posterior end, in being lower and less inflated, in the marked subcentral tubercle and in the presence of ornamental ridges. In *S. cleopatrae* the overlap of the left valve is stronger.

Identical specimens to *Soudanella* sp. are known from Pliocene strata in the Río Negro province. (Echevarría, 1985, pers. comm.).

Repository.—YPF. Lab. Geol. N° 357.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1958

Genus HENRYHOWELLA Puri, 1957

Type species.—*Cythere evax* Ulrich and Bassler, 1904.

Remarks.—In the ostracod evolutionary lines of Argentina, the genus *Henryhowella* appears in the Julian Stage (upper Eocene - lower Oligocene) and according to Bertels (1976), during its evolution the strength of the reticulation is reduced and a coarser tuberculation is acquired.

HENRYHOWELLA CUEUENSE Bertels, 1975a

(Plate 1, figs. P, Q)

Henryhowella cuevense BERTELS, 1975a, p. 278, Pl. 6, figs. 6, 7.

Material.—1 carapace.

Dimensions.—length: 1 mm; height: 0.62 mm; width: 0.50 mm.

Remarks.—This sub-quadrate in outline species shows a widely rounded posterior end and large tubercles superimposed to a primary reticulation. It was originally described from Las Cuevas for the Leonian Stage (Bertels, 1975a). The surface ornamentation of the ECa. X-1 borehole specimen is partly eroded.

Repository.—YPF. Lab. Geol. N° 358.

HENRYHOWELLA aff. EVAX (Ulrich and Bassler, 1904)

(Plate 1, figs. N, O)

Henryhowella aff. *evax* (Ulrich and Bassler). ROSSI DE GRACIA, 1966, p. 200, Pl. 1, figs. 3a-c.

Material.—4 carapaces.

Dimensions.—length, 0.87mm; height, 0.50mm; width, 0.45mm.

Remarks.—This Miocene species, which originally has been described from outcrops of the Entre Ríos Formation in the Victoria locality (Text-fig. 1), shows marked similarities to *Henryhowella evax* (Ulrich and Bassler), Puri (1957), but differs in the surface sculpture (Rossi de García, 1969). It also presents marked similarities to *Henryhowella patagonica* Bertels (1975a), a Julian Stage species, but shows a more obliquely rounded posterior end, a smaller size and a more conspicuous longitudinal alignment of the dorsally widened and flattened tubercles.

It is also known from the Paraná Formation (upper Miocene), in the subsurface of the Santa Fe province (Zabert, 1978) and from upper Miocene strata of the subsurface of the Buenos Aires province (Malumián, 1970). A zone of *Henryhowella evax* was proposed by Sanguinetti (1969) for Miocene strata of the Pelotas basin, southern Brazil.

Repository.—YPF. Lab. Geol. N° 359.

Genus WICHMANELLA Bertels, 1969

Type species.—*Wichmanella meridionalis* Bertels, 1969.

Remarks.—The genus *Wichmanella* appears in Argentina in the upper Cretaceous (lower Maastrichtian) and developes throughout the Paleogene and possibly the Neogene. It is characterized by a reticular surface pattern with superimposed small tubercles. The evolutive tendency seems to be the acquisition of a more ordered ornamental pattern and a crenulation of the hinge-bar (Bertels, 1969, 1976).

WICHMANELLA DELIAE Bertels, 1975a
(Plate 1, figs. J, K)

Wichmanella deliae BERTELS, 1975a, p. 272, Pl. 4, figs. 3, 4.

Material.—7 carapaces.

Dimensions.—(female): length: 0.75 mm; height: 0.47 mm; width: 0.42 mm; (male): length: 0.87 mm; height: 0.45 mm; width: 0.37 mm.

Remarks.—This species was originally described from outcrops of the Monte León Formation in Las Cuevas from the Leonian Stage (Bertels, 1975a).

Repository.—YPF. Lab. Geol. N° 360.

Genus QUADRACYTHERE Hornibrook, 1952

Type species.—Cythere truncula Brady, 1898

QUADRACYTHERE sp.
(Plate 1, figs. L, M)

Material.—1 carapace.

Description.—Subquadrate carapace in lateral view; dorsal margin sinuous; ventral margin straight; anterior end rounded; posterior end pointed, forming a caudal process; antero-dorsal angle rounded; posterodorsal angle acute. Valves of approximately equal size, the left being somewhat larger than the right at the anterior margin and at the anterior and posterior cardinal angles. Surface ornamented with ribs and deep and large sub-circular pits. A sinuous median rib runs the length of the carapace; a second prominent diagonal rib runs from the posterodorsal angle downwards and joins the median rib at the subcentral tubercle; a third and shorter rib runs from the posterior third of the dorsal margin and extends obliquely to the joint-point of the other two ribs. Ventrolateral keel prominent. Ocular tubercle well developed. Carapace inflated in dorsal view with compressed extremities. Internal features not observed.

Dimensions.—length: 0.70 mm; height: 0.40 mm; width: 0.35 mm.

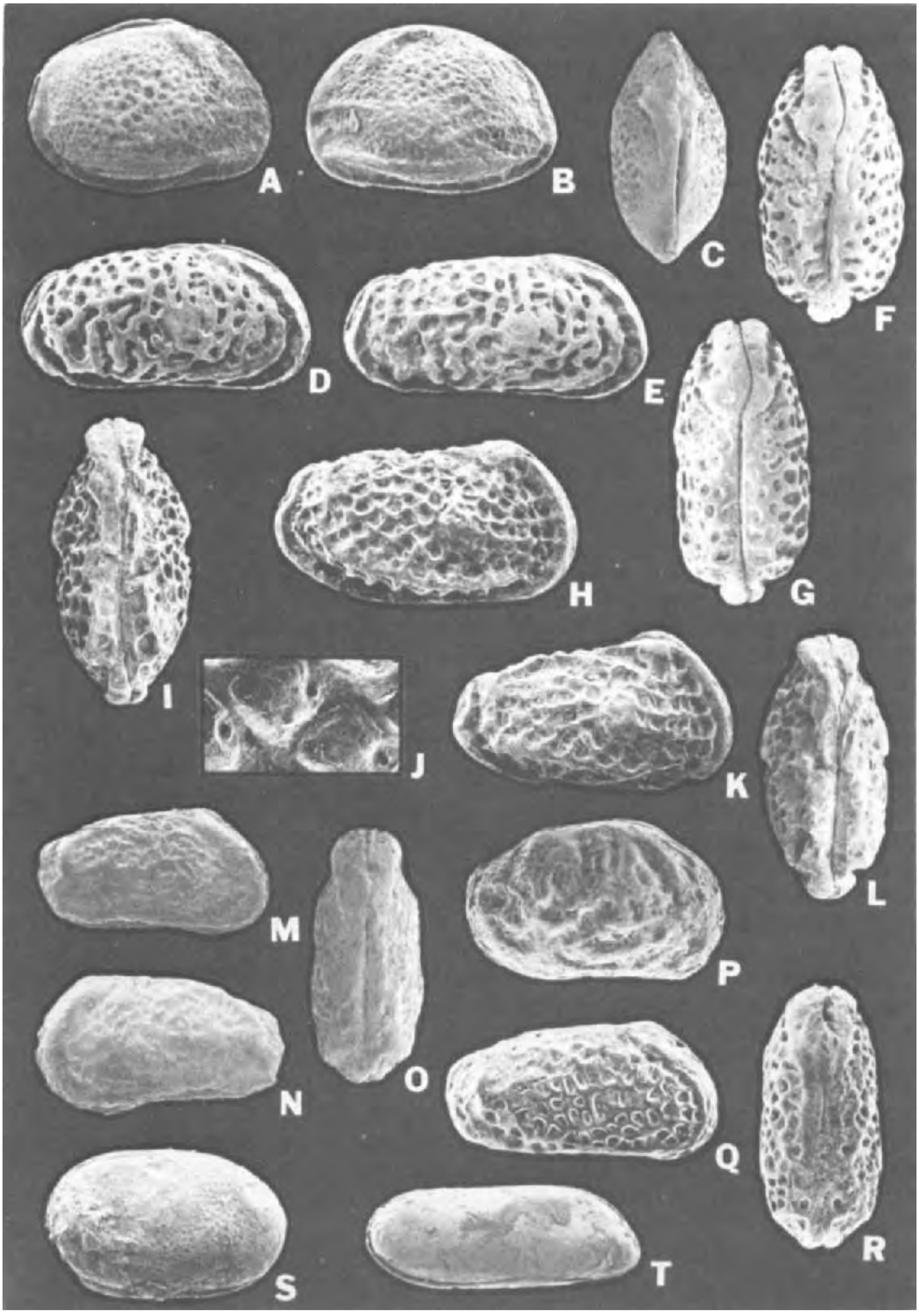
Remarks.—*Quadracythere* sp. presents similarities to *Quadracythere biruga* Hornibrook (1952), described from lower Oligocene to Recent deposits of New Zealand. Differs in being narrower, in the less acute caudal projection which does not show the "two strong and terminal spines" (:45) of Hornibrook's species, in the antero-dorsal angle not being so markedly elevated and in the direction and number of the diagonal ribs. It also shows some similarities to *Quadracythere truncula* (Brady) which displays the same stratigraphic range as *Q. biruga* in the New Zealand Tertiary deposits, but Brady's species differs in the straighter dorsal margin and straighter median rib, in the number and position of the oblique ribs, in the lower anterodorsal angle and in being narrower in dorsal view.

Another similar species, *Quadracythere nealei* Sanguinetti (1979), from the Miocene deposits of the Pelotas basin (Brazil), shows a more obliquely rounded anterior end, a straighter median rib, more elongated pits and a somewhat different dorsal view.

Repository.—YPF. Lab. Geol. N° 361.

Family HEMICYTHERIDAE Puri, 1953
Genus AURILA Pokorny, 1955

Type species.—Cythere convexa Baird, 1950.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AURILA cf. CONVEXA (Baird, 1950)
(Plate 1, figs. R, S)

Mutilus (Aurila) cf. *convexa* (Baird). BECKER, 1964, p. 334, Pl. 4, figs. 2a, b.

Material.—22 carapaces.

Dimensions.—(female): length: 0.65 mm; height: 0.42 mm; width: 0.32 mm; (male): length: 0.67 mm; height: 0.42 mm; width: 0.30 mm.

Remarks.—ECa. X-1 borehole specimens are identical to *Mutilus* (*Aurila*) cf. *convexa* (Baird), a species described from middle Miocene strata of the Austral basin (Becker, 1964). Bertels (1975b) referred Becker's species to the "Patagonian Stage *s. l.*" ostracod assemblage of the Austral basin. According to Doruk (1973), the distribution of Biard's species is Recent in the Atlantic and Mediterranean, Miocene–Quaternary in Europe and Miocene, Pliocene and Recent in Turkey and Cyprus.

Repository.—YPF. Lab. Geol. N° 362.

AURILA MAGALLANICA n. sp.
(Plate 2, figs. A, C)

Brachycythere 1 BECKER, 1964, p. 337, Pl. 5, figs. 5a, b.
Aurila sp. (Becker). BERTELS, 1975b, Pl. 4, figs. 3a, b.

Etymology.—From the Magallanes Formation.

Holotype.—Complete carapace. YPF. Lab. Geol. N° 363/1.

Paratypes.—8 carapaces. YPF. Lab. Geol. N° 363/2.

Diagnosis.—A species of *Aurila* with a strong ventrolateral rib; two short and weak secondary ribs of anteroventral position and one of posteroventral position, subparallel to the ventrolateral rib; pitted surface, (more coarsely in the central portion of the valves) and well developed eye tubercle.

Description.—Carapace subtriangular in lateral view. Anterior end obliquely rounded; posterior end pointed, dorsally concave in the right valve; ventral margin sinuous; dorsal margin convex in the left valve and straight in the right one. Maximum height anterior to the middle. Left valve larger than the right, overlapping it at the dorsal and posterodorsal margins. The ornamentation consists of a strong ventrolateral rib, gently curved and parallel to the ventral margin and short and weak secondary ribs, two of anteroventral position and one of posteroventral position, subparallel to the main rib. The surface of the valves is pitted centrally and strongly punctated toward the margins. Carapace sub-elliptical with compressed ends in dorsal view. In ventral view, carapace swollen by the ventrolateral ribs.

Dimensions.—length: 0.62 mm; height: 0.40 mm; width: 0.27 mm.

Remarks.—Specimens which are identical to *Aurila magallanica* n. sp. except in the more regular surface pitting, have been previously found in Miocene outcrops in Las Cuevas and described as *Brachycythere* 1 by Becker (1964). She observed the following internal features (:332, in Spanish):

PLATE 2—Figs. A–C. *Aurila magallanica* n. sp.; A, RV lateral view, ×60; B, LV lateral view, × 60; C, dorsal view, ×60; holotype YPF. Lab. Geol. N° 363/1. Figs. D–G. *Urocythereis bertelsae* n. sp.; D, female, RV lateral view, holotype YPF. Lab. Geol. N° 364/1, ×60; E, male, RV lateral view, ×60; F, female, dorsal view, holotype YPF. Lab. Geol. N° 364/1, ×60; G, male, dorsal view, ×60. Figs. H–L. *Australicythere* sp. 1 (Becker); H, female, RV lateral view, ×60; I, female, dorsal view, ×60; J, detail of surface reticulation showing normal pores placed at the sides of the ribs, ×100; K, male, RV lateral view, ×60; L, male, dorsal view, ×60. Figs. M–O. *Munseyella santacrucensis* n. sp.; M, RV lateral view, ×60; N, LV lateral view, ×75; O, dorsal view, ×75; holotype YPF. Lab. Geol. N° 368/1. Fig. P. *Callistocythere litoralensis* (Rossi de García). RV lateral view, ×100. Figs. Q–R. *Munseyella* sp.; Q, female, RV lateral view, ×60; R, female, dorsal view, ×60. Fig. S. *Cytherella* aff. *C.* (*Platella*) *fragilis* (Rossi de García), LV lateral view, ×60. Fig. T. *Copytus* sp., RV lateral view, × 60.

"Inner lamella moderately wide. Line of concrescence and inner margin coincident. Radial pore canals numerous, regularly spaced, less numerous in the posterior region. Hinge amphidont/heterodont with strong subcylindrical anterior tooth and elongated crenulated posterior tooth. Deep ocular sockets. Muscle scar pattern not observed".

Bertels (1975b) illustrated Becker's species as *Aurila* sp. and referred it to the upper Oligocene-lower Miocene? ostracod assemblage of the Austral basin.

Aurila magallanica n. sp. shows similarities to *Aurila trigonula* (Jones), as it appears illustrated for Miocene sediments of the Pelotas basin (Brazil) by Sanguinetti (1979), but differs in the centrally pitted instead of regularly punctated surface of the valves, in the better developed eye tubercle and in the presence of ribs. *Aurila variabilepunctata* Swain and Gilby (1974), described from Holocene nearshore samples of Baja California, is another similar species, but the outline is somewhat different and shows "a coarsely reticulate ridge pattern developed posteriorly and a pitted and narrow reticulate pattern anteriorly" (Swain and Gilby, 1974: 305).

Repository.—YPF. Lab. Geol. N° 363.

Genus UROCYTHEREIS Ruggieri, 1950

Type species.—*Cytherina favosa* Roemer, 1838.

UROCYTHEREIS BERTELSAE n. sp.
(Plate 2, figs. D–G)

Urocythereis 1 Becker, 1964, p. 335, Pl. 4, fig. 3.
Urocythereis Becker, BERTELS, 1975b, Pl. 4, figs. 7, 8.

Etymology.—In honour of Dr. Alwine Bertels, who made many valuable contributions to the knowledge of Cretaceous and Tertiary ostracods of Argentina.

Holotype.—Complete carapace. YPF. Lab. Geol. N° 364/1.

Paratypes.—Two carapaces. YPF. Lab. Geol. N° 364/2.

Diagnosis.—*Urocythereis* with subrectangular outline, coarsely foveolate surface; smooth anterior marginal rim; posteroventral oblique ridge and short caudal process.

Description.—Inflated subrectangular carapace in lateral view. Dorsal margin nearly straight; ventral margin slightly concave in the middle of the length, nearly parallel to the dorsal margin; anterior end rounded; posterior end pointed, concave dorsally in the right valve, forming a short caudal process with small marginal denticles. Left valve larger than the right, overlapping it anterodorsally and posterodorsally. Maximum height at the anterior cardinal angle. Subcentral and eye tubercles not conspicuous. Anterior marginal rim smooth and thick. An oblique rib runs from the posterocardinal angle to the posterior sixth of the ventral margin and limits the surficial ornamentation. The surface of the valves is coarsely and irregularly foveolate. Along the anterior margin the foveae are arranged in sub-parallel rows.

Carapace sub-elliptical in dorsal view, with compressed posterior end; maximum width posteriorly, coincident with the oblique ribs. Sexual dimorpism present, the males being longer and narrower than females.

Dimensions.—(female): length: 0.72 mm; height: 0.40 mm; width: 0.43 mm; (male): length: 0.75 mm; height: 0.35 mm; width: 0.35 mm.

Remarks.—Specimens identical to *Urocythereis bertelsae* n. sp. were previously found in Miocene outcrops, in Las Cuevas and Monte Entrance in the Santa Cruz province (Becker, 1964). Becker observed the following internal features (:355, in Spanish): "Inner lamella wide. Line of concrescence and inner margin coincident. Selvage markedly developed. Radial pore canals straight, numerous anteriorly. Muscle-scar pattern composed of three frontal scars and four adductor scars, the second of which is divided. Hinge amphidont/heterodont". Later Bertels (1975b) illustrated Becker's species and referred it to the upper Oligocene–lower Miocene? ostracod assemblage of the Austral basin. The species was also found in "Patagonian" outcrops (Echevarría, 1985, pers. comm.) and in upper Oligocene-lower Miocene subsurface sediments of the northern area of the basin.

Urocythereis bertelsae n. sp. shows similarities to *Urocythereis* sp. (Keij, 1957) described for the Pliocene of France, but differs in the postero lateral outline and in the presence of the posterior oblique rib. It is also similar to *U. bidentata* (Bosquet), known from the lower Miocene of southwestern France (Keij, 1957), but differs in the less conspicuous caudal process and in the arrangement of the secondary ornamental pattern.

Repository.—YPF. Lab. Geol. N° 364.

Genus AUSTRALICYTHERE Benson, 1964

Type species.—*Cythereis polylyca* Müller, 1908.

AUSTRALICYTHERE sp. 1 (Becker, 1964)

(Plate 2, figs. H, L)

Hermanites 1 BECKER, 1964, p. 336, Pl. 5, fig. 3.
Hermanites sp. 1 Becker BERTELS, 1975b, Pl. 4, figs. 9a-c.

Material.—21 carapaces (2 broken).

Description.—Carapace heavy, subrectangular in lateral view. Dorsal margin straight with irregularities caused by the reticular pattern of the surface; ventral margin straight to gently convex; anterior end broadly rounded, bordered by a thick marginal rim; posterior end subrounded, bordered by a narrow marginal rim. Anterior and posterior margins finely denticulated. Cardinal angles well-marked; maximum height at the anterior one. Valves of approximately equal size, the left being somewhat larger than the right at the anterior and posterior cardinal angles. Eye and subcentral tubercles prominent. A ventrolateral ridge extends from the anterior marginal rim to the posterior sixth of the carapace and a vertical ridge extends from the posterior end of the ventrolateral ridge, toward the dorsum. Surface heavily reticulated with normal pores placed at the sides of the ribs of the reticular surface pattern (fig. J). Carapace inflated in dorsal view, with sub-parallel sides. Anterior end thickened by the anterior marginal rim. The posterior end converges sharply from the posterior vertical ridge and is truncated at the posterior margin. Greatest width near the subcentral tubercle.

The sexual dimorphism is strong, the males being longer and narrower than females, subtrapezoidal in lateral view and slightly caudal posteriorly. Other features not observed.

Dimensions.—(female): length: 0.70 mm; height: 0.42 mm; width: 0.30 mm; (male): length: 0.72 mm; height: 0.35 mm; width: 0.25 mm.

Remarks.—*Australicythere* sp. 1 (Becker) shows marked similarities to *Australicythere polylyca* (Müller), a Recent species from the Antarctica (Benson, 1964), but differs in being smaller, in the stronger reticular surface pattern, in the more pointed posterior end and in being narrower in dorsal view. It also presents similarities to *Australicythere bensoni* Sanguinetti (1979), a Miocene species of the Pelotas basin (Brazil), but shows a different ornamental pattern.

Australicythere sp. 1 is known from Miocene outcrops in Las Cuevas and Monte Entrance (Becker, 1964); from La Despedida Formation (Eocene) of Tierra del Fuego island (Echevarría, 1985, pers. comm.) and from upper Oligocene–lower Miocene sediments of the northern area of the Austral basin.

Repository.—YPF. Lab. Geol. N° 365.

Family CYTHERIDEIDAE Sars, 1925
Genus COPYTUS Skogsberg, 1939

Type species.—*Copytus caligula* Skogsberg, 1939.

COPYTUS sp.
(Plate 2, fig. T)

Copytus sp. ZABERT and HERBST, 1977, p. 149, Pl. 3, fig. 10.
Copytus sp. ECHEVARRÍA, 1982, p. 223, Pl. 1, fig. 5.

Material.—5 caparaces.

Dimensions.—length: 0.70 mm; height: 0.25 mm; width: 0.22 mm.

Remarks.—*Copytus* with markedly oblique anterodorsal margin and three weak anteroventral carapace folds. It has been described from lower Miocene outcrops of the Carmen Silva Formation, Tierra del Fuego island (Echevarría, 1982). It is also known from the Paraná Formation (upper Miocene), in the Entre Ríos province (Zabert and Herbst (1977) and from upper Oligocene - lower Miocene subsurface strata of the northern region of the Austral basin.

Repository.—YPF. Lab. Geol. N° 366.

Family LEPTOCYTHERIDAE Hanai, 1957
Genus CALLISTOCYTHERE Ruggieri, 1953

Type species.—*Cythere littoralis* Müller, 1894.

CALLISTOCYTHERE LITORALENSIS (Rossi de García, 1966)
(Plate 2, fig. P)

Perissocytheridea litoralensis. ROSSI DE GARCÍA, 1966, p. 206, Pl. 2, figs. 3a-c.

Material.—2 carapaces.

Dimensions.—length: 0.42 mm; height: 0.25 mm; width: 0.20 mm.

Remarks.—A species of *Callistocythere* ornamented with coarse and sinuous ribs which are perpendicular to the dorsal margin in the upper middle of the carapace and subparallel to the ventral margin in the lower middle of the carapace. It was originally described from Miocene strata of northeastern Argentina (Rossi de García, 1966) and is also known from upper Oligocene - lower Miocene subsurface sediments of the northern area of the Austral basin; from upper Miocene subsurface sediments of the Santa Fē province (Zabert, 1978) and from Miocene subsurface sediments of the Pelotas basin (Sanguinetti, 1979).

Repository.—YPF. Lab. Geol. N° 367.

Family PECTOCYTHERIDAE Hanai, 1957
Genus MUNSEYELLA Van den Bold, 1957

Type species.—*Toulminia hyalokystis* Munsey, 1953.

MUNSEYELLA SANTACRUCENSIS n. sp.
(Plate 2, figs. M–O)

Etymology.—From the Santa Cruz province.

Holotype.—Complete carapace. YPF. Lab. Geol. N° 368/1.

Paratypes.—Two carapaces. YPF. Lab. Geol. N° 368/2.

Diagnosis.—A species with subrectangular outline; obliquely rounded anterior end; truncated posterior end, somewhat oblique posteroventrally; smooth and moderately wide anterior rim;

narrower posterior rim; prominent posterodorsal ridge which curves itself toward the anterior end at the middle of the posterior height, swelling the carapace. The surface of the valves is irregularly reticulated.

Description.—Carapace small, elongate subrectangular in lateral view. Dorsal margin straight to gently convex; ventral margin slightly concave. Anterior end obliquely rounded; posterior end truncated, somewhat oblique ventrally. Maximum height at the anterior cardinal angle. Left valve larger than the right, overlapping it at the anterior, ventral and posterior margins. Anterior marginal rim thick, smooth and moderately wide; posterior rim narrower. A smooth ridge runs dorsally from the posterior third of the carapace, parallel to the dorsal and posterior margins, curving itself toward the anterior end at the middle of the posterior height and swelling the carapace. Surface of the valves irregularly reticulated. Carapace subrectangular in dorsal view, with parallel sides; anterior end thickened by the marginal rim. The posterior end converges sharply from the posterior ridge and is truncated at the posterior margin.

Dimensions.—length: 0.47 mm; height: 0.20 mm; width: 0.17 mm.

Remarks.—*Munseyella santacrucensis* n. sp. is similar in outline to *Munseyella* sp., illustrated by Bertels (1975b) for Pleistocene strata of Argentina, but the last species shows a punctated surface and a different arrangement of ridges. Another Argentine species, *Munseyella laurea* Bertels (1973), described from outcrops of the Roca Formation (lower Danian), in the Río Negro province, presents similar differences and shows a more rounded posterior end and a different dorsal view.

Munseyella santacrucensis n. sp. is also comparable to *Munseyella rectangulata* Swanson (1969) described from the lower Miocene of New Zealand, but the arrangement of ridges and reticular pattern is different. *Munseyella minuta* (Van den Bold), known from Oligocene - Miocene strata of Trinidad (Van den Bold, 1958) and *Munseyella* sp. Van den Bold (1963) from the upper Miocene of Trinidad, show similar outlines but differ in the ornamental pattern.

Repository.—YPF. Lab. Geol. N° 368.

MUNSEYELLA sp.
(Plate 2, figs. Q, R)

Material.—13 carapaces.

Description.—Carapace small, sub-rectangular in lateral view. Dorsal margin straight; ventral margin gently concave at the anterior third of the carapace; anterior end obliquely rounded; posterior end almost straight. Maximum height at the anterior cardinal angle. Left valve larger than the right, overlapping it at the anterodorsal and posterodorsal margins. Anterior marginal rim smooth and moderately wide; ventral and posterior rims smooth and narrower. A short and narrow ridge is developed parallel to the upper part of the posterior margin, swelling the carapace. The surface of the valves is heavily reticulated, longitudinally to the anterior and posterior outline of the carapace. Males are longer and narrower than females. Internal features not observed.

Dimensions.—(female): length: 0.45 mm; height: 0.22 mm; width: 0.18 mm.

Remarks.—*Munseyella* sp. was previously found in the Upper Member of the Carmen Silva Formation (lower Miocene), on Tierra del Fuego Island (Echevarría, 1985, pers. comm.) and in upper Oligocene - lower Miocene subsurface strata of the northern area of the Austral basin. It shows marked similarities to *Munseyella* sp., illustrated by Bertels (1975b) from Pleistocene strata of Argentina, but differs in being less elongated and in some details of the reticular pattern of the surface. *Munseyella* sp. from the upper Oligocene of Australia (McKenzie, 1974) is a similar species, but shows some different sculptural details. The Upper Miocene *Muneyella argentina* Zabert, 1978, known from the subsurface of the Santa Fè province, is another heavily ornamented species but its outline is different and the valves are reticulated at the periphery and pitted centrally.

Repository.—YPF. Lab. Geol. N° 369.

Suborder PLATYCOPINA Sars, 1866
Family CYTHERELLIDAE Sars, 1866
Genus CYTHERELLA Jones, 1849

Type species.—*Cytherina ovata* Roemer, 1840.

CYTHERELLA aff. C. (PLATELLA) FRAGILIS (Rossi de García, 1966)
(Plate 2, fig. S)

Cytherella aff. *C. (Platella) fragilis* (Rossi de Gracía). ECHEVARRÍA, 1982, p. 219, Pl. 1, figs. 1a, b.

Material.—5 carapaces.

Description.—Carapace subelliptical in lateral view. Ventral and dorsal margins subparallel; anterior end rounded; posterior end obliquely rounded dorsally. Right valve larger than the left, overlapping it along the periphery. Surface finely punctated with a slender elongated subcentral depression. In dorsal view carapace elongated, ovoidal. Maximum width posterior to the middle. Other features not observed.

Dimensions.—length: 0.62 mm; height: 0.37 mm; width: 0.22 mm.

Remarks.—This species was previously found in the lower Miocene Carmen Silva Formation (Echevarría, 1982) and in upper Oligocene – lower Miocene subsurface sediments of the northern region of the Austral basin. It shows marked similarities to *Cytherella* (*Platella*) *fragilis* Rossi de García (1966), described from northeastern Argentina, but is somewhat smaller. *Cytherella* (*C.*) sp. (Zabert, 1978), an upper Miocene species from northeastern Argentina, differs in its obliquely rounded anterior end and concentrically arranged surface punctations. *Cytherella* (*C.*) cf. *C.* (*C.*) *punctata* Brady (Zabert, 1978) shows larger punctations and a different outline.

Repository.—YPF. Lab. Geol. N° 370.

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Palaeocene Non-marine Ostracods in China

SHAO-ZENG GUAN
Geological Institute for Chemical Mineral Products,
Ministry of Chemical Industry, P. R. China

Apart from China, Palaeocene non-marine ostracods have been found in few areas of the world. As presently known, they have only been reported from the Gant Range of Ney County in Nevada, the Tongue River Member of the Fort Union Formation of Powder River County in Montana and Palaeocene or Lower Eocene Flagstaff Limestone of Utah in the Western United States, from the white Beds of the Nemegt Basin in the Gobi Desert and the Nalanbulag Formation of Outaltai Gobi in the People's Republic of Mongolia.

In China, the non-marine Palaeocene deposits are well developed and widely distributed in the north, south, northwest and a few other regions, where they are not only exposed in continuous succession, but also yield abundant fossil remains.

In recent years, the Palaeocene ostracod fauna has been separated into an Early-Middle Palaeocene assemblage and a Late Palaeocene assemblage, which are well developed in the Shanghu Formation and the Nongshan Formation in the stratotype section of the Nanxiong Basin, Guangdong. Similar ostracod assemblages have also been found in Jiangsu, Anhui, Zhejiang, Henan, Shandong, Qinghai, Inner Mongolia(?), the Songliao Basin (?) and other regions.

THE SUCCESSION OF THE PALAEOCENE OSTRACOD ASSEMBLAGES

1) The Early-Middle Palaeocene ostracods are represented by the *Porpocypris orbiculata-Cypridea* (*Morinia*) *nanxiongensis-Parailyocypris taizhouensis* assemblage dominated by *Porpocypris orbiculata* Guan, *P. spheroidalis* Guan, *Cypridea* (*Morinia*) *nanxiongensis* Guan, *C.* (*M.*) *elongata* Guan, *C.* (*Pseudocypridina*) *subtera* Hou, *C.* (*P.*) *rigida* Guan, *C.* (*Guangdongia*) *speciosa* Guan, *Parailyocypris taizhouensis* Yang, *Ilyocypris subhuangqiaoensis* Yang, etc. which bears a close resemblance to the Palaeocene ostracod fauna in the Western United States, in containing a great number of genera and species similar to those of the latter group (Guan, 1979).

An assemblage similar to that of the Shanghu Formation has been found in the Dongtang Formation of the Hengyang Basin in Hunan, the Dalongshan Formation of the Sanshui Basin in Guangdong, the Mengyejing Formation in Yunnan, the Taizhou Formation in Jiangsu and so on.

In the Hengyang Basin, this assemblage is represented mainly by *Cypridea* (*Morinia*) *nanxiongensis* Guan, *Porpocypris orbiculata* Guan, *Cypridea* (*Pseudocypridina*) *rigida* Guan, *Sinocypris* cf. *S. excelsa* Guan, *Cyprinotus* cf. *C. xialiushiensis* Guan and *Cypris* sp.

In the Mengyejing Formation of Yunnan, this assemblage consists of *Parailyocypris changzhouensis* Yang et Hou, *P. jiangchengensis* Ye et Jiang, *Cypris* (*Cristocypris*) *zhengdongensis* (Ye), *Cypridea cryptorostrata* Ye et Jiang, *Porpocypris* sp., *Limnocythere menglaensis* Gou, *Ilyocypris dunshanensis* Mandel and *Sinocypris yulongensis* Gou; except for some endemic forms, the other important members are similar to those of the *Porpocypris-Cypridea-Parailyocypris* assemblage. Since the above fossils have been found in different sections, some species may have come from the Upper Palaeocene strata.

Fifty-eight species of 25 genera have been reported from the Taizhou Formation, the important members of which are *Cypridea* (*Cypridea*) *floribunda* Chen, *C.* (*C.*) *orbinoda* Chen, *C.* (*C.*) *semimorula* Chen, *C.* (*C.*) *hebes* Chen, *C.* (*C.*) *modihebes* Chen, *C.* (*C.*) *vitrea* Chen, *C.* (*Morinia*) *xindianensis* Hou, *C.* (*Pseudocypridina*) *subtera* Hou, *Ilyocypris huangqiaoensis* Yang, *Parailyocypris taizhouensis* Yang, *Porpocypris orbiculata* Guan, *P. sphaeroidalis* Guan, *Disapontocypris tralatitia* Chen, *Quadracypris favosa* Hou, etc. (Hou *et al.*, 1982). As regards the age of the Taizhou Formation, there are different opinions. Some geologists assign it to the late Cretaceous, while others put it in the Late Cretaceous to Palaeocene or the Palaeocene. Although the genus *Cypridea,* which was in its acme in the Early Cretaceous, includes over twenty species in the Taizhou Formation, the majority of them exhibit a unique aspect as indigenous forms which occur only in the border area of Jiangsu and Zhejiang Provinces. Other species, such as those of the genera *Porpocypris, Parailyocypris* and *Ilyocypris,* as well as *Cypridea* (*Pseudocypridina*) *subtera* Hou, *C.* (*Morinia*) *xindiaensis* Hou, *C.* (*Guangdongia*) sp. etc., have also been found in the Shanghu Formation. Most of them continue to occur in the overlying 1st Member of the Palaeocene Funing Formation. However, on the evidence of the sporopollen and charophyte floras found in association, a Palaeocene age for the Taizhou Formation is most likely.

TABLE 1—DISTRIBUTION OF LATE PALAEOCENE OSTRACODS IN CHINA.

			ostracoda fossil																										
area	basin	stage	Candona abrupta Guan	C. subcombibo Yang	C. xinzhoangensis Zhang	Cypridea (Pseudocypridina) sp.	Cyprinotus libitus Guan	C. xialushiensis Guan	Cypris sp.	Cyprois sp.	Dogelinella subparallela Guan	Eucypris hengyangensis Guan	E. stagnalis Mandelstam	E. subreticulata Guan	Homoeucypris bucerusa Ho et Zhou	Ilyocypris hengyangensis Guan	Limnocythere nemegtanensis Szczechura	L. sp.	Metacypris changzhouensis Chen	M. luanchuanensis Sun et Li	Neomonoceratina bullata Yang et Chen	Parailyocypris changzhouensis Y. et H.	P. jiangsuensis Yang	P. obesa Yang	Sinocypris excelsa Guan	S. funingensis Ho	S. multipuncta Ho	Sinometacypris sp.	Talicypridea sp.
Guangdong	Nanxiong Basin	Nongshan For.					O					O		O								O			O	O			
	Shanshui Basin	Xinzhuang For.	O		O		O					O		O		O						O			O	O			
	Longgui Basin	Xinzhuang For.								O		O					O					O			O			O	
	Heyuan Basin	Xinzhuang For.										O										O			O				
	Changchang,Hainan	Changchang For.																							O				
	Beibu Wen	Liushagang For.										O										O			O				
Guangxi	Hepu Basin	Shangyang For.										O		O		O		O				O			O				
Hunan	Hengyang Basin	Xialushi For.					O	O				O	O	O		O				O		O			O	O			
	Yunma Basin	Gaocun For.										O													O				
	Dongting Basin	Doumu For.				O			O									O				O			O	O		O	
Hubei	W. Jianghan Basin	Gaangjiachong F.					O	O	O			O		O				O	O	O		O			O				
	C. Jianghai Basin	Shasi For.					O					O				O	O								O				
Sichuan	W. Sichuan Basin	Mingshan For.										O													O				
Jiangxi	Chijiang Basin	Chiliang For.				O			O			O													O				O
Henan	Liguanqiao Basin	Beiying For.							O		O																		
	Lingbao	Xiangcheng For.										O										O							
Anhui	along Yangzi R.	Shuagta For.										O							O		O	O				O			
Jiangsu	N Jiangsu Basin	Funing For.		O								O			O			O	O		O	O	O	O	O	O			
Zhejiang	Hangjiahu area	Changhe G. 1-2F.																				O					O		

2) The Late Palaeocene ostracods represented by the *Sinocypris excelsa-Parailyocypris changzhouensis-Eucypris hengyangensis* assemblage include among their main elements, such species as *Sinocypris excelsa* Guan, *S. funigensis* Ho, *Parailyocypris changzhouensis* Yang et Hou, *Eucypris hengyangensis* Guan, *E. subreticulata* Guan, *E. stagnalis* Mandel, *Cyprinotus xialiushiensis* Guan, *C. libitus* Guan, *Limnocythere nemegtensis* Szczechura, *Metacypris changzhouensis* Chen and so on. Some species of *Sinocypris* in this assemblage are similar to *Hemicyprinotus watsonensis* Swain and *H. watsonensis emaciata* Swain from the Palaeocene to Lower Eocene strata of the Western United States.

This assemblage is extensively distributed in China and is basically identical in taxonomic composition at many different localities as in the Xinzhuang Formation of the Sanshui, Dongwan, Longgui and Heyuan Basins, the Liushagang Formation of Leizhou Peninsula and Beibu Wen of Guangdong, the Shangyang Formation in the Hepu Basin of Guangxi, the Chijiang Formation in the Chijiang Basin of Jiangxi, the Chashanao Member of the Xialushi Formation in the Hengyang Basin, the Gaocun Formation in the Yuanma Basin, the Doumu Formation in the Dongting Basin of Hunan, the Gongjiachong Formation in the Jianghan Basin of Hubei, the Yuguangpo Member of the Mingshan Formation in the western Sichuan Basin, the 2nd to 4th Members of the Funing Formation in Jiangsu, the Shuangta Formation along the Yangzi River of Anhui, the 3rd and 4th Formation of the Changhe Group in the Hangjiahu district of Zhejiang as well as in Xichuan, Linbao of Henan, Yunnan, Qinghai(?) and other places (Table 1). This indicates that these had a similar palaeoenvironment during Late Palaeocene time.

THE NATURE OF THE PALAEOCENE OSTRACODS

The Palaeocene is the first geological period in the Tertiary. Therefore, as a fauna coming into existence at the turning point from Mesozoic to Cenozoic in geological history, the Palaeocene ostracods must show the coexistence of both Mesozoic and Cenozoic taxa with the genera flourishing in the Late Mesozoic gradually declining to their extinction. Those genera having their origin in the Early Cenozoic gradually developed to dominate the fauna. For example, the genus *Cypridea,* originating in the Middle Jurassic and flourishing during the Early Cretaceous, declined in Late Cretaceous times and finally became extinct in the Late Palaeocene (China) or Early Eocene (United States). The genus *Bennelongia* (De Deckker *et al.*, 1981) living today in Queensland, Australia is probably a descendant of *Cypridea* in that remote part of the world.

Among the species of *Cypridea* in the assemblage, *Cypridea* (*Pseudocypridina*) *subtera* has already been found in the Upper Cretaceous Jinjiang Formation of the Yuanma Basin, the Paomagang Formation of the Jianghan Basin, and the Daijiaping Formation of the Hengyang Basin. *Cypridea* (*Morinia*) *nanixongensis* and *C.* (*Pseudocypridina*) *rigida* show a close resemblance to the Late Cretaceous *C.* (*M.*) *xindianensis* Hou and *C.* (*P.*) *gigantea* Ye. In the Shanghu Formation, for example, the number of individuals of *Cypridea* make up about 25% of the total number of ostracods found in it (Guan, 1978).

Talicypridea, which enjoyed its heyday of development in the Late Cretaceous, already has 42 known species of which only two have been discovered in the Palaeocene Nalanblag Formation of the People's Republic of Mongolia and the Mengyejing Formation of Yunnan in Southwestern China respectively.

Porpocypris is an endemic genus, having only been found in Southeastern China where it occurs mainly in the Early-Middle Paleocene strata, although individual species occasionally appear in the Upper Cretaceous, as in the Paomagang Formation of the Jianghan Basin and the Fensuiao Formation of the Dongting Basin.

Ilyocypris, Parailyocypris, Cypris, etc. originated in the Cenozoic, *Ilyocypris* and *Cypris* becoming highly developed and diverse since Palaeocene times with many of their species widespread in various Recent non-marine water bodies all over the world.

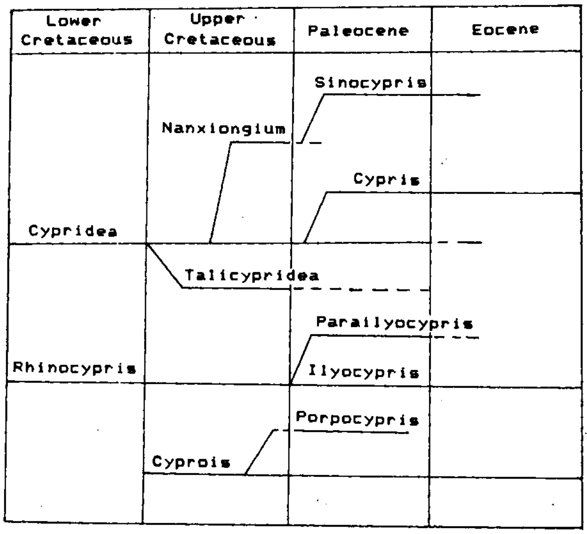
To sum up, this assemblage exhibits aspects of coexistence, namely a transitional character between the Mesozoic and Cenozoic ostracods and differs both from the Late Cretaceous *Talicypridea-Cypridea-Candona* assemblage and the Late Palaeocene *Sinocypris excelsa-Parailyocypris changzhouensis-Eucypris hengyangensis* assemblage.

In the Late Palaeocene, the ostracod fauna underwent a rapid change. *Cypridea* and *Talicypridea*, well developed in the Late Mesozoic, and *Porpocypris*, flourishing in the Early-Middle Palaeocene, no longer existed. However, *Sinocypris, Parailyocypris, Ilyocypris, Sinometacypris*, which were only living in the Cenozoic, and *Eucypris, Cyprinotus, Limnocythere*, which were mainly living in the Cenozoic, gained a dominant position. The Late Palaeocene ostracod fauna shows a closer relationship in terms of genera and species composition with the post-Palaeocene ostracod fauna than with the Early-Middle Palaeocene ostracod fauna.

THE EVOLUTION OF OSTRACODS IN THE PALAEOCENE

From the Mesozoic to the Cenozoic a distinct change took place in the ostracod fauna. Some old genera and species became extinct and a lot of new forms came into being. Their evolutionary relationships are shown in Text-fig. 1.

Rhinocypris, ranging from the Late Jurassic to Cretaceous on the Eurasian continent, disappeared by the end of the Cretaceous. It was characterised by its small-sized carapace, inconspicuous dorsal sulcus and weak reticulation on the valve surface. *Parailyocypris* and *Ilyocypris* are considered to be two lineal descendants of *Rhinocypris*. The former has a large carapace, broadly ovate in side view with a shallow dorsal sulcus, on both sides of which large nodes are developed. *Ilyocypris* possesses a medium-sized carapace, rectangular in lateral view, distinct dorsal sulcus, well developed dorsal and ventral nodes and reticulation on the valve surface. The geological range of *Parailyocypris* is from the Paleocene to Early Eocene, while *Ilyocypris* ranges from the Early Tertiary to Recent. The latter rests on the soft mud on the bottom of lakes and ponds and was one of the most common non-marine genera in the Cenozoic.



TEXT-FIG. 1—Evolution of Palaeocene Ostracods.

The main characteristic feature of *Cypridea* is its anteroventral beak. In order to distinguish the various forms of *Cypridea,* a number of subgenera have been identified. In the early Late Cretaceous, an evolutionary change in the beak of the subgenus *Cypridea* (*Cypridea*) took place resulting in the occurence of the cristate protuberance or lip-like structure of *Talicypridea.* The genus *Talicypridea,* established and discribed by Khand, 1977, existed over thirty million years, most species dying out at the end of the Late Cretaceous with only a few survivors continuing to exist in the Palaeocene. The genus *Cypris* ranges from the beginning of the Tertiary to Recent times. It has been supposed that *Talicypridea* was an intermediate form between *Cypridea* and *Cypris* on the basis of the lip-like structure developed at the anterior end of the *Cypris* carapace which is similar to that of *Talicypridea,* and according to the geological range of the two genera, *Cypris* appeared as a successor of *Talicypridea.* However, *Cypris,* which is subtriangular in lateral view and subglobose in dorsal view, differs distinctly from *Talicypridea,* which is subrectangular in side view and wedge-shaped in dorsal view. Judging from the ontogeny of *Cypris* (Guan, 1984), its early larval shell shows no relationship with *Talicypridea.* Thus *Cypris* must originate directly from *Cypridea.* The subgenus *Cypridea* (*Bisulcocypridea*) has two parallel transverse sulci in the dorsal part and flourished in the Cretaceous period. Its immediate descendant is probably *Cypridea* (*Guangdongia*) Guan, 1978, which has three transverse sulci arranged in a radial pattern in the dorsal part.

Nanxiongium (namely *Quadracypris*) probably originates from one of the unbeaked types of the genus *Cypridea* (Hou, 1983).

Sinocypris, which has a medium-sized shell, is ovate in lateral view with a shallow depression in the central anterior part of the valve and a smooth or reticulate valve surface. It bears a strong resemblance to *Nanxiongium,* except that the carapace of *Sinocypris* is larger with the surface reticulation not well developed. As regards the time distribution, *Nanxiongium* reached its maximum development mainly in the Late Cretaceous while *Sinocypris* appeared at the beginning of the Tertiary. Thus *Sinocypris* may be considered to have originated from *Nanxiongium.*

Porpocypris is characterised by its small carapace, subcircular in lateral view and swollen in its central part, which sometimes looks likes a bubble or sometimes forms a node, and by a narrow frill along the anterior margin. Judging from the aspect of outline and anterior frill, *Porpocypris* is similar to *Cyprois. Cyprois* appeared in the Late Cretaceous and flourished in the Cenozoic while *Porpocypris* existed mainly in the Palaeocene, so the latter is probably a descendant of *Cyprois.*

From the evolutionary relationships between the genera discussed above, the following conclusions may be drawn:

1) Increase of shell size is one of the evolutionary trends of genera in the same lineage.

2) The shell ornamentation of descendant forms is more developed than that of their ancestors.

3) The specialization or extreme development of the valve structures of an ostracod may lead to its extinction as is probably the case with *Talicypridea* which had a large crest-like protuberance at the anterior end of the right valve, *Porpocypris* with a strong central swelling which forms a bundle or node, and *Parailyocypris* which had a wide thick and heavy shell with bulky nodes and spines.

4) Most of the above mentioned genera belong to the Order Podocopida, Superfamily Cypridacea. All of them possess simple hingement and inner lamellae which remain almost unchanged from ancestral to descendant forms. This pehnomenon is probably due to the calm environment in non-marine water bodies with weak hydrodynamic energy, which are inhabited by these ostracods.

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Biostratigraphy of Paleogene Non-marine Ostracoda from East China

JUN-DE HE, DONALD S. VAN NIEUWENHUISE AND FREDERICK M. SWAIN
Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing, P. R. China,
Amoco Production Company Research Center, Tulsa and University of Delaware, Newark, U.S.A.

ABSTRACT

In eastern China, five non-marine ostracode zones can be recognized from the Paleocene to the Oligocene. These are discussed and compared with Paleogene ostracode assemblages in the western United States. Two of the assemblages can be subdivided into freshwater non-marine and marginal marine or saline lake types.

INTRODUCTION

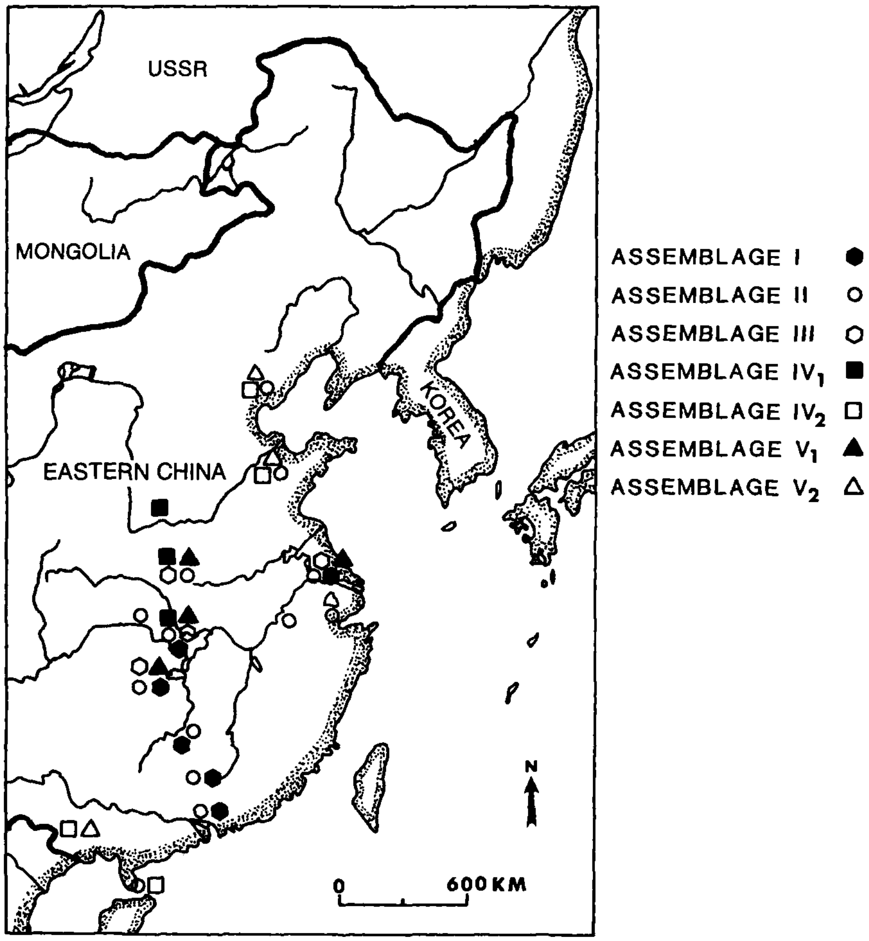
Non-marine sediments deposited during the Early Tertiary in East China consist mostly of detrital clastics and localized carbonates and evaporites that have yielded abundant endemic ostracode faunas. These show: (1) definable assemblages, (2) obvious stratigraphic and lateral facies changes, and (3) significance in both stratigraphic subdivision and correlation of the Early Tertiary subsurface oil-bearing strata. Problems of correlation and assemblage relationships exist in all the faunas to be discussed. Correlation between China and North America are based on generic similarities. Many of the Chinese taxa may be congeneric with the more broadly defined North American genera, but only the first author has seen both the Chinese and the North American taxa. Solution of these problems will aid in the exploration for petroleum in the widespread Cenozoic rocks of East China (Text-fig. 1). Comparison of Chinese material with North American material is necessary to resolve these problems.

CHARACTER, DISTRIBUTION AND CORRELATION OF ASSEMBLAGES

From Paleocene to Oligocene, five stratigraphically significant ostracode assemblages are recognized. Further, the Late Eocene and Oligocene assemblages can be subdivided into non-marine and marginal marine or saline lake ostracode subassemblages (Text-fig. 2). They are given below:

I. *Porpocypris subglobra–Parailyocypris taizhouensis–Cypridea* (*Cypridea*) *xindianensis* assemblage of the Paleocene.

II. *Sinocypris funingensis–Cypris farosa–Eucypris stagnalis–Parailycypris changzhouensis–Limnocythere spinisalata* assemblage of the Early Eocene.



Text-fig. 1—Localities in East China from which ostracode assemblages were obtained.

III. *Echinocypris fabaeformis–Cyprinotus* (*Heterocypris*) *jianglingensis* assemblage of the Middle Eocene.

IV$_1$. Non-marine type: *Cyprinotus* (*Heterocypris*) *macronefandus–Cyprinotus* (*Heterocypris*) *igneus* assemblage of the Late Eocene.

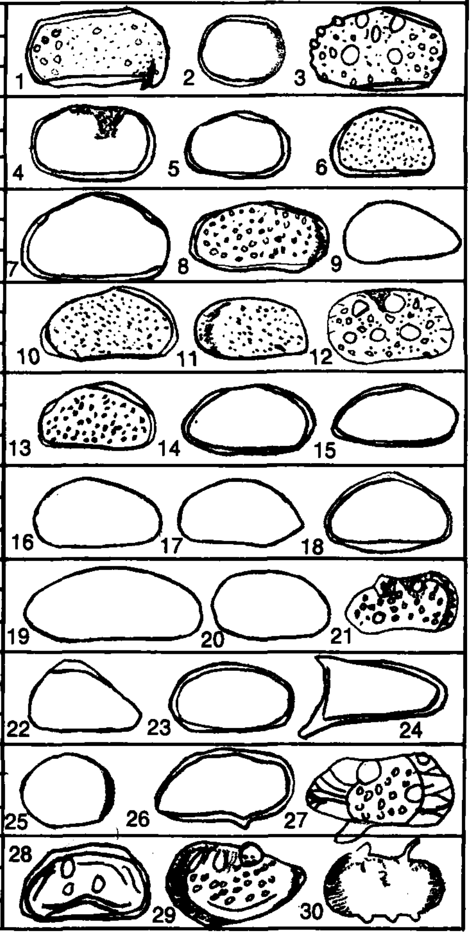
IV$_2$. Marginal marine type: *Cyprinotus* (*Heterocypris*) *yongningensis–Austrocypris levis–Chinocythere subcornuta* assemblage of the Late Eocene.

V$_1$. Non-marine type: *Cyprinotus* (*Cyprinotus*) *hubeieniss–Cyprinotus* (*Heterocypris*) *jinheensis–Pinnocypris postiacuta* assemblage of the Oligocene.

V$_2$. Marginal marine type: *Hebeinia–Huabeinia–Dongyinia-Candona–Parachinocythere–Chinocythere* assemblage of the Oligocene.

Assemblage I was first found in the Shanghu Formation of the Nanxiong Basin in 1964 (Guan, 1978). During the Paleocene, the most abundant and widespread Mesozoic forms, such as *Cypridea* and *Talicypridea* species, dwindled and vanished. They were replaced with similar Cenozoic genera, *Cypridea* (*Cypridea*) *xindianensis* Hou, 1978, *C.* (*Guangdongia*) *speciosa* Guan, 1978, *C.* (*Pseudocypridina*) *subtera* Hou, 1978, *Parailyocypris taizhouensis* Yang, 1982, *Ilyocypris sub-*

PALEOCENE	EOCENE			OLIGOCENE	Figure Number	EARLY TERTIARY OSTRACODES OF EAST CHINA
	LOWER	MIDDLE	UPPER			
■					1	*Cypridea (Cypridea) xindianensis*
■					2	*Porpocypris subglobra*
■					3	*Parailyocypris taizhouensis*
	■				4	*Sinocypris funingensis*
	■				5	*Sinocypris excelsa*
	■				6	*Sinocypris reticulata*
	■	▥	■		7	*Cypris decaryi*
	■				8	*Cypris favosa*
	■				9	*Eucypris stagnalis*
	■				10	*Eucypris subtriangularis*
	■				11	*Limnocythere spinisalata*
	■				12	*Parailyocypris changzhouensis*
		■			13	*Echinocypris fabaeformis*
		■			14	*Cyprinotus (Heterocypris) jianglingensis*
		■	▥	■	15	*Cyprinotus (Heterocypris) jintanensis*
		■	■		16	*Cyprinotus (Heterocypris) formalis*
			■		17	*Cyprinotus (Heterocypris) igneus*
			■		18	*Cyprinotus (Heterocypris) macronefandus*
			■		19	*Austrocypris levis*
			■		20	*Cyprinotus (Heterocypris) yongningensis*
			■		21	*Chinocythere subcornuta*
				■	22	*Cyprinotus (Cyprinotus) hubeiensis*
				■	23	*Cyprinotus (Heterocypris) jinhensis*
				■	24	*Pinnocypris postiacuta*
				■	25	*Cyprois xiangxiangensis*
				■	26	*Candona (Caspiocypris) directa*
				■	27	*Parachinocythere cornispinata*
				■	28	*Dongyingia inflexicostata*
				■	29	*Chinocythere sinucarinata*
				■	30	*Chinocythere wutangensis*

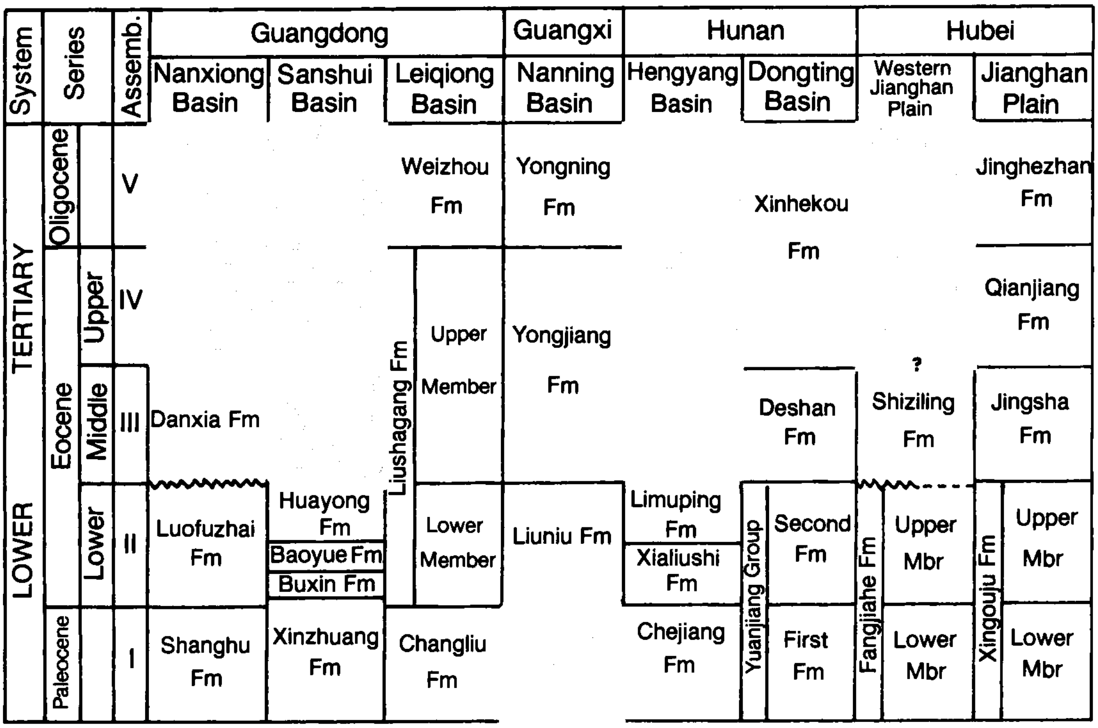


TEXT-FIG. 2—Stratigraphic ranges of Early Tertiary ostracodes of East China.

huanggianoensis Hou and Yang, 1982, *Porpocypris subglobra* (Zhou), 1982, and *Cyprois depressa* Chen, 1982 (Guan, 1978; He, 1979).

The greatest resemblance among the Paleocene ostracode species is found in those from the Chejiang Formation in Hengyang Basin of Hunan, the Lower Member of Fangjiahe Formation in the marginal region of the Yang tze-Han River Plain of Central Hubei and in the First Formation of the Funning Group in Northern Jiangsu (Text-fig. 3). They are characterized by the presence of rare *Cypridea* and by several Cenozoic genera. The assemblage can be correlated with similar ostracodes in Fort Union Formation in the Western Interior of the United States (Swain *et al.*, 1971). Assemblages from both regions contain bisulcate *Cypridea,* such as *Cypridea* (*Guangdongia*) *speciosa* Guan, 1978, which is closely similar to *Cypridea nyensis* Swain, 1964.

Assemblage II has a widespread distribution and a preponderance of typical Cenozoic genera

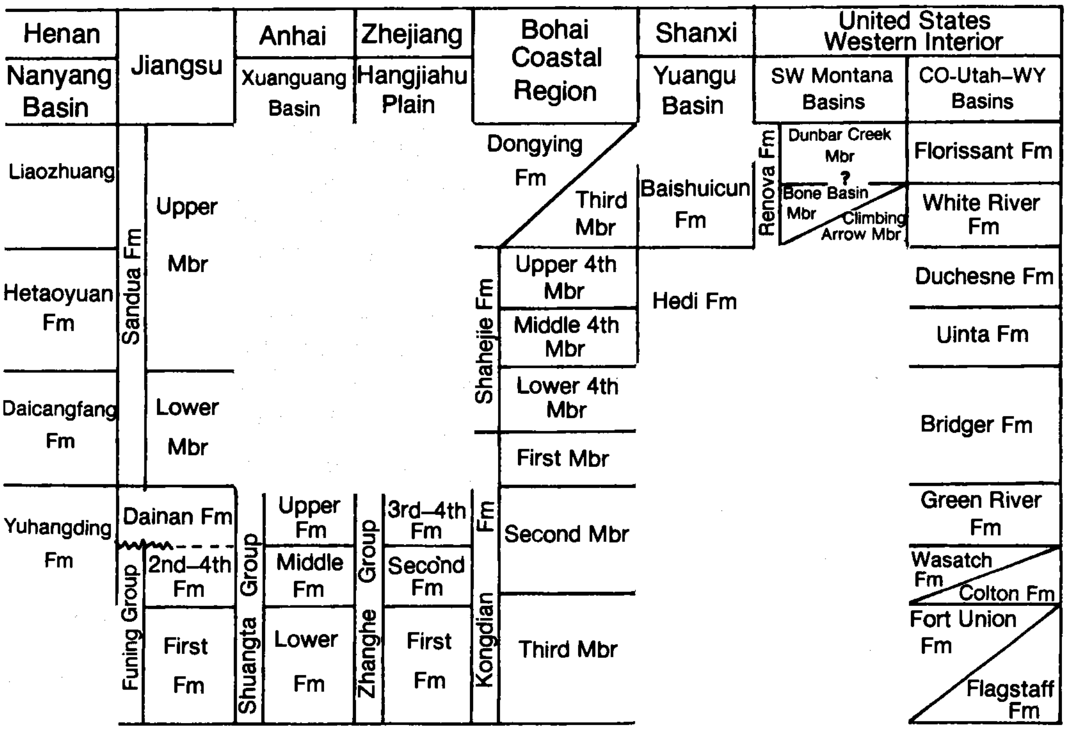


TEXT-FIG. 3—Correlation of the Early Tertiary strata bearing non-marine ostracods in East China.

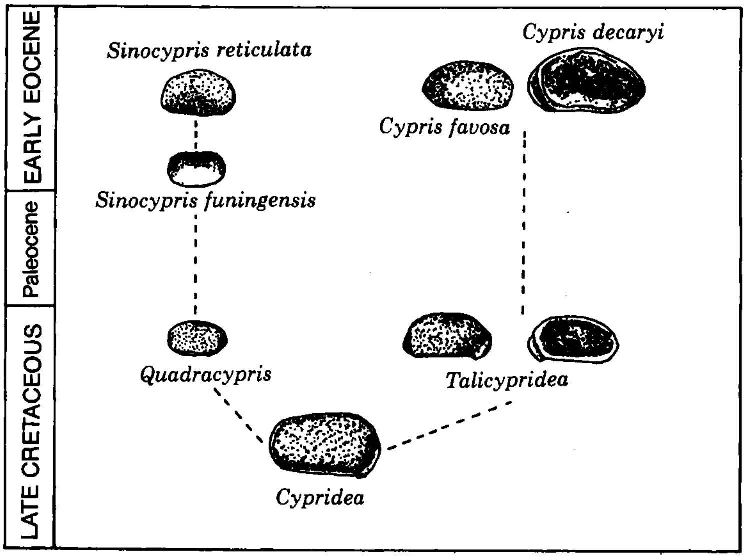
and species. The assemblage consists mainly of *Cypris decaryi* Gauthier, 1933, *C. favosa* Ye, 1978, *Eucypris stagnalis* Mandelstam, 1963, *Eucypris subtriangular* Ye, 1978, *Sinocypris funingensis* Ho, 1982, *S. Parailyocypris changzhouensis* Yang and Hou, 1982, *Limnocythere hubeiensis* Ye, 1978, and *L. spinisulata* Ye, 1978 (Hou *et al.*, 1978, 1982).

Sinocypris is the most abundant ostracode throughout the entire Lower Eocene, but especially in the lower part of the Lower Eocene. A non-marine ostracode assemblage very similar to this assemblage is known from the Colton and Wasatch formations in the Western Interior of the United States (Swain, 1964) and the White Bed of Nemegt Basin in Mongolia (Szczechura, 1971). An important form, such as *Sinocypris funingensis* Ho, 1982, is very similar to *Hemicyprinotus watsonensis* Swain in its weakly reticulate surface. Other species of the assemblage, such as *Cypris favosa* Ye, 1978, are very similar to *Pseudoeucypris pagei* (Swain, 1956) of the Colton Formation in the Western Interior of the United States. *Hemicyprinotus watsonensis* and *Pseudoeucypris pagei* are zonally significant in the Colton Formation in Colorado, Utah, and Wyoming. In the Western Interior of the United States, *Cypridea*-like species are rarely found in the Eocene and Paleocene.

Some of the Cenozoic non-marine ostracodes probably evolved from *Cypridea* (Text-fig. 4). In morphology, especially the compressed mid-dorsal area and inner microstructure, *Sinocypris* is related to *Quadracypris*. Among the other significant forms of *Sinocypris* is *S. reticulata* Zhang and Guan, 1978. *Sinocypris reticulata* may have evolved from *S. funingensis*; it is subtriangular in outline, highest anteromedially; the left valve is slightly larger than the right, overlapping along free margins, especially the anterodorsal margin. These morphological features are quite similar to other types of Late Paleogene and Neogene ostracodes. It is suggesteed that *Sinocypris reticulata* is more advanced than *Sinocypris funingensis* and it has a greater geographic distribution. Follo-



wing the evolutionary development of *Sinocypris,* the ostracode assemblage of the Early Eocene can also be separated into two subassemblages. The lower Early Eocene subassemblage includes *Sinocypris funingensis* Ho, 1982, *S. multipuncta* Ho, 1982, and is associated with many other Cenozoic species. This subassemblage occurs in the Second, Third and Fourth Formations of the



Text-fig. 4—Possible evolutionary relationships of several taxa.

Funning Group of Jiangsu, the Buxin Formation of Sanshui Basin, the Luofuzhai Formation of Nanxion Basin and the Lower Member of the Liushagang Formation of Leiqiong subregion, the Xialiushi Formation of Hengyang Basin, the Second Formation of the Zhanghe Group of Zhejiang and the Middle Member of the Shuangta Group of Xuanguang Basin. The subassemblage of ostracodes from the upper part of the Early Eocene consists mainly of *Sinocypris reticulata* Zhang and Guan, 1978. This species is widely distributed in the Dainan Formation of Jiangsu, the Limuping Formation of Hengyang Basin, the Huayong Formation of Sanshui Basin, the Upper Member of the Fangjiahe Formation of Hubei and the Upper Member of the Shuangta Group of Xuanguang Basin.

Worthy of notice is that the Early Eocene Continental Basin in East China can separated into two biogeographic regions: the northern and the southern, with the area from Lianyunguang to Quinling Moutains as the borderland. The two regions can easily be distinguished from each other by the presence of *Sinocypris* in the southern region and its absence in the northern region.

Assemblage III is the Middle Eocene assemblage. Following the extinction of *Sinocypris* at the end of the Early Eocene, *Echinocypris* and *Cyprinotus* became the dominant non-marine ostracodes, possessing strongly endemic characteristics. This assemblage consists of *Echinocypris elongata* Jiang and Li, 1978, *E. fabaeformis* Li, 1978, *Cyprinotus* (*Heterocypris*) *jianglingensis* He and Zhang, 1982, *C.* (*H.*) *formalis* Schneider, 1963, and a few specimens of *Candona, Ilyocypris, Eucypris* and *Limnocythere* (He *et al.*, 1982). Assemblage III has been found at several localities such as in the Jingsha Formation of the Jianghan Plain, the Deshan Formation of Dongting Basin, the Daicangfang Formation of Nanyang Basin and the Lower Member of the Sanduo Formation of Jiangsu. However, *Echinocypris* is mostly limited to Hubei, Hunan and Henan Provinces. The echinulate forms have not been seen in the First Member of Sanduo Formation. Both are characterized by the presence of numerous species and individuals of *Cyprinotus*, especially in the Jiangsu Province. The faunas can be correlated with each other on the basis of *Cyprinotus* spp.

Middle Eocene Land Mammals were found in the Daicangfang Formation of Henan. These include *Coryphodon* sp., *Palaeosyops* sp., cf. *Breviodon* sp. and *Euryodon minimus* Xu *et al.*, 1979 (Li and Ting, 1983).

Besides the above-mentioned series of ostracode bearing rocks in East China, there are nonfossiliferous rock sequences which consist of reddish-brown sandstones and conglomerates, such as the Danxia Formation of Nanxiong Basin, the Shiziling Formation of the Western Jianghan Plain, and the First Member of the Kongdian Formation to the lower part of the Fourth Member of the Shahejie Formation of the Coastal Region of Bohai. Present interpretations are that these strata overlie the *Cypris–Sinocypris–Eucypris–Parailyocypris–Limnocythere* assemblage of Early Eocene. The nonfossiliferous strata series seem to be Middle Eocene.

Assemblage IV_1. (Non-marine type) In this assemblage, the *Cyprinotus* (*Heterocypris*) spp. are very diverse in species with abundant populations, represented chiefly by *Cyprinotus* (*Heterocypris*) *macronefandus* Li, 1978, and *C.* (*H.*) *igneus* Hou *et al.*, 1978. The assemblage occurs in the Qianjiang Formation of the Jianghan Plain, in the Hetaoyuan Formation of Nanyang Basin, in the middle part of the Fourth Member of the Shahejie Formation of the Coastal Region of Bohai and in the Hedi Formation of Yuanqu Basin. However, the genera and species of assembage IV are different in the East China Region. For example, the assemblage of the Jianghan Plain consists of *Cypris decaryi* Gauthier, 1933, *C.* (*H.*) *gonganensis* He and Zhang, 1982, *Pseudostenocypria*? *triangularis* He and Zhang, 1982, *Paracandona euplectella* (Brady and Norman, 1889), *Ilyocypris biplicata* Sars, 1838, *I. cornae* Mandelstam, 1961 and *Virgatocypris ovata* He and Zhang, 1982. (He *et al.*, 1982). In the Coastal Region of Bohai, ostracodes are less abundant. There, *Cyprinotus* (*Heterocypris*) *igneus* Hou *et al.*, 1978, is associated with a few species of *Cypris, Eucypris* and *Cyprois* (Hou *et al.*, 1978).

In addition, a rich Late Eocene land mammal assemblage co-occurring with ostracode assemblage IV_1 was recently discovered in the Hetaoyuan Formation of Henan and in the Hedi Formation of Yuangu Basin (Li and Ting, 1982). Characteristic fossils are *Ictopidium lechei* Zdansky, 1930, *Hoanghonius stehlini* Zdansky, 1930, *Cricetodon schaubi* Zdansky, 1930, *Hyaenodon yuanchuenesi* Young, 1937, *Chailicyon crassidens* Chow, 1975, *Rhinotitan mongoliensis* (Osborn, 1925), ?*Amynodon mongoliensis* (Osborn, 1930), *Sianodon sinensis* (Zdansky, 1930), *Anthracokeryx sinensis* (Zdansky, 1930).

Assemblage IV_2 has only been found in a few localities which are the upper part of the Fourth Member of the Shahejie Formation in Coastal Region of Bohai, the Upper Member of the Liushagang Formation of Leiquiong subregion and the Yongning Formation of Nanning Basin. This assemblage is allied to, but distinct from, both non-marine freshwater ostracode assemblages and sub-littoral marine ones. In other places, only a few taxa and individuals occur. The Yongning Formation is represented by *Xiyingia cuneata* He, 1981, *Cyprinotus* (*Heterocypris*) *yongningensis* He, 1981, *Ilyocpris jinjiensis* He, 1981, *Chinocythere xixiangtangensis* He, 1981 and *C. subcornuta* He, 1981 (He, 1981). Ostracodes from the upper part of the Fourth Member of the Shahejie Formation are represented by *Cypris postilonga* Hou *et al.*, 1978, *Candona acclivis* Hou *et al.*, 1978, *Austrocypris levis* Hou *et al.*, 1978, *A. posticaudata* Hou *et al.*, 1978, *Pterygocypris caudata* Hou *et al.*, 1978, *Miniocypris subaequalis* Hou *et al.*, 1978, *Limnocythere longipilerformis* Hou *et al.*, 1978, *L. nodosa* Hou *et al.*, 1978, *L. striatituberosa* Hou, *et al.*, 1978, *Chinocythere longicymbiformis* Hou *et al.*, 1978, *C. ventricostata*, Hou *et al.*, 1978. (Hou *et al.*, 1978). This fauna is abundant and diverse. Ostracodes are rare in the Upper member of the Liushagang Formation, which includes mainly species of *Eucypris* and *Chinocythere* (South Sea Branch of Petroleum Corporation of the People's Republic of China *et al.*, 1981).

The characteristics of assemblage IV_2 are summarized as follows:

1) Assemblage IV_2 is characterized by species of a few common freshwater genera such as *Cypris, Cyprinotus, Candona, Ilyocypris* and *Limnocythere* as well as new forms, such as *Austrocypris, Xiyingia, Pterygocypris, Miniocypris,* and *Chinocythere.* The new forms bear some of the same carapace features as nearshore marine and brackish forms, for example, *Chinocythere* resembles *Leptocythere*, which is a marine genus. *Chinocythere* is quite similar to saline non-marine forms of *Elkocythereis* found in the upper and middle parts of the Humboldt Formation of northeastern Nevada in the United States. *Austrocypris* bears some resemblance to *Cytherura*, the latter being a shallow-marine form. In addition, in the Coastal Region of Bohai and in the same horizons with the above-mentioned ostracodes, there have also been reported foraminifera—*Deflandrea* and *Cladosiphonia*—but, curiously enough, no typical marine ostracodes have been discovered (Hou *et al.*, 1978). The marginal marine or saline lake assemblage seems to be related more to saline than to fresh-water masses, suggesting that there may have been a sea invasion at that time, or that the lakes evaporated significantly and became saline enough to support foraminifera.

2) *Austrocypris, Chinocythere* and *Xiyingia* are brackish-water genera that seem to have originated in the Coastal Bohai Basin, Nanning Basin and Leiquiong subregion and are not found elsewhere in China.

3) Assemblage IV_1 (Non-marine) and assemblage IV_2 (marginal marine) have several similar genera and species. For example, *Cyprinotus* (*Heterocypris*) sp. 1 from the Hedi Formation of the Yuangqu Basin (unpublished manuscript). Thus the ostracode assemblage of the transitional type can be correlated with the ostracode assemblage of the continental type and on the basis of land mammal ages (LMA) they are regarded as Late Eocene.

Assemblage V_1 (Non-marine type) is represented chiefly by *Cyprinotus* (*Cyprinotus*) *hubeiensis* He, 1982, *C.* (*Heterocypris*) *jingheensis* (Li, 1978), *C.* (*H.*) *jintanensis* He, 1982, *Pinnocypris postiacuta* Zhou, 1982, *P. alata* Zhou and *Cyprois xiangxiangensis* Guan, 1978, which are associated with a few species of *Cypris, Eucypris, Pseudoeucypris, Ilyocypris* and *Limnocythere.* The species of *Cyprinotus* are numerous and widely distributed. The assemblage is believed by Chinese scientists to be Oligocene on the basis of charophytes and ostracodes. The abundant species of this assemblage are very similar to those of the Renova Formation of the Jefferson Basin in the United States. The same or closely similar species of *Cyprinotus* (*Heterocypris*), *Cyprois* and *Ilyocypris* are also found in the Renova Formation. The principal difference between the two regions is that the species of the subgenus *Cyprinotus* (*Cyprinotus*) and the genus *Pinnocypris* do not occur in the Renova Formation of the Jefferson Basin.

Assemblage V_2 (Transitional type) This assemblage is very rich in both species and individuals. New forms, such as *Huabeinia, Tuozhuangia, Hebeinia, Dongyingia, Camarocypris, Ninghainia, Glenocypris, Xiyingia, Berocypris, Crepocypris, Megacypris, Guangbeinia, Fusocandona, Phacocypris, Ammocypris, Chinocythere, Potamocyprella, Pterygocypris, Minocypris, Nexypria, Stipitalocythere, Parachinocythere, Nanningcythere* are most abundant, as well as a few common freshwater species of *Cypris, Eucypris, Virgatocypris, Herptocyprella, Cyprinotus, Candona, Paracandona, Tuberocyproides, Cycloscypris, Cypria, Cyprois, Ilyocypris, Ilyocyprimorpha, Metacypris* and *Limnocythere.* This assemblage was first found in the First, Second and Third members of the Shahejei Formation and in the Dongying Formation in Coastal Region of Bohai (Hou *et al.*, 1978). Later it was recorded from the Weizhou Formation of Leiquiong subregion and the Yongning Formation of Nanning Basin. (South Sea Branch of Petroleum Corporation of the People's Republic of China *et al.*, 1981; He, 1981). The generic components of the Third Member of the Shahejie Formation up to and including Dongin Formation are numerous, but the Weizhou Formation and Yongning Formation, although similar on the whole, have only a few genera.

From the character of the ostracode assemblages, assemblages V_2 and IV_2 are alike, but assemblage V_2 embraces many new forms which reach their peak of diversity in the assemblage. The marine organism *Leglunia, Pentagonus,* fossil tubes of *Serpulimorpha* and foraminifera have also been discovered in the Coastal Region of Bohai (Hou *et al.*, 1978). Additionally, some results from Early Tertiary shales of the Yongning Formation in Guangxi (He, 1981), indicate that the "equivalent boron" is around 200 ppm (see Walker and Price, 1963), suggesting an oligohaline marginal marine or saline lake environment.

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Cretaceous and Palaeogene Ostracod Biostratigraphy in Xining and Minhe Basins of China

YI-CHUN HAO
Beijing Graduate School of Wuhan College, P. R. China

ABSTRACT

The Xining and Minhe Basins bordering on each other around Ledu in northwestern China cover a wide area from the west of Lanzhou in Gansu province to the east of Xining in Qinghai province (Text-fig. 1). In these inland basins, Mesozoic–Cenozoic terrestrial deposits of great thickness and rich in mineral resources such as coal, oil and salt, have been deposited. The Cretaceous and Palaeogene strata, which range from about 1,400 to 3,400 meters in thickness, contain abundant remains comprising microfossils such as non-marine ostracods, charophytes, spores and pollen, as well as macrofossils including freshwater bivalves, gastropods, estherians, freshwater fishes, reptiles and plants.

In the present paper, biostratigraphy of the Cretaceous and the Palaeogene is discussed in terms of ostracod and charophyte assemblages.

CRETACEOUS AND PALAEOGENE LITHOSTRATIGRAPHY (TABLE 1)

The Cretaceous is divided in ascending order into the Datonghe Formation which includes part of the Upper Jurassic, the Hekou Formation and the Minhe Formation (Hao *et al.*, 1982, 1983).

The Datonghe Formaion is mainly represented by greyish-green and greyish-white, sandy conglomerate and sandstone with interbedded brown mudstones in its lower part; by brown and brownish-red mudstone and siltstone with intercalations of greyish-green and brown sandstone and variegated shale in its middle part, and by brick-red sandstone and conglomerate with intercalations of thin-bedded brown silty mudstone in its upper part.

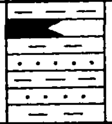
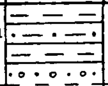
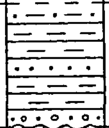
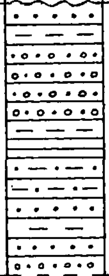
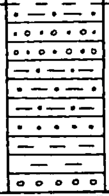
The Hekou Formation comprises reddish-brown sandstone and sandy conglomerate in its lower part; reddish-brown and green mudstone with variegated shale containing interbedded sandstone in its middle part, and reddish-brown mudstone, reddish-brown, orange conglomeratic sandstone and sandy conglomerate with intercalated reddish-brown mudstone in its upper part.

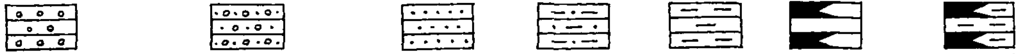
The Minhe Formation is lithologically subdivided into two parts. The lower part consists of reddish-brown sandy conglomerate and the upper part of reddish-brown mudstone and siltstone with interbedded greyish-green sandstone and gypsum.

The Palaeogene strata comprise in ascending order the Qijiachuan Formation, the Honggou Formation and the Mahalagou Formation (Hao *et al.*, 1983).

The Qijiachuan Formation consists of clastic deposits mainly represented by dark brown mudstone, silty mudstone and greyish-brown greyish-green sandstone with gypsolite intercalations and brown coloured basal conglomerate.

TABLE 1—CRETACEOUS AND LOWER TERTIARY STRATIGRAPHY AND FOSSIL ASSEMBLAGE SEQUENCES IN XINING AND MINHE BASINS.

System	Formation/Epoch	Strati-graphic Column	Fossil Assemblages	
			Ostracoda	Charophyta
Lower Tertiary	Mahalagou Formation E_3		*Ilyocypris ellipsoidea—Eucypris milagouensis* Song—*Cyprinotus jucundus* Song Assemblage	*Moedlerisphaera chinensis* Huang and Xu—*Grovesichara minheensis* Yang Assemblage
	Honggou Formation E_2^{2-3}		*Limnocythere hubeiensis* Ye—*L. languida languida* Song Assemblage	*Gyrogona qianjiangica* Z. Wang—*Sphaerpchara minheensis* Yang Assemblage
	Qijiachuan Formation E_1^2–E_2^1		*Cypris decaryi* Gautheir—*Limnocythere hubeiensis* Ye Assemblage	*Stephanochara breviovlis* Lin and Huang—*Neochara squalida* Z. Wang and Lin Assemblage
Cretaceous	Minhe Formation K_2		*Talicypridea reticulata* (Hou)—*Cypridea* (*Cypridea*) *cavernosa* Galeeva—*Cypridea* (*Pseudocypridina*) *longa* Hou—*Eucypris qinghaiensis* Song Assemblage	*Latochara curtula* Z. Wang—*Gyrogona hubeiensis* Z. Wang—*Charites guanpingensis* Z. Wang Assemblage
	Hekou Formation K_1		Upper *Cypridea* (*Cypridea*) *sanmachiensis* Song—*Rhinocypris ventriconcava* Hao—*Ziziphocypris costata* (Galeeva) Assemblage Middle *Cypridea* (*Cypridea*) *unicostata* Galeeva—*Cypridea* (*Ulwellia*) *koskulensis* Mandelstam Assemblage Lower *Lycopterocypris infantilis*—*L. flaccida* Song Assemblage	Middle *Flabellochara jurongica* S. Wang and Zhang—*Aclistochara caii* S. Wang—*Mesochara stipitata* Assemblage
Upper Jurassic	Datonghe Formation J_3–K_1		*Minheella minheensis* Song and Cheng—*Jingguella hutouyaiensis* Hao—*Damonella huangshuiensis* Hao—*Protolimnocythere pingua* Cheng Assemblage	Upper *Minhechara columelaria* Wei—*Multispirochara subovalis* Assemblage Lower *Aclistochara datongheensis* Wei—*A. bransoni* Peck Assemblage



Conglomerate Sandy conglomerate Sandstone Siltstone Mudstone Gypsum Gypsum mudstone

The Honggou Formation is a series of interbedded mudstones, silty mudstones and sandstones. The mudstone and silty mudstone are reddish-brown or brown, while the sandstone is light brown, greyish-green and gypseous.

The Mahalagou Formation consists of light reddish-brown mudstone and light variegated gypsolite with intercalated brown and yellowish-grey sandstone.

OSTRACOD AND CHAROPHYTE ASSEMBLAGES (TABLE 1)

Ostracod Assemblage 1, the *Minheella minheensis–Jingguella hutouyaiensis–Damonella huangshuiensis–Prolimnocythere pinoua* assemblage occurs in the middle part of the Datonghe Formation, where ostracod fossils are preserved in abundance. In the lower and upper parts of the formation ostracods are rarely found (Hao *et al.,* 1983).

The endemic genus *Minhella* is very rich and diversified in the assemblage, next to it are *Damonella* and *Jingguella*; another indigenous form, *Prolimnocythere,* is as abundant as *Minheella,* but less diversified. *Minheella minheensis* Song and Cheng, *Jingguella hutouyaineis* Hao, *Damonella huangshuiensis* Hao and *Prolimnocythera pinoue* are the species which dominate the assemblage. Other important taxa occurring in association are *Minheella ligulata* Song, *M. plicata* Cheng, *M. aurita* Song, *Damonella ovata* Gou, *Jingguella ovata* Gou, *J. ovalis* Song, *Darwinula oblonga* (Roemer), *Ousocypris arca* Song and Cheng, *Lycopterocypris eggeri* Mandelstam (Hao *et al.,* 1983) (Table 2).

Two charophyte assemblages are recognized in the Datonghe Formation. The lower one, the *Aclistochara datongheansis–A. bransoni* assemblage, occurs in the lower part below the horizon containing the ostracod assemblage. The upper one, the *Minhechara columelaris–Multispirochara subovalis* assemblage, is found in the middle part together with the ostracod assemblage. In addition to the most prevalent species which give their names to the assemblage, the other important

TABLE 2—OSTRACOD AND CHAROPHYTE ASSEMBLAGES OF THE DATONGHE FORMATION (J_3–K_1).

Formation \ Fossil Assemblages	Ostracoda		Charophyta	
	Characteristic Components	Important Components	Characteristic Components	Important Components
Datonghe Formation (J_3–K_1)	*Minheella minheensis* Song and Cheng *Jingguella hutouyaiensis* Hao *Damonella huangshuiensis* Hao *Prelimnocythere pingua* Cheng	*Minheella ligulata* Song *M. plicata* Cheng *M. surita* Song *Damonella ovata* Gou *Jingguella ovata* Gou *Djungarica ovalis* Song *Darwinula oblonga* (Roemer) *Ousocypris area* Song and Cheng *Lycopterocypris eggeri* Mandelstam	Upper *Minhechara columelaris* Wei *Multispirochara subovalis* Hao Lower *Aclistochara datongheensis* Wei *A. bransoni* Peck	Upper *Mesochara paragranulifera* (S. Wang) *M. ammoena* (Madler) *Nodosoclavator qinghalenensis* Yang Lower *Aclistochara datongheensis* Wei *A. xiangtangensis* Wei *A. platyglobata* Hao *A. obovata* (Peck) *A. yunnanensis* (Z. Wang *et al.*) *Forochara maedleri* Yang

TABLE 3—OSTRACOD AND CHAROPHYTE ASSEMBLAGES OF THE HEKOU FORMATION AND MINHE FORMATION (K_{1-2}).

Fossil Assemblages / Formation	Ostracoda		Charophyta	
	Characteristic Components	Important Components	Characteristic Components	Important Components
Minhe Formation K_2	*Talicypridea reticulata* (Hou) *Cyprides* (*Cypridea*) *cavernosa* Galeeva *Cypridea* (*Pseudocypridina*) *longa* Hou *Eucypris qinghaiensis* Song	*Talicypridea amoena* (Liu) *T. laliovata* (Hou) *Cypridea* (*Morinina*) *xindianensis* Hou *C.* (*Pseudocypridina*) *gigantea* Ye *Eucypris minheensis* Song *E. debiloides* Ye	*Latochara curtula* Z. Wang *Cyrogona hubeiensis* Z. Wang *Charites guanpingensis* Z. Wang	*Latochara yuananensis* Z. Wang *Charites tenuis* Z. Wang *Grambastichara communis* Z. Wang
Hekou Formation K_1	Upper *Cypridea* (*Cypridea*) *sanmachiensis* Song *Rhinocypris ventriconcava* Hao *Zisiphocypris costata* (Galeeva)	Upper *Rhinocypris jurassica jurassica* (Martin) *Cypridea* (*Cypridea*) *deflecta* Song *C.* (*C.*) *sanmachiensis* Song *C.* (*Ulwellia*) *chuankouensis* Hao *Candoniella candida* Hao *Cypridea* (*Bisulcocypridea*) *skeeteri* (Peck)		
	Middle *Cyrpidea* (*Cypridea*) *unicostata* Galeeva *Cypridea* (*Ulwellia*) *koskulensis* Mandelstam	Middle *Cypridea* (*Cypridea*) *vitimensis* Mandelstam *C.* (*U.*) *meneveensis* Anderson *Rhinocypris jurassica jurassica* (Martin)	Middle *Flabellochara jurongica* S. Wang and Zhang *Aclistochara caii* S. Wang *Mesochara stipitata* (S. Wang)	Middle *Aclisto laiae* S. Wang *A. huangshuiensis* Yang *Mesochara xuanziensis* Yang
	Lower *Lycopterocypris infantilis* *L. flaccida* Song			

components include *Aclistochara umbonata* Wei, *A. xiangtangensis* Wei. *A. platyglobata* Hao, *A. obovata* (Peck), *A. yunnanensis* (Z. Wang *et al.*) and *Porochara maedleri* Yang in the lower assemblage and *Mesochara xuanziensis* Yang, *M. paragranulifera* (S. Wang), *M. ammoena* (Maedler) and *Nodosoclavator qinghaiensis* Yang in the upper assemblage (Hao *et al.*, 1983) (Table 2).

Ostracod Assemblage 2, the *Lycopterocypris infantilis–L. flaccida* assemblage is recognized in the lower part of the Hekou Formation and is monotonous in taxa (Hao *et al.*, 1983) (Table 3).

Ostracod Assemblage 3, the *Cypridea* (*Cypridea*) *unicostata–Cypridea–Ulwellia*? *koskulensis* assemblage appearing in the middle part of the Hekou Formation, is dominated by the genus *Cypridea* in high diversity and abundance. In addition to the most prevalent species, *Cypridea* (*Cypridea*) *unicostata* Galeeva and *Cypridea* (*Ulwellia*) *koskulensis* Mandelstam, the other important forms in the assemblage are *Cypridea* (Cypridea) *vitimensis* Mandelstam, *C.* (*Ulwellia*) *menevensis* Anderson and *Rhinocypris jurassica jurassica* (Martin) (Hao *et al.*, 1983) (Table 3).

Ostracod Assemblage 4, the *Cypridea* (*Cypridea sanmachiensis–Rhinocypris ventriconcava–Ziziphocypris costata* assemblage, is found in the upper part of the Hekou Formation. In this Formation *Cypridea* still maintains its predominance and the new taxon, *Candoniella*, which reached its acme of development in the Cenozoic, makes its first appearance. Besides the characteristic forms such as *Cypridea* (*Cypridea*) *sanmachiensis* Song, *Rhinocypris ventriconcava* Hao and *Ziziphocypris costata* (Galeeva), there are other important components in the assemblage, such as *Cypridea* (*Cypridea*) *deflecta* Song, *C.* (*Ulwellia*) *chuankouensis* Hao, *Candoniella candida* Hao and *Rhinocypris jurassica jurassica* (Martin) (Hao *et al.*, 1983) (Table 3).

Charophytes are only reported from the middle part of the Hekou Formation occurring in association with ostracod Assemblage 3. This *Flabellochara jurongica–Aclistochara caii–Mesochara stipitata* assemblage also includes *Aclistochara laiae* S. Wang. *A. huangshuiensis* Yang and *Mesochara xuanziensis* Yang (Hao *et al.*, 1983) (Table 3).

Ostracod Assemblage 5, the *Talicypridea reticulata–Cypridea* (*Cypridea*) *cavernosa–C.* (*Pseudocypridina*) *longa–Eucypris qinghaiensis* assemblage, occurs in the Minhe Formation with *Talicypridea* as the most important component of high diversity and abundance. In association with the predominant species, *Talicypridea reticulata* (Hou), *Cypridea* (*Cypridea*) *cavernosa* Galeeva, *Cypridea* (*Pseudocypridina*) *longa* Hou and *Eucypris qinghaiensis* Song, other important components in the assemlage are *Talicypridea amoena* (Liu), *T. latiovata* (Hou), *Cypridea* (*Morinina*) *xindianensis* Hou, *C.* (*Pseudocypridina*) *gigantea* Ye, *Eucypris minheensis* Song and *Eucypris debiloides* Ye (Hao *et al.*, 1983) (Table 3).

Charophyte remaines are very rich and are represented by the *Latochara curtula–Gyrogona hubeiensis–Charites quanoingensis* assemblage in the Minhe Formation. This assemblage consists of *Latochara curtula* Z. Wang, *Gyrogona hubeiansis* Z. Wang and *Charites quanpingensis* Z. Wang, as the most common components and *Latochara yunnanensis* Z. Wang, *Charites cenuis* Z. Wang and *Grambastichara communis* Z. Wang as important components (Hao *et al.*, 1983) (Table 3).

Ostracod Assemblage 6, the *Cypris decaryi–Limnocythere hubeiensis* assemblage, is recognized in the Qijiachuan Formation. It is monotonous in taxa with *Cypris decaryi* Gautheir as the predominant components and distributed mainly in the upper part of the formation. In the lower part only *Limnocythere* has been found in large numbers but preservation is poor.

Charophytes are found coexisting with the ostracod assemblage only in the uppermost part of the Qijiachuan Formation. The *Stohanochara breviovalis–Neochara squalida* assemblage is not abundant and is poorly preserved. Besides those species which give their name to the assemblage, the other important components include *Peckichara serialis* Z. Wang, *Rhabdochara kisgyonensis* (Rasky) and *Sphaerochara parvula* (Reid and Groves) (Hao *et al.*, 1983) (Table 4).

Ostracod Assemblage 7, the *Limnocythere hubeiensis–L. languida* assemblage of the Honggou Formation, comprises very few taxa with *Limnocythere hubeiensis* Ye and *L. languida* Song as the most abundant components together with subordinante *Limnocythere pengzhenensis* Ye and *Ilyocypris bradyi* Sars (Hao *et al.*, 1983) (Table 4).

Ostracod Assemblage 8, the *Ilyocypris ellipsoidea–Eucypris milagouensis–Cyprinotus jucundus* Assemblage, occurring in the Mahalagou Formation is the most abundant assemblage of the Palaeogene formation in the Xining and Minhe Basins. With *Ilyocypris* as the predominant and most diversified genus, it also includes *Ilyocypris ellipsoidea* Song, *Eucypris milagouensis* Song and *Cyprinotus jucundus* Song as characteristic members and *Ilyocypris manasensis confrogosa* Bodina, *I. errabundia* Mandelstam, *Eucupris koktalensis* Bodina and *Cyprinotus gregarius* Bodina as less important members (Hao *et al.*, 1983) (Table 4).

Charophyte flora of the Mahalagou Formation and its underlying Honggou Formation are similar in taxa comprising *Maedlerisphaera chinensis* Huang and Xu, *Grovesichara minheensis* Yang,

TABLE 4—OSTRACOD AND CHAROPHYTE ASSEMBLAGES OF THE LOWER TERTIARY QIJIACHUAN FORMATION, HONGGOU FORMATION AND MAHALOGOU FORMATION (E_1^2–E_3).

Fossil Assemblage Formation	Ostracoda		Charophyta	
	Characteristic Components	Important Components	Characteristic Components	Important Components
Mahalagou Formation E_3	Mahalagou Formation		Mahalagou Formation	
	Ilyocypris ellipsoidea Song	*Ilyocypris manasensis confrogosa* Bodina	*Maedlerisphaera chinensis* Huang and Xu	*Gyrogona qianjiangica* Z. Wang
	Eucypris milagouensis Song	*Cyprinotus gregarius* Bodina		*Sphaerochara minheensis* Yang
	Cyprinotus jucundus Song	*Eucypris koktalensis* Bodina	*Grovesichara minheensis* Yang	*Pseudolatochara aechma* Lu
		Ilyocypris errabundis Mandelstam		*Charites minutissium* (Madler)
Honggou Formation E_2^{2-3}	Honggou Formation		Honggou Formation	
	Limnocythere hubeiensis Ye	*Ilyocypris bradyi* Sars		
	L. languida Song		*Gyrogona qianjiangica* Z. Wang *Sphaerochara minheensis* Yang	*Moedlerisphaera chiensis* Huang and Xu
				Grovesichara minheensis Yang *Pseudolatochara aechma* Lu *Charites minutissium* (Madler)
Qijiachuan Formation E_1^2–E_2^1	Qijiachuan Formation		Qijiachuan Formation	
	Cypris decaryi Gautheir			
	Limnocythere hubeiensis Ye		*Stephanochara breviovalis* Lin and Huang	*Peckichara serialis* Z. Wang *Rhabdochara kisgyonensis* (Rasky)
			Neochara squalida Z. Wang and Lin	*Sphaerochara parvula* (Reid and Groves)

Gyrogona gianjiangica Z. Wang, *Sphaerochara minheensis* Yang, *Pseudolotochara aechma* Lu and *Charites minutissium* (Maedler), but the most prevalent species are *Maedlerisphaera chinensis* and *Grovesichara minheensis* in the Mahalagou Formation and *Gyrogona gianjiangica* and *Sphaerochara minheensis* in the Honggou Formation (Hao *et al.*, 1983) (Table 4).

STRATIGRAPHICAL SIGNIFICANCE OF THE FOSSIL ASSEMBLAGES

Ostracod Assemblage 1 exhibits the aspect of a mixed group of Late Jurassic and Early Cretaceous taxa with some forms ranging from Jurassic to Cretaceous. Among its dominant genera, *Damonella* is one of the important forms of the Purbeckian Ostracoda prevailing in horizons below the Cinder Beds in England (Anderson, 1973) and frequently encountered in equivalent horizons in Yunnan, Sichuan, Xinjiang, Anhui and many other localities in China (Hao *et al.*, 1982, 1983;

Shi and He, 1963; Ye *et al.*, 1977). *Jingguella* was first reported from the Late Jurassic to Early Cretaceous Jingxing Formation in western Yunnan (Hao *et al.*, 1982; Ye *et al.*, 1977) and in recent years has been found in the Lower Cretaceous of different localities in Sichuan. *Jingguella ovata*, which occurs in the Datonghe Formation, is widespread in all these localities. *Pinnocypridea*, which was first described from the ostracod fauna from the Lower Cretaceous Hanyangpu Formation in northern Sichuan (Shi and He, 1963), is widely distributed in the Lower Cretaceous, of Central Yunnan and Western Sichuan (Ye *et al.*, 1977). *Djungarica*, which was first found in the Lower Cretaceous Tugulu Group (Hao and Guan, 1984) in the Junggar Basin of northern Xinjiang, has wide distribution in northwestern and southwestern China, ranging from Middle Jurassic to Early Cretaceous. *Minheella*, which was considered to be a form endemic to the Minhe Basin, has also been recently found in some other regions in China (Hao *et al.*, 1983). For instance, *Minheella minheensis* and *M. liqulata* have been found in the Jingxing Formation of Yunnan. *M. plicata* and *M. aurita* have come from the Lower Cretaceous and Upper Jurassic of Sichuan and Xinjiang respectively.

Charophytes occurring in the lower part of the Datonghe Formation represent a Late Jurassic flora, among which *Aclistochara bransoni* and *A. obovata* are important members of the charophyte flora of the Upper Jurassic Morrison Formation in the United States (Peck, 1957) and are also found in Late Jurassic strata in the western part of Mongolia (Kyansep-Romashkina, 1975).

In accordance with the micropalaeontological evidence above, it is reasonable to consider the Datonghe Formation as a transitional series from Upper Jurassic to Lower Cretaceous.

Ostracod Assemblages 2, 3 and 4, recognized respectively in the lower, middle and upper parts of the Hekou Formation, show the typical aspect of Early Cretaceous faunas. *Cypridea*, which enjoyed its heyday of development in the Early Cretaceous, dominates Assemblages 3 and 4; some of the prevailing species, such as *Cypridea* (*Cypridea*) *unicostata*, *C.* (*C.*) *vitimensis* and *C.* (*Ulwellia*) *koskulensis* are index forms in the Early Cretaceous ostracod fauna of eastern Mongolia, the west Siberian lowland and the Far East Vitim platform of the Soviet Union respectively (Hao, 1982; Galeeva, 1955; Lubimova, 1956). They are also widespread in the Lower Cretaceous of northeastern and northwestern China (Hao *et al.*, 1974). Some less common species, such as *Cypridea* (*Ulwellia*) *menevensis*, *C.* (*U.*) *ultima* and *C.* (*Cypridea*) *montoriana* are reported from the Lower Cretaceous in the south of the United States, the northwest of Congo, Stanleyville (Grekoff, 1957) and Spain (Brenne, 1976) respectively. *Cypridea* (*Bisulcocypridea*) *skeeteri* is frequently encountered in the Bear River Formation in the Rocky Mountain region of the United States (Peck, 1951) and some late Early Cretaceous strata in Zhejiang and Anhui of eastern China. *Lycopterocypris infantilis* was first reported from the Lower Cretaceous Junbaiyin formation of Mongolia (Lubimova, 1956) and is commonly encountered in the lower Lower Cretaceous of northeastern and northwestern China (Hao *et al.*, 1974, 1982). *Ziziphocypris costata* it widely distributed in the upper Lower Cretaceous of northern and northeastern China (Hao *et al.*, 1974).

Among the charophytes found in association with Ostracod Assemblage 3, *Aclistochara laiae* and *Mesochara stipitata* are important components of charophyte flora in the Lower Cretaceous of West Siberia, while the less common form, *Mesochara symmetrica* was first known from the Aptian of south Dakota in the United States (Peck, 1957). Most other important forms have been found from the Lower Cretaceous of many other regions in China.

The Hekou Formation is shown by its ostracod and charophyte content to be part of the Lower Cretaceous.

Talicypridea, which dominates Ostracod Assemblage 5, ranged from late early Cretaceous to Early Palaeocene and reached its acme of development in the Late Cretaceous. An assemblage of this genus along with *Cypridea* (*Pseudocypridina*), *Cypridea cavernosa* and some precursors of

Cenozoic cypridids, is characteristic of almost all non-marine Late Cretaceous strata known in China and Mongolia. Therefore, Ostracod Assemblage 5 serves as the basis for assigning the Minhe Formation to the Upper Cretaceous.

The charophyte asemblage in the Minhe Formation represents a mixed flora comprising mainly Cretaceous taxa and some forerunners of Cenozoic forms. A similar assemblage is widespread in the Upper Cretaceous of Hubei, Hunan, Kuangdong, Anhui and Jiangsu in China (Huang, 1973; Wang, 1978a, 1981; Zhang *et al.*, 1978).

Ostracod Assemblage 6 in the Qijiachuan Formation consists of a few Cenozoic forms with no relics of the Late Cretaceous taxa. Its main components, *Cypris decaryi* and *Limnocythere hubeiensis*, are widespread in Late Palaeocene and Early Eocene strata of south China, such as the Xingouju and the Fangjiahe Formations in the Yangtze and Han River Basin, the Dainan Formation in Jiangsu and the Sanshui and the Buxin Formations in Kuangdong etc. (Guan, 1979; Hou *et al.*, 1978, 1982).

The most important elements among the charophyte asemblage in the Qijiachuan Formation, such as *Stephanochara breviovalis, Peckichara serialis* and *Rhabdochara kisgyonensis*, have a distinct surface ornamentation of spiral cells, which is a special feature of the Late Palaeocene and the Early Eocene Charophyta. This assemblage is very similar to those found in Late Palaeocene and Early Eocene non-marine formations at different localities in south China (Huang, 1973; Wang, 1978a, b; Zhang *et al.*, 1978).

The age of the Qijiachuan Formation is ascertained to be Late Palaeocene to Early Eocene based on its ostracod and charophyte fossil contents.

In Ostracod Assemblage 8 from the Mahalagou Formation, the genus *Ilyocypris* is predominant over all other components; the subspecies *Ilyocypris manasensis confrogosa* together with *Ilyocypris errabundis, Cyprinotus gregarius* and *Eucypris koktalensis* are frequently encountered in the Oligocene deposits of northern Xinjiang and the coastal region of Bohai Bay (IPED, 1978) in China as well as in some inland basins of the Central Asian part of the Soviet Union.

Charophytes in association with this ostracod assemblage are similar to those of the underlying Honggou Formation, among which *Maedlerisphaera chinensis*, prevailing in the Mahalagou Formation is an important member of the Oligocene flora in Jiangsu, Hubei, Hunan and the coastal region of Bohai Bay as well as in France (Castel, 1967). *Gyrogona ginjiangensis*, more abundant in the Honggou Formation, is the main component of the Middle to Late Eocene charophyte flora which is widespread in southern and southwestern China and also in the coastal region of Bohai Bay in northern China.

On the basis of the above micropalaeontological evidence and the discovery of Early Miocene mammalian remains in the overlying Xiejia Formation (Li, 1980), the Mahalagou Formation belongs to the Oligocene. In the underlying Honggou Formation, Ostracod Assemblage 7 lacks stratigraphically significant taxa, and its age is provisionally regarded as Middle to Late Eocene on the basis of its charophyte flora and its stratigraphical position.

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The Cretaceous Ostracod Faunas from the Fuxin Basin, Liaoning Province

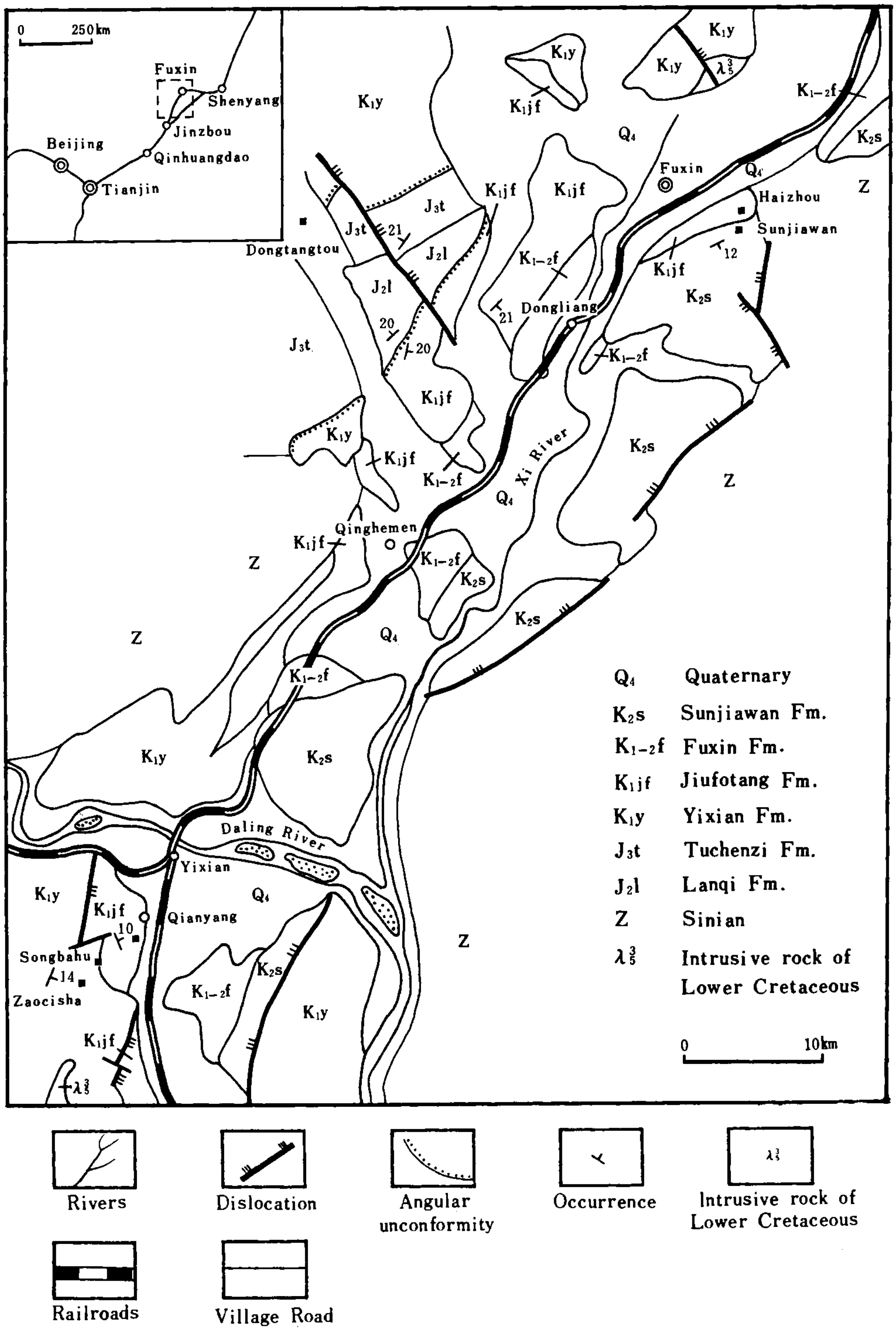
YOU-GUI LI[1], DE-YING SU[1] AND LI-JUN ZHANG[2]
[1] *Chinese Academy of Geological Sciences, Beijing, and*[2] *Shenyang Institute of Geology and Mineral Resources, Shenyang, China*

The Fuxin Basin, 120 km long and 8–10 km wide, is located in the western part of Liaoning Province. It extends from Jinzhou in the south to Xinqiu in the north, and from Mount Yiwulu in the east to Mount Sungling in the west. It occurs as a narrow, elongated, intermontane basin with rolling hills stretching in a NE-SW direction. The most important lineament in this district is represented by the Daba-Jinzhou fault, approximetely parallel to the strike of the basin. This fault penetrates the basin along its eastern margin, and the strike of the strata shows a trend of 30° - 45° east of north with a dip angle of 10°–30°. The structures do not seem to be very complicated.

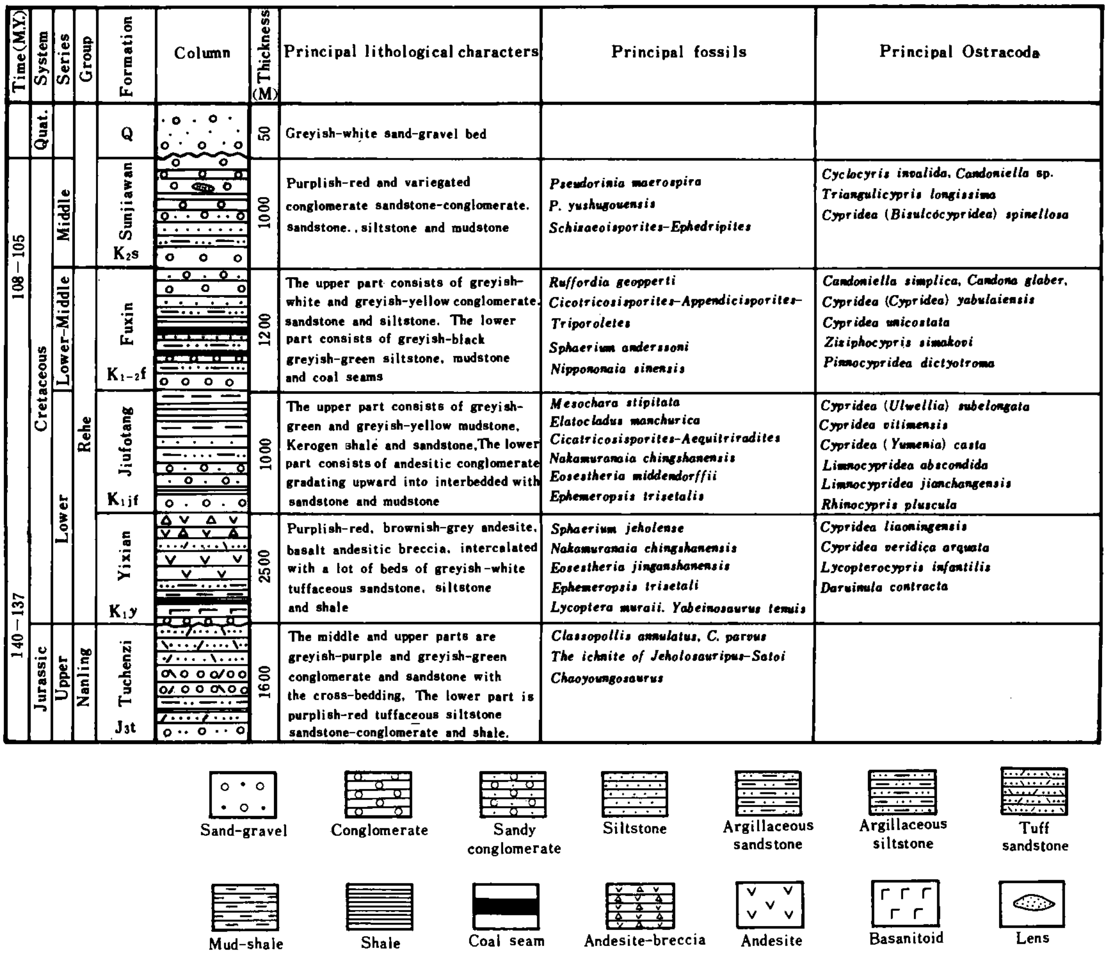
In this basin, the Cretaceous continental deposits are well developed and are represented by a sequence of volcanic-sedimentary formations with a total thickness of more than 5000 metres, resting upon the Upper Jurassic Tuchengzi Formation or unconformably on Sinian strata and containing abundant faunas and floras and rich coal resources. The sequence can be subdivided in ascending order into the Yixian Formation, the Jiufotang Formation, the Fuxin Formation and the Sunjiawan Formation. A brief account of each of them is given as follows:

The Yixian Formation is the lowest stratum of the Cretaceous in this district, and consists mainly of purplish-red and brownish-grey andesite, basalt andesitic breccia, intercalated with beds of greyish-white tuffaceous sandstone, siltstone and shale with a total thickness of about 2500 metres. The tuffaceous sandstone, siltstone and shale yield abundant bivalves such as *Sphaerium jeholense, Nakamuranaia chigshanensis*; the conchostracan *Eosestheria jingangshanensis*; the insect *Ephemeropsis trisetalis*; the fish *Lycoptera muraii*; the reptile *Yabeinosaurus tenuis* and abundant and well preserved ostracods. The ostracods collected from this basin and neighbouring districts (Sanguanmiao and Liujiawopu) mainly consist of *Cypridea venustata, C. ganzhaoensis, C. veridica arquata, C. sulcata, C.* aff. *delicatula, C. (C.) deflecta, Lycopterocypris infantilis* and *Darwinula contracta*, etc.

The Jiufotang Formation is characterised by lacustrine deposits. Its lower part consists of purplish-red andesitic conglomerate passing upwards into interbedded sandstone and mudstone. The upper part is composed of greyish-green and greyish-yellow mudstone, oil shale and sandstone containing Charophyta: *Mesochara stipitata*; plant: *Elatocladus manchurica*; pollen and spores: *Cicatricosisporites–Aequitriradites*; bivalve: *Nakamuranaia chingshanensis*; conchostracan: *Eosestheria middennaia chingshanensis*; and *Ephemeropsis trisetalis* fossils as well as abundant and well preserved ostracods. The most common species of ostracods found in this formation are *Cypridea vitimensis, C. prognata, C. (Yumenia) casta, C. unicostata, C. rostella, Cheilocypridea trapezoidea, C. (Ulwellia) subelongata, Limnocypridea abscondida, L. grammi, L. jianchangensis, Rhinocypris pluscula, R. echinata, Clinocypris obliquetruncata, Lycopterocypris circulata* and *Ziziphocypris costata* etc. This formation, conformably overlying the Yixian Formation, is about 1000 meters in thickness.



TEXT-FIG. 1—Geological sketch map of the Fuxin Basin of Liaoning Province.



Time (M.Y.)	System	Series	Group	Formation	Column	Thickness (M)	Principal lithological characters	Principal fossils	Principal Ostracoda
	Quat.			Q		50	Greyish-white sand-gravel bed		
108 – 105	Cretaceous	Middle		Sunjiawan K_2s		1000	Purplish-red and variegated conglomerate sandstone-conglomerate. sandstone., siltstone and mudstone	*Pseudorinia macrospira* *P. yushugouensis* *Schizaeoisporites–Ephedripites*	*Cyclocyris invalida*, *Candoniella* sp. *Triangulicypris longissima* *Cypridea* (*Bisulcócypridea*) *spinellosa*
		Lower-Middle	Rehe	Fuxin $K_{1-2}f$		1200	The upper part consists of greyish-white and greyish-yellow conglomerate, sandstone and siltstone. The lower part consists of greyish-black greyish-green siltstone, mudstone and coal seams	*Ruffordia geopperti* *Cicotricosisporites–Appendicisporites–Triporoletes* *Sphaerium anderssoni* *Nippononaia sinensis*	*Candoniella simplica*, *Candona glaber*, *Cypridea* (*Cypridea*) *yabulaiensis* *Cypridea unicostata* *Ziziphocypris simakovi* *Pinnocypridea dictyotroma*
		Lower		Jiufotang K_1jf		1000	The upper part consists of greyish-green and greyish-yellow mudstone, Kerogen shale and sandstone,The lower part consists of andesitic conglomerate gradating upward into interbedded with sandstone and mudstone	*Mesochara stipitata* *Elatocladus manchurica* *Cicatricosisporites–Aequitriradites* *Nakamuranaia chingshanensis* *Eosestheria middendorffii* *Ephemeropsis trisetalis*	*Cypridea* (*Ulwellia*) *subelongata* *Cypridea vitimensis* *Cypridea* (*Yumenia*) *casta* *Limnocypridea abscondida* *Limnocypridea jianchangensis* *Rhinocypris pluscula*
140 – 137				Yixian K_1y		2500	Purplish-red, brownish-grey andesite, basalt andesitic breccia, intercalated with a lot of beds of greyish-white tuffaceous sandstone, siltstone and shale	*Sphaerium jeholense* *Nakamuranaia chingshanensis* *Eosestheria jingganshanensis* *Ephemeropsis trisetali* *Lycoptera muraii*. *Yabeinosaurus tenuis*	*Cypridea liaoningensis* *Cypridea veridica arquata* *Lycopterocypris infantilis* *Darwinula contracta*
	Jurassic	Upper	Nanling	Tuchenzi J_3t		1600	The middle and upper parts are greyish-purple and greyish-green conglomerate and sandstone with the cross-bedding. The lower part is purplish-red tuffaceous siltstone sandstone-conglomerate and shale.	*Classopollis annulatus*, *C. parvus* *The ichnite of Jeholosauripus–Satoi* *Chaoyoungosaurus*	

TEXT-FIG. 2—Composite column of the Jurassic–Cretaceous system in the Fuxin Basin.

The Fuxin Formation, conformably overlying the Jiufotang Formation, is represented by lacustrine swamp deposits composed mainly of grey, greyish-white conglomeratic sandstone, conglomerate, sandstone and greenish-grey siltstone, sandy-shale, and dark grey mudstone with six intercalated coal-measure units. It yields abundant fossil plants such as *Ruffordia geopperti*, the pollen and spores *Cicatricosisporites–Appendicisporites–Triporoletes* and sparse bivalves such as *Spherium anderssoni* and *Nippononaia sinensis* as well as some ostracods. The ostracods mainly include *Cypridea unicostata*, *C.* (*C.*) *yabulaiensis*, *C.* (*Pseudocypridina*) *globra*, *C.* (*P.*) *haizhouensis*, *Ziziphocypris simakovi*, *Z. costata*, *Pinnocypridea dictyotroma*, *Candona*? *dungliangensis* and *Candoniella simplica* etc. The thickness of this formation is approximately 1200 metres.

The Sunjiawan Formation is characterised by fluvio-lacustrine deposits, consisting mainly of purplish-red and variegated conglomerate, sandy-conglomerate, sandstone, siltstone and mudstone, lying conformably upon the Fuxin Formation with a total thickness of about 100 metres. The sandstone, siltstone and mudstone contain sparse plants, the pollen and spores *Schizaeoisporites–Ephedripites*, gastropods and ostracods. The Ostracoda consist of *Cypridea* (*Bisulcocypridea*) *edentula tumidula*, *Rhinocypris pluscula*, *Triangulicypris longissima*, *Candona praevara* and *Cyclocypris invalida*.

For more than half a century, many Chinese and foreign geologists have conducted a lot of investigations in this district. Their research results have provided valuable data for present-day geological and stratigraphical studies. In recent years, great endeavours have been made in this field by the Shenyang Institute of Geology and Mineral Resources, the Regional Survey Party of the Liaoning Geological Bureau, the 107 Geological Party of the Liaoning Corporations of Geology and Coal Field Exploration and the Haizhou Coal Mine Bureau, with encouraging results.

In the ostracod studies of this district, Hou Youtang (1958) described and illustrated 2 new species of *Cypridea* from the upper part of the Jiufotang Formation; Hao Yichun (1962) studed some ostracod species from the Jiufotang Formation and the Fuxin Formation in an unpublished scientific report; Chen Deqiong (1965) described a new genus *Ziziphocypris* from the upper part of the Jiufotang Formation; and Su Deying *et al.* (1981) studied some species of Ostracoda from the Yixian Formation and the Jiufotang Formation of western Liaoning. Some species of ostracods from the Jiufotang Formation and the Fuxin Formation have been described and illustrated by Zhang Lijun (1982, 1984); Dai Hanlin and Ge Yuhua (1984) drew up a fossil list of the Cretaceous ostracods from the Fuxin and Zhangwu regions.

The above-mentioned geological, stratigraphical and ostracod studies are undoubtedly very conducive to the further study of the Cretaceous ostracods in the Fuxin Basin.

OSTRACOD ASSEMBLAGES

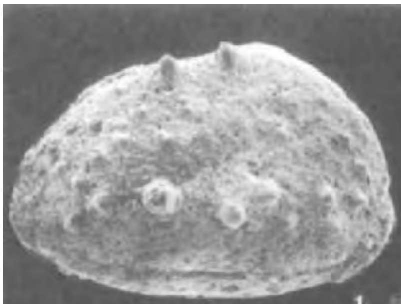
The Cretaceous ostracods in the Fuxin Basin are abundant and dominated by numerous species of *Cypridea*. Based on the difference in taxa and their stratigraphical distribution, four ostracod assemblages are recognized as follows:

The assemblage of the Yixian Formation (Assemblage 1) is relatively abundant. The genus *Cypridea* is represented by the following forms:

a) The medium-sized, spinose, punctate-shelled form *Cypridea venustata* with a subtrapezoid profile, which is similar to *Cypridea dunkeri carinata* from the Middle Berriasian in northern German Democratic Pepublic (Wienholz, 1968) and from the middle Purbeck Bed in southern England (Anderson, 1971); it also bears a resemblance to *Cypridea accommodata* from the Lower Cretaceous in eastern Mongolia.

b) The high-shelled, large, punctate, multi-spinose and tuberculate species *Cypridea ganhzaoensis* resembles *Cypridea tuberculata longtonensis* from the Middle Purbeck Beds in southern England (Anderson, 1971) and from the Berriasian in northern Spain (Brenner, 1976). It is also similar to *Cypridea jonesi* (Wolburg, 1959) from Wealden 4 Bed in northwestern Germany and has a close resemblance to *Cypridea regia* (Lubimova, 1956) from Lower Cretaceous deposits in eastern Mongolia.

PLATE 1— Fig. 1. *Cypridea venustata* Su and Li. Lateral view of right valve (LY8421, DLW11, Yixian Formation) ×48. Fig. 2. *Cypridea sulcata* Mandelstam. Lateral view of right valve (LY8422, DLW12, Yixian Formation) ×40. Fig. 3. *Cypridea ganzhaoensis* Su and Li. Lateral view of right valve (KZ8451, DLW13, Yixian Formation) ×40. Fig. 4. *Cypridea regia* Lubimova. Lateral view of right valve (OL8112, Jiufotang Formation) ×34. Fig. 5. *Cypridea vitimensis* Mandelstam. Lateral view of left valve (BG8491, DLW15, Jiufotang Formation) ×40. Fig. 6. *Cypridea justa* Lubimova. Lateral view of right valve (OL8115, Jiufotang Formation) ×36. Fig. 7. *Cypridea (C.) veridica arquata* Zhang. Lateral view of right valve (ZC8471, DLW14, Yixian Formation) ×40. Fig. 8. *Cypridea koskulensis* Mandelstam. Lateral view of left valve (OL8113, Jiufotang Formation) ×48. Fig. 9. *Cypridea unicostata* Galeeva. Lateral view of right valve (OL816, Jiufotang Formation) ×36. Fig. 10. *Cypridea prognata* Lubimova. Lateral view of right valve (OL818, Jiufotang Formation) ×36. Fig. 11. *Cypridea (Ulwellia) ihsienensis* Hou. Lateral view of left valve (OL8114, Jiufotang Formation) ×36. Fig. 12. *Cypridea (C.) rostella* Zhang. Lateral view of right valve (YJ848x, DLW16, Jiufotang Formation) ×40. Fig. 13. *Cypridea (C.) veridiva veridiva* Zhang. Lateral view of left valve (YJ8496, DLW17, Jiufotang Formation) ×42.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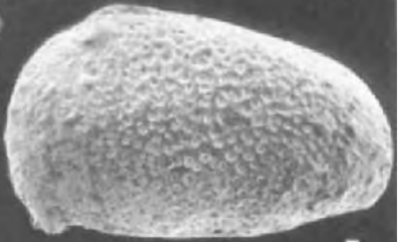
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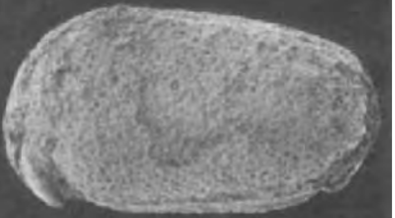
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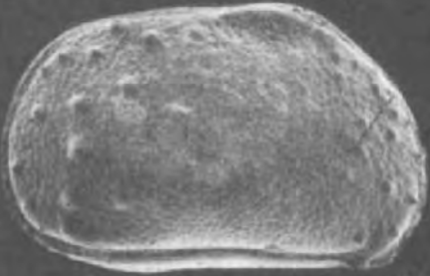
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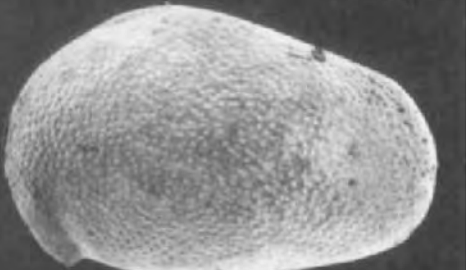
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c) The medium-sized, smooth, uni-spinose form *Cypridea sulcata* is very close to *Cypridea bispinosa bimammata* (Wolburg, 1959), and *Cypridea spinigera* (Neale, 1971). Other genera such as *Lycopterocypris infantilis* and *Darwinula contracta,* which have been found in the Lower Cretaceous of other districts of China, the USSR and MNR, are also abundant in this basin. Based on the characteristics of Assemblage 1 and their resemblance to known species found in other countries, the plausible age for the Yixian Formation is from Middle Berriasian to Valanginian. In addition, volcanic samples for isotopic studies were collected from the bottom of the Yixian Formation, west of Zhuanchengzi, and the result of Rb-Sr isochron dating gives 140 M.Y. while K-Ar isochron dating gives 136.9 M.Y. The palaeomagnetic determination made with samples from the same locality and horizon showed the palaeomagnetic pole to be at 148.9° E longitude and 65° N latitude. According to both isotopic data and palaeomagnetic determination, the Yixian Formation should be Early Cretaceous in age (Wang Dongfang, 1982, 1983).

The assemblage of the Jiufotang Formation (Assemblage 2) is abundant. The genus *Cypridea* includes the following species:

a) The medium-sized, sparsely tuberculate form *Cypridea vitimensis* with an anterodorsal node is widely distributed in the Barremian of the Vitimu Basin and Baikol region of USSR, eastern Mongolia and other regions of China. This species resembles *Cypridea granulos protogranulosa* (Anderson, 1971) from the Middle Purbeck Beds of southern England.

b) The inverse, medium-sized, punctate form *Cypridea koskulensis* with well-developed cyathus is widely distributed in the Far East and W. Siberia and Kazakh province of USSR, eastern Mongolia and other regions of China. This form resembles *Cypridea bogdenensis* and *Cypridea valdensis* which have been found in southern England (Kilenyi and Neale, 1978), the Cretaceous of the Paris Basin (Oertli, 1963) and the Wealden 4 Beds in northwestern Germany (Wolburg, 1959).

c) The small, tuberculate, spined form *Cypridea just* with a marked anterodorsal angle; the medium-sized, multi-tuberculate species *Cypridea regia* with a marked anterodorsal angle; and the large, punctate, large-beaked form *Cypridea prognata* with marked cyathus, have all been reported from the Barremian of eastern Mongolia (Lubimova, 1956).

d) Besides the species of *Cypridea,* this assemblage also contains *Rhinocypris echinata* and *Ziziphocypris costata* which are widely distributed in the Barremian of the W. Siberia and Kazakh province of USSR, eastern Mongolia and other regions of China.

e) The large, smooth, subtriangular shelled form *Cheilocypridea trapezoidea* with a marked "anterior lip" is very like *Mantelliana*? *uniensis* (Brenner, 1976) from the Barremian-Aptian in northeastern Spain.

Based on the characteristics of Assemblage 2 and their resemblance to known Cretaceous

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PLATE 2—Fig. 1. *Lycopterocypris infantilis* Lubimova. Lateral view of right valve (LY8423, DLW18, Yixian Formation) ×40. Fig. 2. *Darwinula contracta* Mandelstam. Lateral view of right valve (LY8424, DLW19, Yixian Formation) ×40. Fig. 3. *Rhinocypris pluscula* Li. Lateral view of right valve (SG130158, Sunjiawan Formation) ×60. Figs. 4, 5. *Timiriasevia* sp. 4. Lateral view of right valve; 5. Dorsal view of carapace (DL8441, DLW20, Fuxin Formation) ×40. Fig. 6. *Ziziphocypris simakovi* (Mandelstam). Lateral view of right valve (DL8442, DLW 21, Fuxin Formation) ×40. Fig. 7. *Ziziphocypris costata* (Galeeva). Lateral view of right valve (DL8443, DLW22, Fuxin Formation) ×40. Fig. 8. *Candona* sp. Lateral view of left valve (SJ8461, DLW23, Sunjiawan Formation) ×40. Fig. 9. *Lycopterocypris circulata* Lubimova. Lateral view of right valve (SG130220, Jiufotang Formation) ×48. Fig. 10. *Candoniella simplica* Zhang. Lateral view of right valve (DL8444, DLW24, Fuxin Formation) ×40. Fig. 11. *Cheilocypridea trapezoidea* Zhang. Lateral view of right valve (OL8127, Jiufotang Formation) ×37. Figs. 12, 13. *Cypridea* (*Bisulcocypridea*) *edendula tumidula* Zhang. 12. Lateral view of right valve; 13. Dolsal view of carapace (SG130103, Sunjiawan Formation) ×49. Fig. 14. *Rhinocypris echinata* (Mandelstam). Lateral view of right valve (OL130157, Jiufotang Formation) ×60. Figs. 15, 16. *Limnocypridea jianchangensis* Su and Li. 15. Lateral view of right valve; 16. Dorsal view of carapace (JC8431, DLW25, Jiufotang Formation) ×40. Fig. 17. *Limnocypridea grammi* Lubimova. Lateral view of right valve (SG130129, Jiufotang Formation) ×36. Fig. 18. *Limnocypridea abscondida* Lubimova. Lateral view of right valve (SG130127, Jiufotang Formation) ×36.


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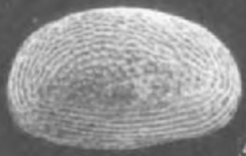
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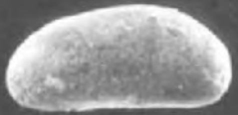
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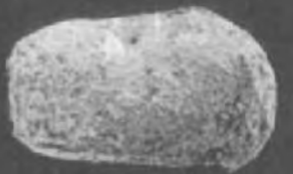
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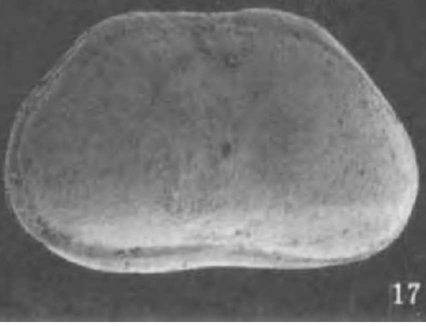
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species from other countries, the age of the Jiufotang Formation is probably from Hauterivian to Barremian.

The assemblage of the Fuxin Formation (Assemblage 3) is represented by sparse species of the genus *Cypridea* and several forms of other genera such as:

a) The medium-sized, subtriangular, smooth-shelled, flat-ventered *Cypridea (C.) yabulaiensis,* which has been found in the middle Cretaceous of Mongol autonomous region in China.

b) The large, smooth-shelled, small-beaked *Cypridea (Pseudocypridina)? globra* has been reported from the Lower-Middle Cretaceous of Gansu and Ningxia in China.

c) The small, flat-shelled *Ziziphocypris costata* and *Z. simakovi* with distinct striated ornamentation are widely distributed in the Middle Cretaceous of other parts of China, eastern Mongolia and W. Siberia and Kazakh province of USSR.

d) In addition, there are species of the Cenozoic genera *Candona* and *Candoniella* in this assemblage. Based on the characteristics of this assemblage and the geological distribution of the known species, the Fuxin Formation could be of Barremian to Aptian age.

In the assemblage of the Sunjiawan Formation (Assemblage 4) the ostracod fauna is limited.

a) The genus *Cypridea* is represented by several small-shelled, bisulcate forms such as *Cypridea (Bisulcocypridea) edentula tumidula.* The species of the subgenus *Bisulcocypridea* have been found in the non-marine middle and Upper Cretaceous to Lower Tertiary of America, Asia and Africa.

b) Other than very few species of *Cypridea,* this assemblage also contains *Rhinocypris pluscula* and several Cenozoic forms such as *Candona praevara* and *Cyclocypris invalida.* Based on the characteristics of this assemblage and the geological distribution of the known species, the Sunjiawan Formation can be Aptian to Albian in age.

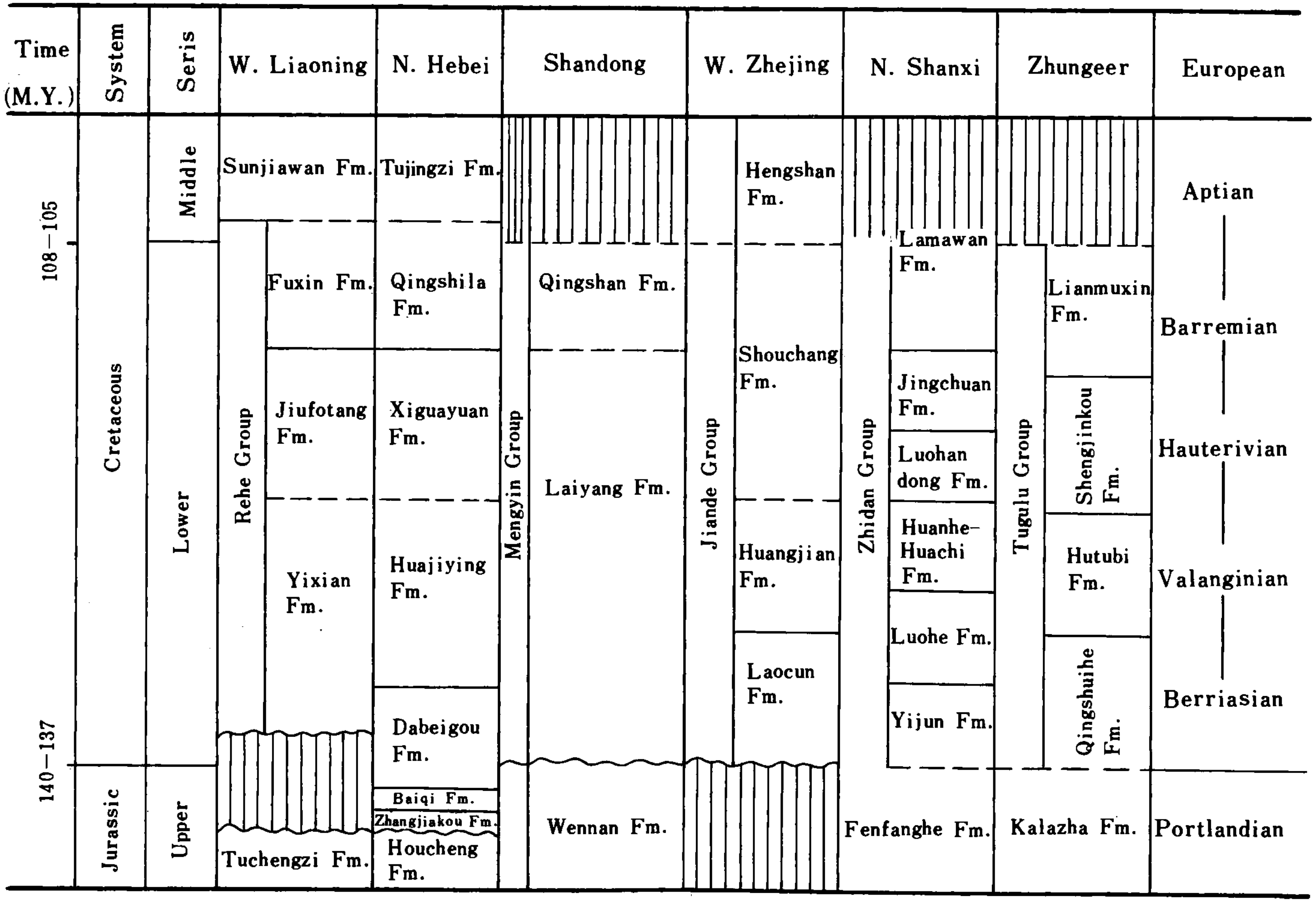
FACIES PRELIMINARY ANALYSIS

Based on sedimentary and palaeontological characteristics and geochemical data, the Cretaceous strata in the district studied could be roughly subdivided into the following four sedimentary facies: shallow lacustrine deposits, lacustrine deposits, lacustrine-swamp deposits and fluvio-lacustrine deposits.

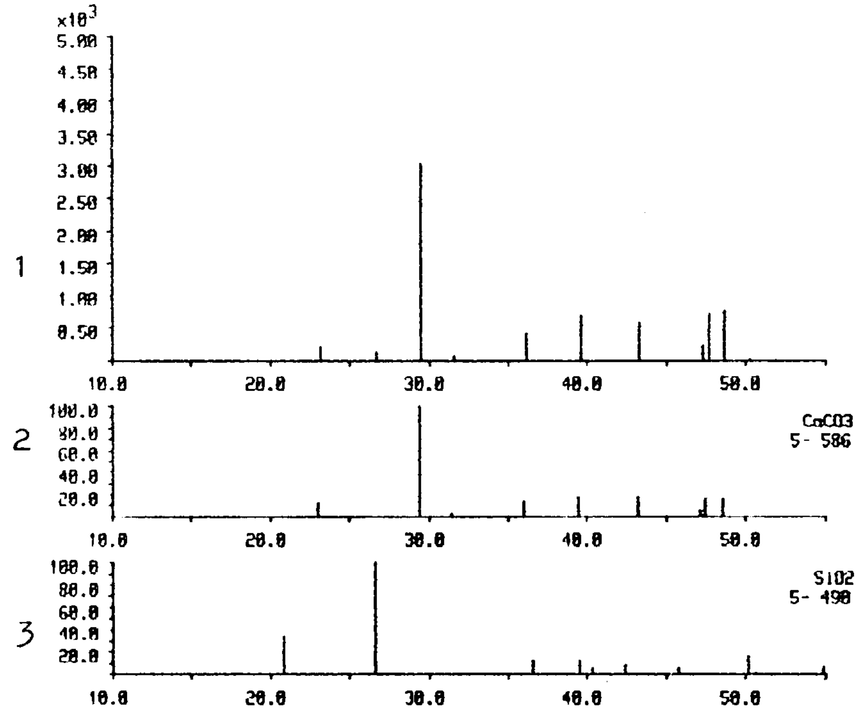
The shallow lacustrine deposits, accumulated in a reducing environment, are represented by the Jingangshan Bed of the Yixian Formation, and mainly distributed in Jingangshan, Toutai, Yusi and Zidutai. The rocks are mainly siltstone and fine granular sandstone, with intercalated thin beds of shale, showing flat bedding and minor cross bedding in moderate thickness. The greyish-white tuffaceous shale in the lower part of the Jingangshan Bed yields abundant specimens of the lacustrine bivalve *Nakamuranaia chingshanensis,* the conchostracan *Eosestheria jingangshanensis,* Insecta *Ephemeropsis trisetalis,* Pisces *Lycoptera muraii* and well-preserved ostracods in very low diversity and high abundance. Ostracoda are dominated by *Cypridea* forms of Cyprididae with very sparse Cytheridae. The ornamentation of these ostracods is generally not strong. They are characterised by smooth or punctate, finely-reticulate and small spinose shells, the hinge is adont and lophodont, and sieve-type normal pores and eye spots are absent.

Trace-element analysis of the ostracod shell of *Cypridea (C.) veridica arquata* by emission spectrometry (after analyst Chen Shanke) shows that the B content is less than 1 ppm (less than 0.001 %) while laser spectrometry (after analyst Duan Yuran and Li Wei hua) shows that the Mg content is 2%, Fe is 0.5%, Ca is 47%, Sr is 0.5%; Sr/Ca ratio is 0.012, and the Ca/Mg ratio is 23.5. Analysis of *Lycopterocypris infantilis* using the same method shows that the Mg content is 2%, Fe is 0.3%, Ca is 38%; Ca/Mg ratio is 19.000 and the Sr/Ca is 0.005.

The phase identification of the powder of the ostracod shells of *Cypridea (C.) veridica arquata*



TEXT-FIG. 3—Correlation of non-marine Lower-Middle Cretaceous in different parts of China.



Text-fig. 4—Comparative patterns of phase identification. 1, The pattern of phase identification of *Cypridea* (*C.*) *veridica arquata* from the Jinganshan Bed of the Yixian Formation at Zaocishan of Yixian; 2, The pattern of $CaCO_3$; 3, The pattern of α-SiO_2.

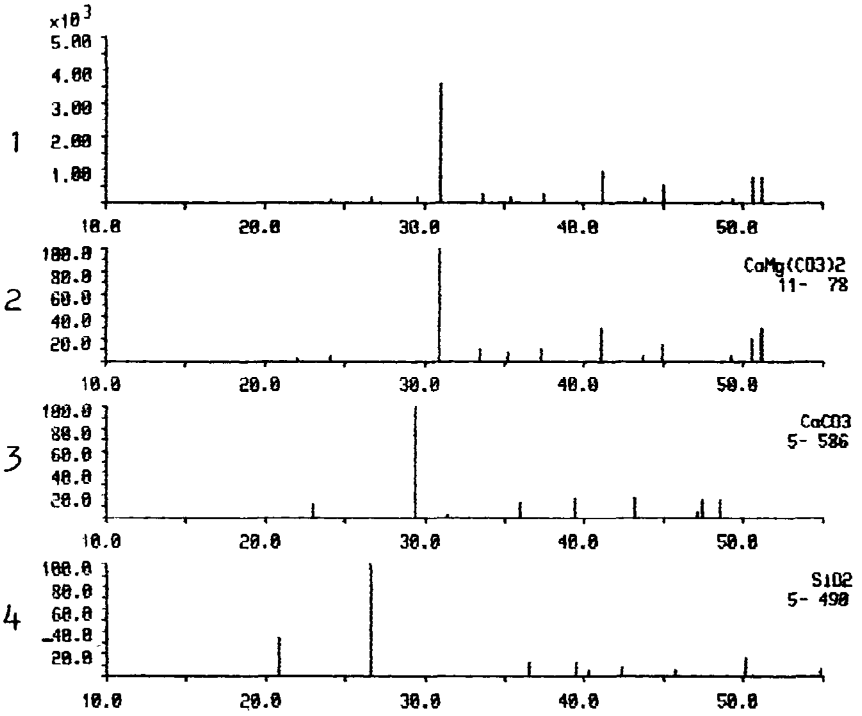
by X-ray diffraction (after analyst Zhu Xiaoling) shows a large amount of $CaCO_3$ with very little α-SiO_2, as shown in Text-fig. 4.

The lacustrine deposits of a reducing environment are represented by the Jiufotang Formation, mainly at Nihezi in Yixian. The rocks are mainly mudshale, siltstone and sandstone with intercalated thin coal seams, oil shale and asphalt, showing paper flat bedding witha total thickness of several hundred metres. They contain abundant specimens of the lacustrine bivalve *Nakamuranala Chingshanensis*, Gastropoda *Viviparus* spp., Conchostracan *Eosenstheria middendorfii*, Insecta *Ephemeropsis trisetalis*, Pisces *Lycoptera* spp. and well-preserved ostracods which are dominated by *Cypridea* species of the family Cyprididae, while forms of the family Cytheridae are very sparse. The ornamentation of these ostracods is smooth or punctate and reticulate; sieve-type normal pores and eye spots are absent. The hinge is lophodont or adont.

Trace-element analysis of the ostracod shell of *Cypridea* (*C.*) *veridica veridica* by laser spectrometry shows that the Mg content is 14%, Fe is 1%, Ca is 34%, Sr is 0.3%; Ca/Mg ratio is 2.420 and Sr/Ca is 0.0088. Analysis of *Limnocypridea jianchangensis* using the same method shows that the Mg content 2%, Fe is 2%, Ca is 37%, Sr is 0.2; Ca/Mg ratio is 18.500 and Sr/Ca is 0.005.

The phase identification of the powder of the ostracod shells of *Cypridea* (*C.*) *veridica veridica* by X-ray diffraction shows a large amount of $CaMg(CO_3)_2$ with very little $CaCO_3$ and α-SiO_2, as shown in Text-fig. 5.

The lacustrine-swamp deposits accumulated in a reducing environment and are represented by the Fuxin Formation, and mainly distributed round Haizhou and Dong liangzhen in Fuxin. These rocks consist mainly of sandstone and mud-shale showing flat bedding and cross bedding. The up-



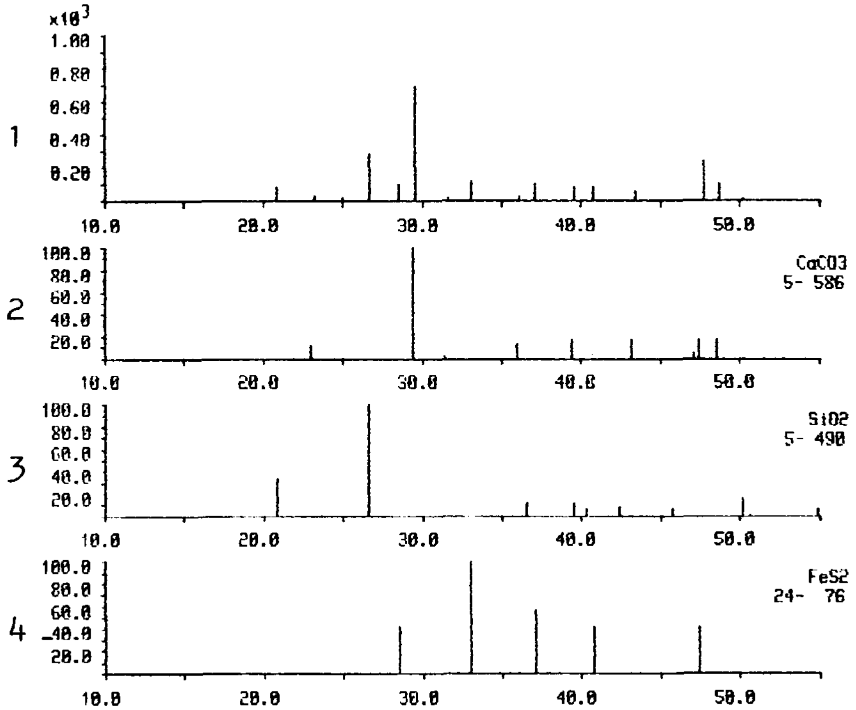
Text-fig. 5—Comparative patterns of phase identification. 1, The pattern of phase identification of *Cypridea* (*C.*) *veridica veridiva* from the Jiufotang Formation at Yujiagou in Yixian; 2, The pattern of $CaMg(CO_3)_2$; 3, The pattern of $CaCO_3$; 4, The pattern of α-SiO_2.

per part is greyish-white sandstone and conglomerate, the middle part greyish-black, greyish-green sandstone and mud-shale with six thick coal seams, and the lower part greyish-yellow sandstone with intercalated conglomerate. These deposits yield abundant plants (*Ruffordia geopperti*) and pollen-spores (*Cicatricosisporites-Appendicisporites-Triporoletes*), sparse vivalves (*Spherium andersson, Nippononaia sinensis*) and ostracods including species of *Cypridea, Candoniella* and *Ziziphocypris*. Their ornamentation is smooth or distinctly striated; the hinge is generally adont or lophodont and sieve-type normal pores and eye spots are absent.

Analysis of the trace elements of the ostracod shell of *Limnocypridea qinghemenensis* by laser spectrometry shows that the Mg content is 1 %, Fe is 8 %, Ca is 40 %, Sr is 0.8 %; Sr/Ca ratio is 0.02 and Ca/Mg ratio is 40. Analysis of *Ziziphocypris simakovi* using the same method shows that the Mg content is 2 %, Fe is 8 %, Ca is 40 %, Sr is 0.3 %; Sr/Ca ratio is 0.007 and Ca/Mg is 20.

The phase indentification of the powder of the ostracod shells of *Ziziphocypris simakovi* by X-ray diffraction shows a large amount of $CaCO_3$ with very little α-SiO_2 and FeS_2, as shown in Text-fig. 6.

The fluvio-lacustrine deposits are represented by the Sunjiawan Formation, and mainly distributed round Sunjiawan in Fuxin and Badaohau in Yixian. These deposits are composed of purplish-red conglomerate with intercalated thin beds of sandstone and mud-shale with major cross bedding. The gravels have not been very well sorted and rounded. Grain size of the sediments becomes finer and finer upwards and their thickenss may range from hundreds of metres to more than one thousand metres. The deposits have retained their purplish-red colour because the anhydrous ironstone has not been hydrated in the sedimentary process.



TEXT-FIG. 6—Comparative pattern of phase identification. 1, The pattern of phase identification of *Ziziphocypris simakovi* from the Fuxin Formation; 2, The pattern of $CaCO_3$; 3, The pattern of α-SiO_2; 4, The pattern of FeS_2.

TABLE 1—TRACE-ELEMENTS OF CRETACEOUS OSTRACOD SHELLS FROM THE FUXIN BASIN.

Environment	Formation	Species	Trace-element (%)					Ca/Mg	Sr/Ca
			Ca	Fe	Mg	Sr	B		
Fluviolacustrine	Sunjiawan	*Candona* sp.	23	0.3	26	0.5		0.884	0.021
Lacustrine-swamp	Fuxin	*Ziziphocypris simakovi*	40	8	2	0.3		20	0.007
		Limnocypridea qinghemenensis	40	8	1	0.8		4.0	0.020
Lacustrine	Jiufotang	*Cypridea* (*C.*) *veridica veridica*	34	1	14	0.3		2.420	0.008
		Limnocypridea jianchangensis	37	2	2	0.2		18.500	0.005
Shallow lacustrine	Yixian	*Cypridea* (*C.*) *veridica arquata*	47	0.5	2	0.5	0.0001	23.5	0.012
		Lycopterocypris infantilis	38	0.3	2	0.2		19.000	0.005

The Sunjiawan Formation may have accumulated in an oxidizing environment and the climate was relatively arid at that time. This formation contains sparse plants, pollen-spores, gastropods and ostracods. The valves of ostracods such as *Candona* and *Cyclocypris* are smooth and those of *Cypridea* (*Bisulcocypridea*) are punctate and bisulcate, generally simple in structure.

Analysis of the trace elements of the ostracod shell of *Candona* sp. by laser spectrometry shows that the Mg content is 26%, Fe is 0.3%, Ca is 23%, Sr is 0.5%; Ca/Mg ratio is 0.884 and Sr/Ca is 0.021.

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DISCUSSION

Colin: In your presentation you compare some of your species with some European species. I see some problems concerning the identification due to different overlapping of valves. *Cypridea bimamata* and *Cypridea dunkeri carinata* compared respectively with *C. sulcata* and *C. venustata* are typically reverse species (RV > LV) whereas from your illustrations the Chinese forms have a normal overlap (RV < LV).

Li Yougui: I think that overlap, whether normal or reverse, is not important in the species that I distinguished. Following Mandelstam, in the USSR, for example, the Lower Cretaceous species *Cypridea koskulensis* Mandelstam has both right and left overlap.

The Biostratigraphy of Cretaceous Ostracods from Oman

J. ATHERSUCH
BP Research Centre, Sunbury, England

ABSTRACT

Fifty-three species of ostracods from the Cretaceous (Aptian–Maastrichtian) of Oman are identified and illustrated. Their value as stratigraphical indices is demonstrated and their stratigraphical ranges and distribution throughout the Middle East and N. Africa are reviewed. Some aspects of ostracod palaeogeography in Tethys during the Cretaceous are also discussed.

INTRODUCTION

This paper primarily concerns the use of "Middle" to Late Cretaceous ostracods (Aptian–Maastrichtian) as indices for stratigraphical correlation in shelf carbonate sequences of Oman.

Traditionally, biostratigraphy of shallow carbonate shelf sediments in the Cretaceous of the Middle East has relied almost entirely on the examination of foraminifera. However, many of these are long-ranging and require thin-sectioning for accurate determination. The advantages of using ostracods are that they are numerous, morphologically diverse, often short-ranging and easily recognisable in "the-round". Nevertheless, they are, like foraminifera, highly facies-controlled and, moreover, are not identifiable in thin section.

There are now a large number of published and unpublished works currently available which deal with Cretaceous ostracods in this region (see bibliography), but to date there has been no detailed account of the ostracods from Oman. The use of ostracods as biostratigraphical indices in the Middle East has been recognised for many years (*e.g.* Sayyab, 1956) and more recently, formal zonation schemes have been developed (*e.g.* Rosenfeld and Raab, 1974; Bismuth *et al.*, 1981).

A number of stratigraphical index species have been identified in the Cretaceous succession of Oman, a large proportion of these being previously described from rocks of similar ages in other parts of the region. In addition, several undescribed forms have been recognised. The species considered in this paper are only a small proportion of the total number reported from this area.

Because of the proprietary nature of the data used in this study the provenance of the illustrated material and the detailed distribution of species in wells cannot be disclosed. For this reason, previously undescribed taxa appear in open nomenclature and are not formally described herein.

Sources of Data

The biostratigraphical data presented herein is based on observations of cuttings samples from 6 wells in the western part of Oman bordering Saudi Arabia (Text-fig. 1).

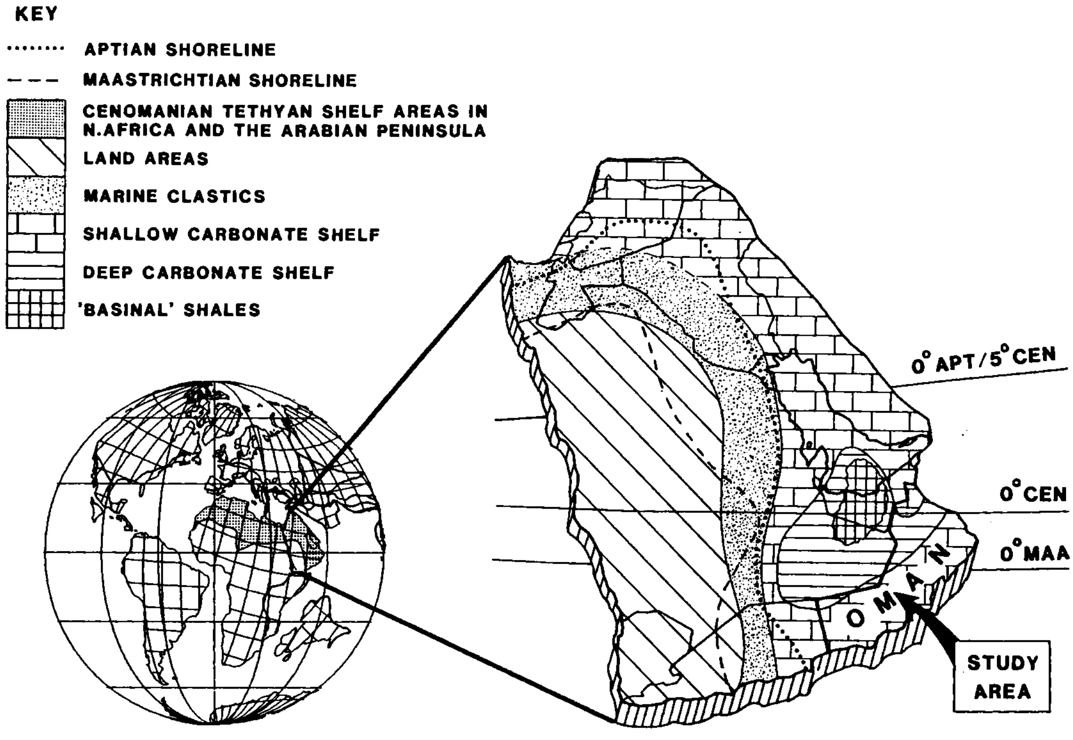
These data are summarised on Text-fig. 2 which records the stratigraphical ranges of the first downhole occurrences of each species. Selected index species are also depicted in Text-fig. 5.

All the species listed in Text-fig. 2 are illustrated on Plates 1–5.

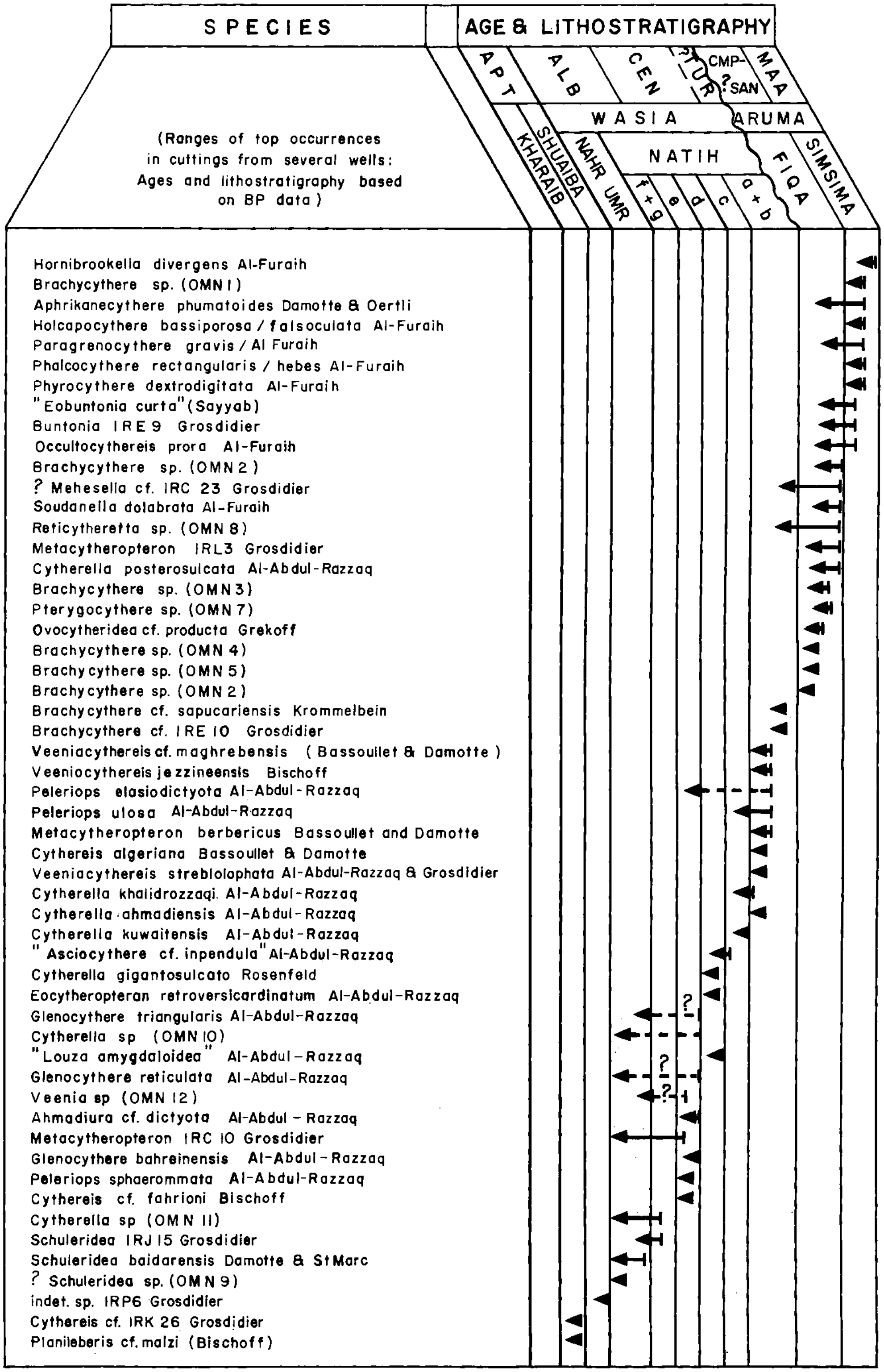
Text-figures 3 and 4 compare the stratigraphical ranges of each of these species from Oman with their previously recorded distributions in the Middle East and North Africa. The text provides information from a variety of sources on their geographical distribution and stratigraphical significance. The ages quoted from non-BP sources are those provided by the originating authors, and in the case of the Oman wells, formation "ages" are in-house assignments based on palaeontological and regional geological considerations.

References to taxomonic names from unpublished literature are enclosed by quotation marks, thus " ". Previously undescribed species have been given BP (Sunbury) reference codes with the prefix OMN and all of the illustrated specimens are housed in the BP (Sunbury) reference collection.

Text-figure 1 shows a global reconstruction and a lithofacies map of the Arabian Peninsula for



Text-fig. 1—Lithofacies map of the Arabian Peninsula during the Cenomanian (data from various sources).



TEXT-FIG. 2—Stratigraphical distribution of Cretaceous ostracods from Oman.

the Cenomanian, with relative positions of Aptian, Cenomanian and Maastrichtian shorelines and equators. Data used in the compilation of this map come from numerous sources including Murris (1980), Saint-Marc (1978) and the BP palaeoreconstruction data base.

OSTRACOD BIOSTRATIGRAPHY IN OMAN

Only one well yielded ostracods in the Kharaib and Shu'aiba Formations. The sparse fauna included *Cythereis* cf. IRK26 Grosdidier and *Planileberis* cf. *malzi* Bischoff (Kharaib) and indet. gen. IRP6 Grosdidier (Shu'aiba). Both of these species have been previously recorded from the Aptian of Iran. Further work on these formations may identify other species of stratigraphical importance.

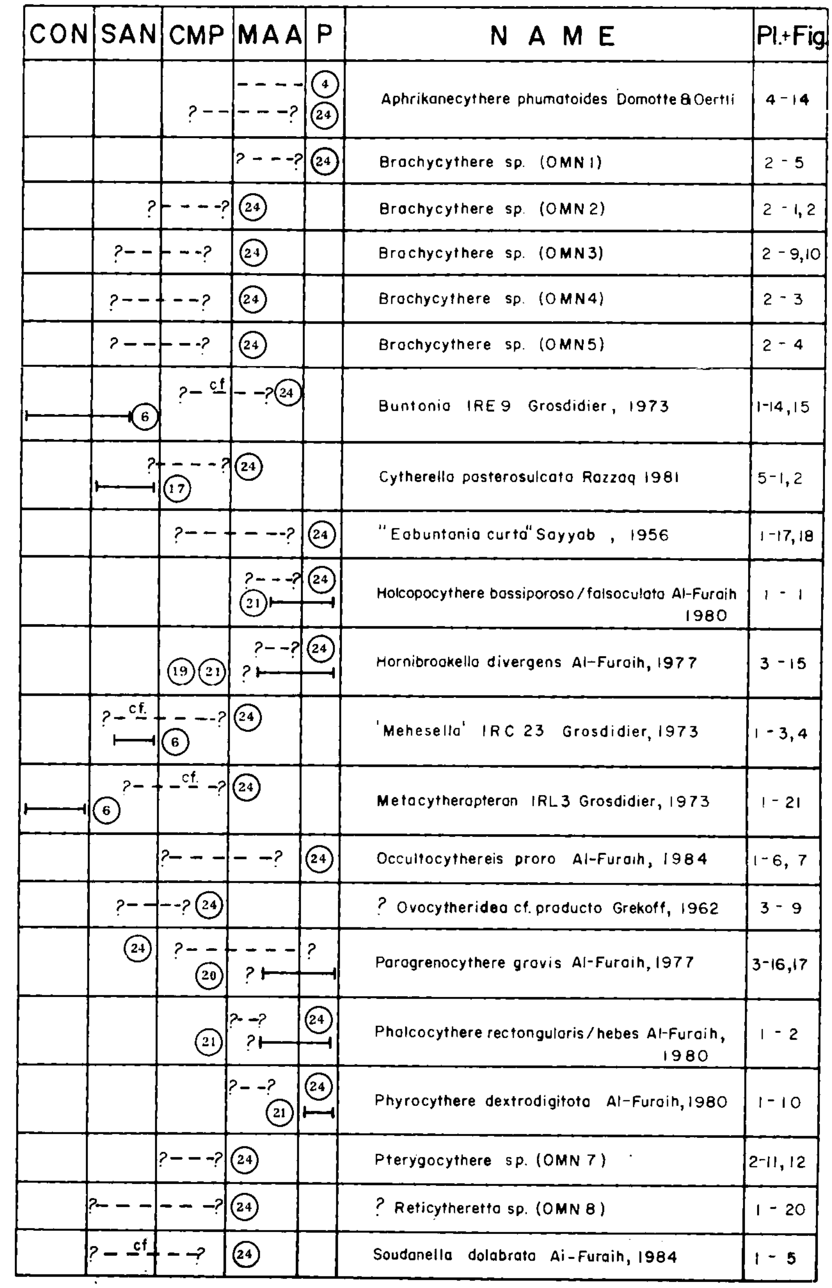
The Nahr Umr Formation in Oman has a presumed Early Albian age. It is characterised by *Schuleridea baidarensis* Damotte and Saint-Marc and *S.* sp. OMN9. According to Standring (1972), the Nahr Umr in Oman is divisible into three units using ostracods, but the identity of the index forms used is not known to the present author, and no such subdivision was recognised from the available material.

Following BP's practice, the Natih Formation is divided into seven members. Members 'g', 'f' and the lower part of 'e' are thought to be Albian in age; Members 'g' and 'f' are characterised by the first downhole occurrence of *Cytherella* sp. OMN 11 and *Schuleridea* IRJ15 Grosdidier in the lower part and by *Metacytheropteron* IRC10 Grosidier throughout. Member 'e' is characterised by *Metacytheropteron* IRC10 Grosdidier, *Cythereis* cf. *fahrioni* Bischoff and *Glenocythere* spp. together with a number of rarer species. Member 'd' typically contains the first downhole occurrences of *Eocytheropteron retroversicardinatum* Al-Abdul-Razzaq, *Cytherella gigantosulcata* Rosenfeld and "*Louza amygdaloidea*" Al-Abdul-Razzaq each of which has a well documented Early Cenomanian to Albian age throughout the Middle East. Member 'c' and the lower part of the combined 'a+b' member are considered to be of Late Cenomanian age and are characterised by a large number of species in Oman which have been previously recorded from the Middle East and, in some cases, from N. Africa as well. They include *V. jezzineensis* (Bischoff), *Veeniacythereis* cf. *maghrebensis* (Bassoullet and Damotte) *V. streblolophata* Al-Abdul-Razzaq and Grosdidier, *Peleriops ulosa* Al-Abdul-Razzaq, *P. elassiodictyota* Al-Abdul-Razzaq, *Cythereis algeriana* Bassoullet and Damotte, *Metacytheropteron berbericus* Bassoullet and Damotte, *Cytherella khalidrazzaqi* Al-Abdul-Razzaq, *C. ahmadiensis* Al-Abdul-Razzaq and *C. kuwaitensis* Al-Abdul-Razzaq. The upper part of the combined 'a+b' member contains *Brachycythere cf. sapucariensis* and *B.* cf. IRE10 Grosdidier in some wells. These are the only index species from the presumed latest Cenomanian to Turonian in Oman.

Few of the species of Coniacian to Early Santonian age from Iran or elsewhere in the Arabian Gulf area are also known from Oman. This may be considered as evidence for the absence of sediments of this age from Oman and supports the notion of a regional unconformity between Turonian and younger Senonian sediments.

The Fiqa Formation in Oman is probably ?Santonian to Campanian in age and is characterised by a large number of *Brachycythere* spp. most of which are not attributable to previously described species. They are accompanied by *Soudanella* cf. *dolabrata* Al-Furaih, *Pterygocythere* sp., "*Mehesella*" cf. IRC23 Grosdidier and sometimes by *Reticytheretta* sp. and *Cytherella posterosulcata* Al-Abdul-Razzaq.

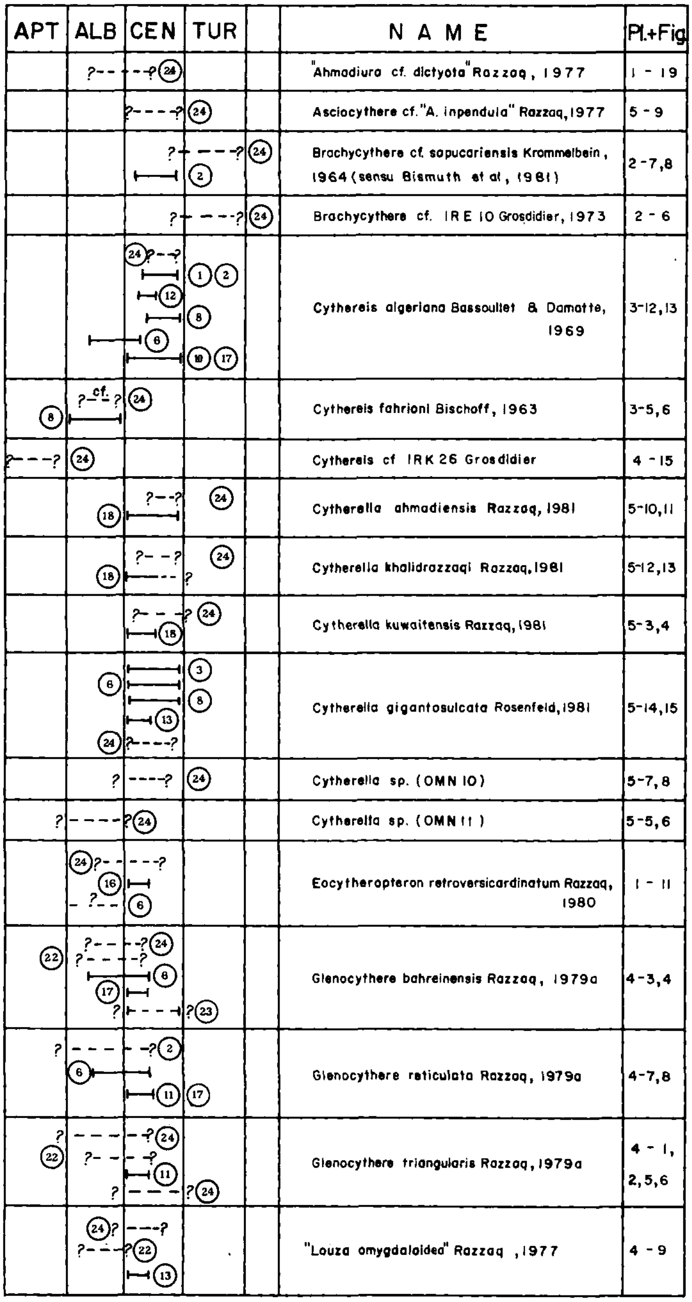
The Simsima Formation is probably Maastrichtian in age and contains large numbers of reticulate trachyleberid ostracods including *Hornibrookella divergens* Al-Furaih and *Paragrenocythere gravis* Al-Furaih as well as *Holcopocythere* sp., *Phalcocythere* sp. and *Phyrocythere dextrodigitata* Al-Furaih. Many of the species from this formation are known to cross the Cretaceous/Tertiary



CON	SAN	CMP	MAA	P	NAME	Pl.+Fig.
		? - -	- - - - - - - ?	④ ㉔	Aphrikanecythere phumatoides Domotte & Oertli	4 - 14
			? - - -?	㉔	Brachycythere sp. (OMN 1)	2 - 5
	?	├ - - -?	㉔		Brachycythere sp. (OMN 2)	2 - 1, 2
	?- -	├ - -?	㉔		Brachycythere sp. (OMN3)	2 - 9,10
	?- - -	- -?	㉔		Brachycythere sp. (OMN4)	2 - 3
	? - - -	- -?	㉔		Brachycythere sp. (OMN5)	2 - 4
├────	────⑥	?- cf	- -?㉔		Buntonia IRE 9 Grosdidier, 1973	1-14,15
	? ├───┤	- - - -? ⑰	㉔		Cytherella posterosulcata Razzaq 1981	5-1,2
		?- - -	- - -?	㉔	"Eobuntonia curta" Sayyab, 1956	1 -17, 18
			?- - -? ㉑├────	㉔ ───┤	Holcopocythere bassiporosa/falsoculata Al-Furaih 1980	1 - 1
		⑲㉑	?- -? ? ├────	㉔ ───┤	Hornibrookella divergens Al-Furaih, 1977	3 - 15
	?- cf. - ├──┤	- - - -? ⑥	㉔		'Mehesella' IRC 23 Grosdidier, 1973	1 - 3,4
├────┤	?- - ⑥	- cf. -?	㉔		Metacytheropteron IRL3 Grosdidier, 1973	1 - 21
		?- - -	- -?	㉔	Occultocythereis proro Al-Furaih, 1984	1-6, 7
	?- -	- -?㉔			? Ovocytheridea cf. producta Grekoff, 1962	3 - 9
	㉔	?- - ⑳	- - - - ? ├────	? ───┤	Paragrenocythere gravis Al-Furaih, 1977	3-16,17
		㉑	?- -? ? ├────	㉔ ───┤	Phalcocythere rectangularis/hebes Al-Furaih, 1980	1 - 2
			?- -? ㉑	㉔ ├─┤	Phyrocythere dextrodigitata Al-Furaih, 1980	1 - 10
		?- - -?	㉔		Pterygocythere sp. (OMN 7)	2-11, 12
	?- - -	- - -?	㉔		? Reticythereta sp. (OMN 8)	1 - 20
	? - - cf	- -?	㉔		Soudanella dolabrata Al-Furaih, 1984	1 - 5

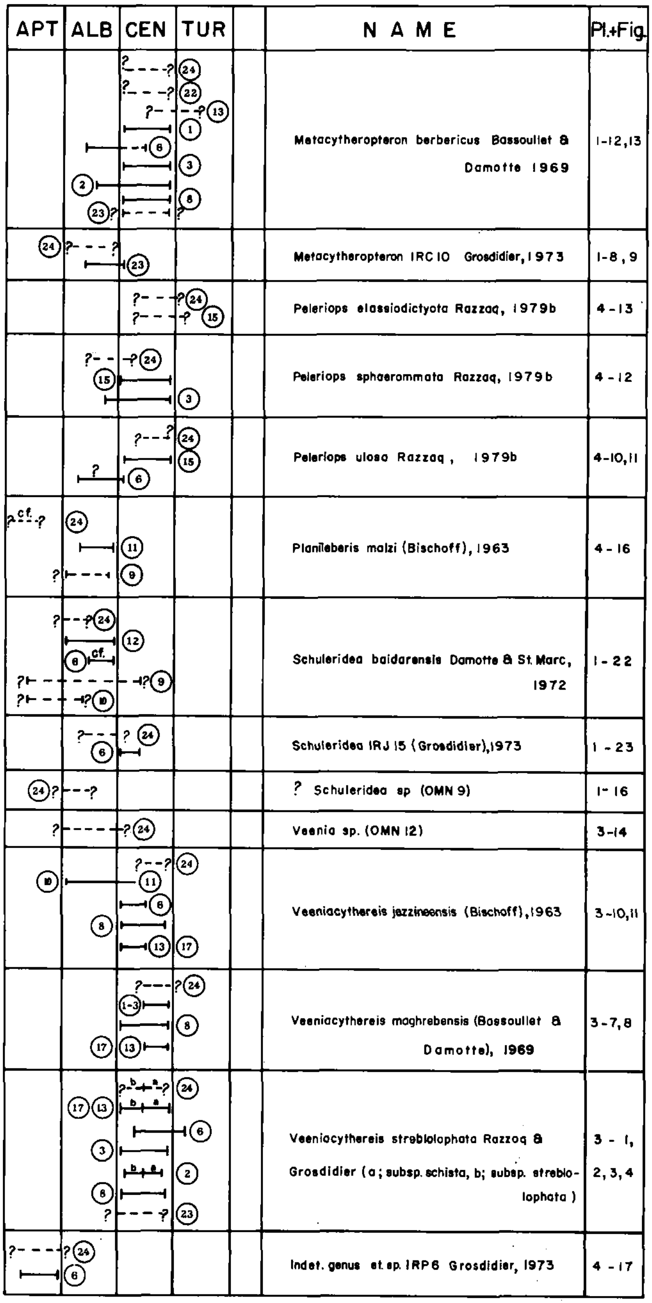
TEXT-FIG. 3—Comparison of stratigraphical ranges of Late Cretaceous ostracods in the Middle East and North Africa (in alphabetical order).

ALGERIA—1, Bassoullet and Damotte, 1969; 2, Bismuth *et al.*, 1981; 3, Glintzboeckle and Magne, 1959; 4, Donze *et al.*, 1982. EGYPT—5, Van den Bold, 1964. IRAN—6, Grosdidier, 1973. IRAQ—7, Al-Sheikly, 1980. ISRAEL—8, Rosenfeld and Raab, 1974; 9, Rosenfeld and Raab, 1984; 10, Hirsch *et al.*, 1983. LEBANON—11, Bischoff, 1963; 12, Damotte and St. Marc, 1972. KUWAIT—13, Al-Abdul-Razzaq, 1977; 14, Al-Abdul-Razzaq, 1979a; 15, Al-Abdul-Razzaq, 1979b; 16, Al-Abdul-Razzaq, 1980; 17, Al-Abdul-Razzaq and Grosdidier, 1981; 18, Al-Abdul-Razzaq, 1981. SAUDI ARABIA/S. ARABIAN GULF—19, Al-Furaih, 1977; 20, Siddiqui and Al-Furaih, 1980; 21, Al-Furaih, 1980; 22, Sayyab, 1956; 23, Al-Furaih, 1983. OMAN—24, this paper.



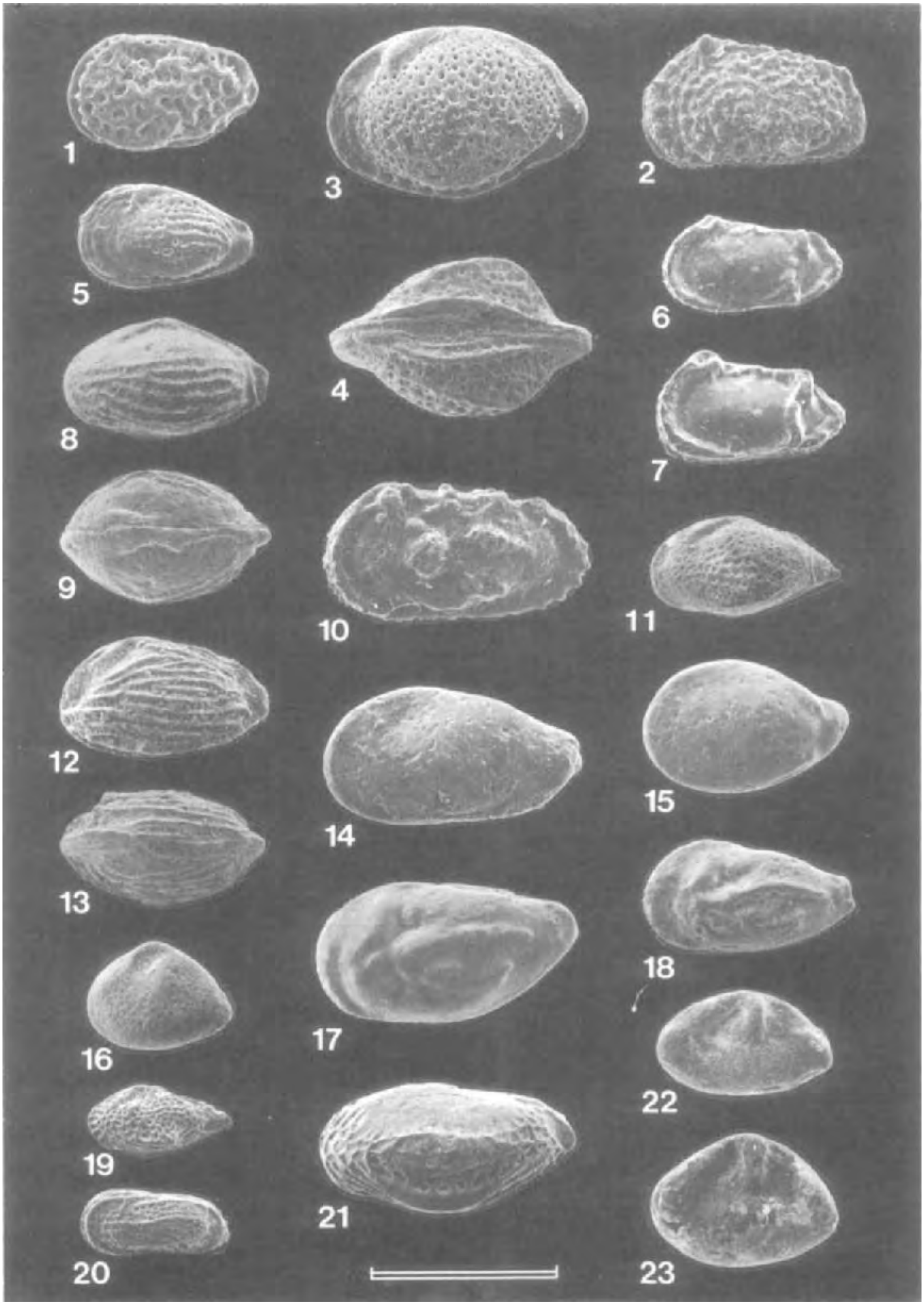
TEXT-FIG. 4a—Comparison of stratigraphical ranges of Middle Cretaceous ostracods in the Middle East and North Africa (in alphabetical order).

ALGERIA—1, Bassoullet and Damotte, 1969; 2, Bismuth *et al.*, 1981; 3, Glintzboeckle and Magne, 1959; 4, Donze *et al.*, 1982. EGYPT—5, Van den Bold, 1964. IRAN—6, Grosdidier, 1973. IRAQ—7, Al-Sheikly, 1980. ISRAEL—8, Rosenfeld and Raab, 1974; 9, Rosenfeld and Raab, 1984; 10, Hirsch *et al.*, 1983. LEBANON—11, Bischoff, 1963; 12, Damotte and St. Marc, 1972. KUWAIT—13, Al-Abdul-Razzaq, 1977; 14, Al-Abdul-Razzaq, 1979a; 15, Al-Abdul-Razzaq, 1979b; 16, Al-Abdul-Razzaq, 1980; 17, Al-Abdul-Razzaq and Grosdidier, 1981; 18, Al-Abdul-Razzaq, 1981. SAUDI ARABIA/S. ARABIAN GULF—19, Al-Furaih, 1977; 20, Siddiqui and Al-Furaih, 1980; 21, Al-Furaih, 1980; 22, Sayyab, 1956; 23, Al-Furaih, 1983. OMAN—24, this paper.



TEXT-FIG. 4b—Comparison of stratigraphical ranges of Middle Cretaceous ostracods in the Middle East and North Africa (in alphabetical order).

ALGERIA—1, Bassoullet and Damotte, 1969; 2, Bismuth *et al.*, 1981; 3, Glintzboeckle and Magne, 1959; 4, Donze *et al.*, 1982. EGYPT—5, Van den Bold, 1964. IRAN—6, Grosdidier, 1973. IRAQ—7, Al-Sheikly, 1980. ISRAEL—8, Rosenfeld and Raab, 1974; 9, Rosenfeld and Raab, 1984; 10, Hirsch, *et al.*, 1983. LEBANON—11, Bischoff, 1963; 12, Damotte and St. Marc, 1972. KUWAIT—13, Al-Abdul-Razzaq, 1977; 14, Al-Abdul-Razzaq, 1979a; 15, Al-Abdul-Razzaq, 1979b; 16, Al-Abdul-Razzaq, 1980; 17, Al-Abdul-Razzaq and Grosdidier, 1981; 18, Al-Abdul-Razzaq, 1981. SAUDI ARABIA/S. ARABIAN GULF—19, Al-Furaih, 1977; 20, Siddiqui and Al-Furaih, 1980; 21, Al-Furaih, 1980; 22, Sayyab, 1956; 23, Al-Furaih, 1983. OMAN—24, this paper.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boundary in Saudi Arabia, but *Occultocythereis prora* Al-Furaih and *Aphrikanecythere phumatoides* Damotte and Oertli apparently signify the presence of Maastrichtian or older sediments. Another important marker is "*Eobuntonia curta*" Sayyab.

PALAEOGEOGRAPHICAL DISTRIBUTION

A comprehensive study of the palaeogeography of Tethyan Cretaceous ostracods is beyond the scope of this paper which deals principally with the species represented in Oman. Nevertheless, the data presented herein are sufficient to allow some speculation on the palaeogeographical distribution of these faunas. The following remarks are tentative since the extent to which the known occurrences reflect the actual distributions is uncertain. This is due mainly to incomplete research in many areas.

As a result of a gradual marine transgressive trend throughout the Aptian to Cenomanian (see Text-fig. 1), a broad carbonate platform developed along the southern shore of Tethys (Saint-Marc, 1978). In the Aptian and Early Albian there was some similarity between the ostracod faunas of Oman, Iran and, to a lesser extent, between Oman, Lebanon and Iraq (see Text-fig. 3).

During Late Albian to Cenomanian times, very similar assemblages of ostracods characterise a vast palaeogeographical province comprising Algeria, Tunisia, Libya, Egypt, Israel, Lebanon, Iraq, the Arabian Gulf, Iran, Oman, Somalia and N. Ethiopia. This area is coincident with the known extent of the southern shelf of Tethys at that time (see Text-fig. 1). A notable exception is the distribution of the genus *Glenocythere* which is characteristic of the Arabian Gulf Coast area, but which is absent from N. Africa and the Levant. The fauna as a whole differs from those known from France, Spain and Syria to the north, Morocco and Senegal to the west and Tanzania to the south.

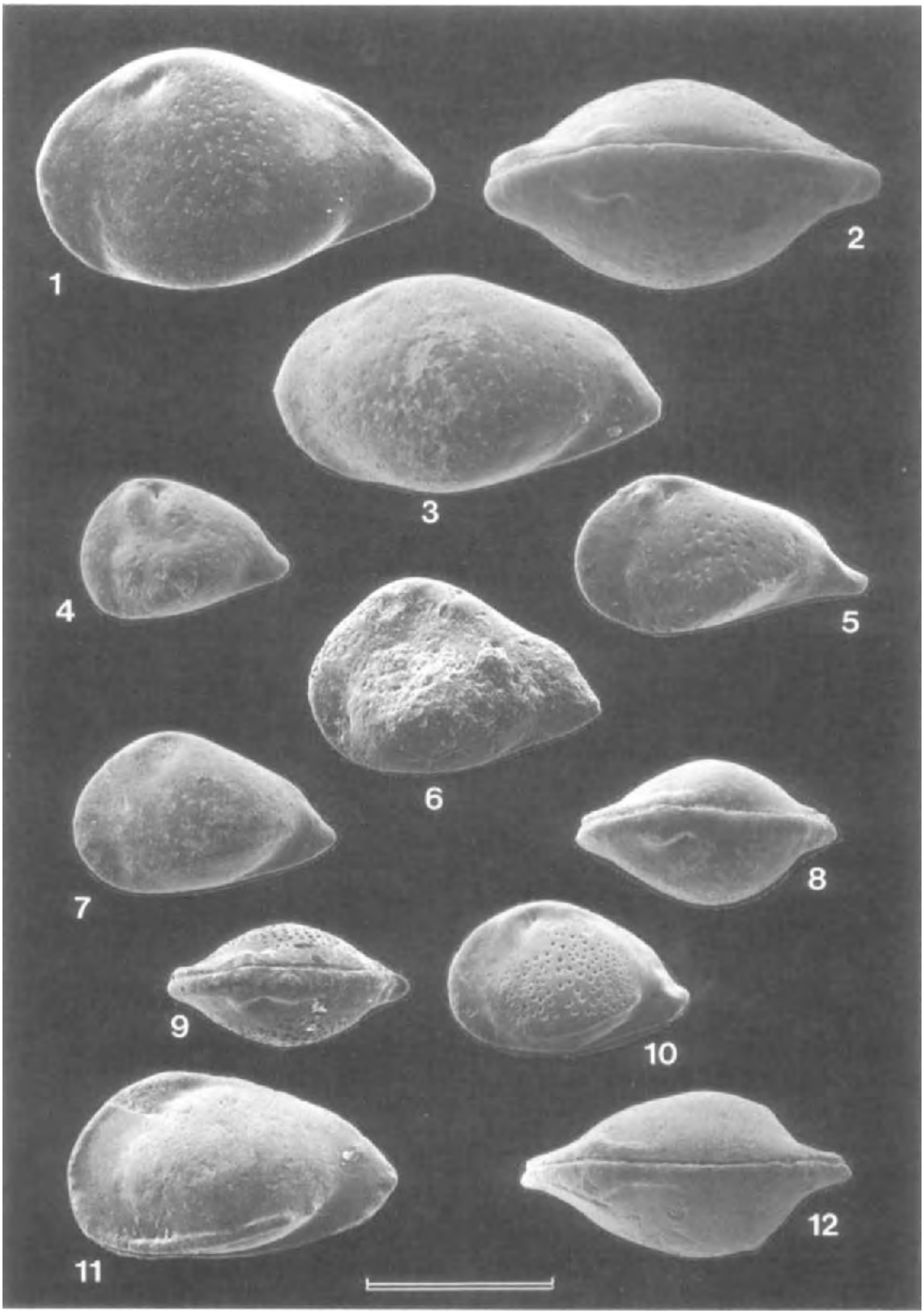
So few ostracods are known from the latest Cenomanian to Turonian of this area that the full extent of their distributions is largely unknown. This is probably largely due to epiorogenic movements during the Turonian and early Senonian which resulted in widespread nondeposition or erosion of Turonian sediments. However, *Brachycythere sapucariensis* and similar forms are known from Brazil, W. Africa, N. Africa and the Middle East at this time, a fact which has been used to support the idea of a trans-saharan marine passage during the Turonian.

In Oman, the study area appears to have been emergent during early Senonian times, as evidence for Conacian to Santonian sediments is missing.

The great similarity between the faunas of the coastal Fars region of Iran and Oman seen during the Late Albian to Cenomanian is lost by the ?Santonian/Campanian, presumably as a result of basinal facies developing throughout the region of the Arabian Gulf and northern Oman (Saint-Marc, 1978).

During the Campanian and Maastrichtian, essentially the same faunas are seen in Oman, N.

PLATE 1—Fig. 1. *Holcopocythere bassiporosa/falsoculata* Al-Furaih. Simsima Fm. Fig. 2. *Phalcocythere rectangularis/hebes* Al-Furaih. Simsima Fm. Figs. 3, 4. "*Mehesella*" cf. *M.* IRC23 Grosdidier. Fiqa Fm. Fig. 5. *Soudanella* cf. *dolobrata* Al-Furaih. Fiqa Fm. Figs. 6, 7. *Occultocythereis prora* Al-Furaih. Fiqa Fm. Figs. 8, 9. *Metacytheropteron* IRC10 Grosdidier. Natih 'f+g' Fm. Fig. 10. *Phyrocythere dextrodigitata* Al-Furaih. Simsima Fm. Fig. 11. *Eocytheropteron retroversicardinatum* Al-Abdul-Razzaq. Natih 'd' Fm. Figs. 12, 13. *Metacytheropteron bergericus* (Bassoullet and Damotte). Natih 'd' Fm. Figs. 14, 15. *Buntonia* cf. IRE9 Grosdidier. Fiqa Fm. Fig. 16. *Schuleridea* sp. [OMN9]. Shu'aiba Fm. Fig. 17. "*Eobuntonia curta* Sayyab". Fiqa Fm. Fig. 18. *Eobuntonia* cf "*E. curta* Sayyab". Fiqa Fm. Fig. 19. *Ahmadiura* cf "*A. dictyota* Al-Abdul-Razzaq". Natih 'e' Fm. Fig. 20. ?*Reticytheretta* sp. [OMN8]. Natih 'a+b' Fm. Fig. 21. *Metacytheropteron* IRL3 Grosdidier. Fiqa Fm. Fig. 22. *Schuleridea baidarensis* (Damotte and St. Marc.) Nahr Umr Fm. Fig. 23. *Schuleridea* IRJ15 (Grosdidier). Natih 'e' Fm. (scale bar = 500 μm). Fm.=Formation.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Ethiopia, Somalia and Saudi Arabia. No extensive survey of the literature outside these areas was made, but it would appear that the ostracod faunas of this region are significantly different from those of the rest of the Middle East and N. Africa at this time (see Text-fig. 4), although there are apparently some species which are found in Tunisia/Algeria and Oman (*e.g. A. phumatoides* and ? '*Eobuntonia curta*'). This marked endemism may result from the irregular submarine topography which developed on the shelf as a result of tectonism and differential subsidence during Turonian and early Senonian times, and which may have isolated various parts of the shelf and the associated ostracod faunas.

Variations in the distribution patterns of ostracods throughout this time may also be related to changes in oceanic circulation in Tethys or to changes in climate due to the northward drift of the Arabian plate (see Text-fig. 1).

REMARKS ON SELECTED INDEX SPECIES

The stratigraphical ranges of index taxa in Oman are shown in Text-fig. 2; distributions and ranges of these taxa for all areas are tabulated in Text-figs. 3 and 4. The following remarks provide additional data which affect the overall knowledge of stratigraphical and geographical distributions of these species.

THE LATE CRETACEOUS (? SANTONIAN–MAASTRICHTIAN)

Aphrikanecythere phumatoides Damotte and Oertli, 1982 (Pl. 4, fig. 14): First illustrated by Sayyab (1956) as "*Anchycythereis quadrata*" from the Upper Cretaceous of the Gulf Coast of Saudi Arabia and Qatar. Similar to *Peleriops levisulcata* of Al-Sheikly (1980) and *P. nodosa* Al-Furaih (1984a) from the Maastrichtian of Iraq and Saudi Arabia, respectively. Comparable specimens occur in the Sadi Formation and the Tanuma Formation in Iraq of ?Campanian and ?Coniacian ages, respectively.

Cytherella posterosulcata Al-Abdul-Razzaq (1981) (Pl. 5, figs. 1, 2): Described by Al-Abdul-Razzaq (1977; 1981) from the Santonian Gudair Formation of Kuwait. Also present in Somalia/Ethiopia, Iran and Iraq where it has a Santonian to Coniacian age range (unpublished data).

"?*Eobuntonia curta*" Sayyab, 1956 (Pl. 1, figs. 17, 18): Probably identical with *Buntonia* B816 of Bellion, Donze and Guiraud (1973) from the Campanian of Algeria. Described by Sayyab (1956) from the Late Cretaceous of the S. Arabian Gulf coast area; occurs in the Campanian Sadi Formation and the ?Coniacian Tanuma Formation, Iraq and the Santonian–Coniacian of Ethiopia (unpublished data).

Holcopocythere bassiporosa/falsoculata Al-Furaih, 1980 (Pl. 1, fig. 1): Resembles both *H. bassiporosa* Al-Furaih (1980) and *H. falsoculata* Al-Furaih (1980) from the Late Maastrichtian and Early Palaeocene of Saudi Arabia.

?'*Mehesella*' cf. '*Mehesella*' IRC23 Grosdidier, 1973 (Pl. 1, figs. 3, 4): Unpublished data indicate its presence in Somalia and Ethiopia and a stratigraphical range of Santonian to Coniacian.

Occultocythereis prora Al-Furaih, 1984a (Pl. 1, figs. 6, 7): It is similar but not identical to

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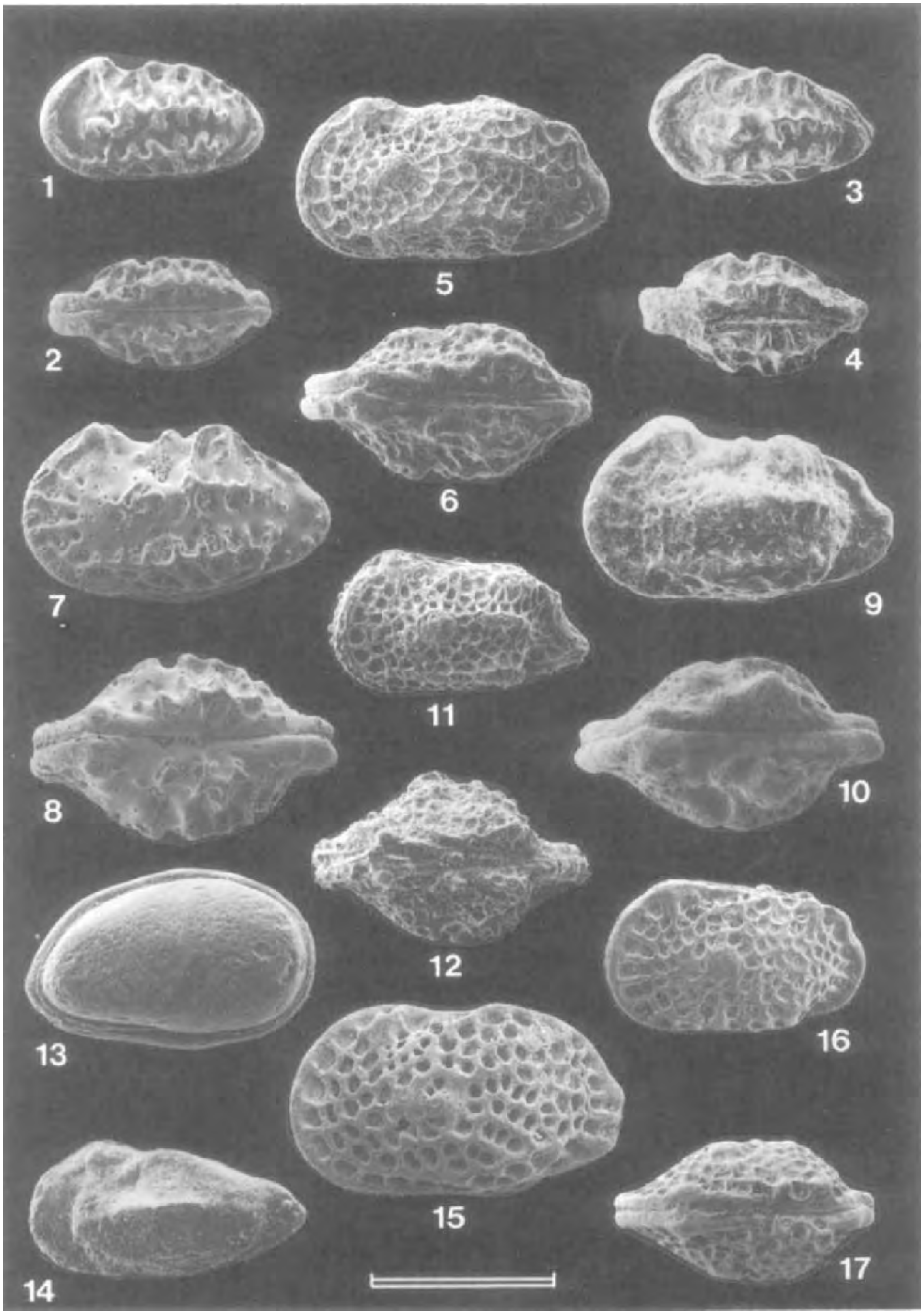
PLATE 2—Figs. 1, 2. *Brachycythere* sp. [OMN2]. Fiqa Fm. Fig. 3. *Brachycythere* sp. [OMN4]. Fiqa Fm. Fig. 4. *Brachycythere* sp. [OMN5]. Fiqa Fm. Fig. 5. *Brachycythere* sp. [OMN1]. Simsima Fm. Fig. 6. *Brachycythere* cf. B. IRE10 Grosdidier. Natih 'a+b' Fm. Figs. 7, 8. *Brachycythere* cf. *sapucariensis* Krommelbein (*sensu* Bismuth *et al.*) Natih 'a+b' Fm. Figs. 9, 10. *Brachycythere* sp. [OMN3]. Fiqa Fm. Figs. 11, 12. *Pterygocythere* sp. [OMN 7]. Fiqa Fm. (scale bar = 500 μm). Fm. = Formation.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"*Occultocythereis asymmetra*" Al-Abdul-Razzaq (1977) from the Santonian Gudair Formation of Kuwait, *Planileberis*? IRE23 Grosdidier from the Early Campanian to Late Santonian of Iran and "*Occultocythereis makhulaensis* Al-Sheikly" (1980) from the Maastrichtian of Iraq. Unpublished data indicate that species similar to *O. asymmetra* are recorded from the Santonian–Coniacian of Somalia/Ethiopia, Oman, Iran, Kuwait, Iraq and Algeria.

?*Ovocytheridea* cf. *O. producta* Grekoff, 1962 (Pl. 3, fig. 9): Also questionably the same as *Ovocytheridea* IRJ8 Grosdidier (1973) from the ?Coniacian of Iran and to unpublished records from the Early Santonian to Coniacian of Somalia/Ethiopia, Oman, Iran, Egypt and Algeria.

Phalcocythere rectangularis/hebes Al-Furaih, 1980 (Pl. 1, fig. 2): Similar to both *P. rectangularis* and *P. hebes* from the Maastrichtian and Early Palaeocene of Saudi Arabia.

Pterygocythere sp. [OMN 7] (Pl. 2, figs. 11, 12): Similar, but not identical, to *P. claustrata* Al-Furaih, 1984b from the Maastrichtian of Saudi Arabia. Questionably also from the Santonian of Somalia/Ethiopia (unpublished data).

?*Reticytheretta* sp. [OMN 8] (Pl. 1, fig. 20): Similar to, and possibly identical with, ?*Dumontina* IRE18 Grosdidier (1974) from the Early Santonian to Coniacian of Iran.

THE MIDDLE CRETACEOUS (APTIAN–TURONIAN)

Asciocythere cf. "*A. inpendula*" Razzaq, 1977 (Pl. 5, fig. 9): Also found in Somalia/Ethiopia, Iran and Algeria in Early Santonian to Late Coniacian sediments (unpublished data).

Brachycythere cf. *B. sapucariensis* Krommelbein, 1964 (Pl. 2, figs. 7, 8): *B. sapucariensis* s.s. was originally described from the Early Turonian of Brazil and the ?Coniacian of Gabon by Krommelbein (1964). Bate and Bayliss (1968) illustrated a similar form from the Turonian of Tanzania which was further illustrated by Neufville (1973) who recorded it from the Early Turonian of Gabon, Nigeria and Brazil. Specimens illustrated by Bismuth *et al.*, (1981) from the Cenomanian of Tunisia are referable to *B.* cf. *sapucariensis,* herein. Prestat and Riche (1980) recorded *B.* aff. *sapucariensis* from S.E. Iraq, and questionably from Iran and Oman.

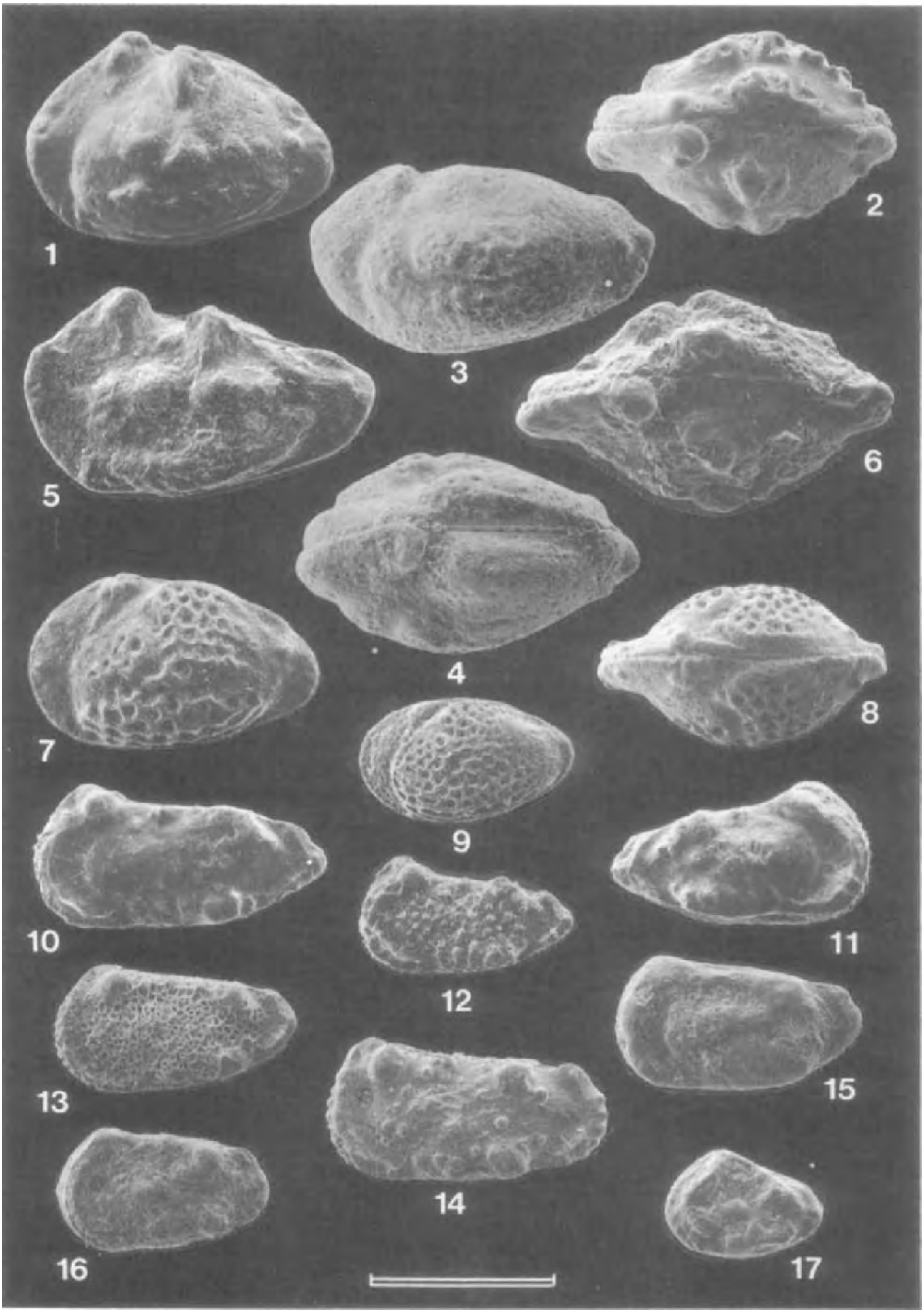
Unpublished data suggest that forms similar to *B. sapucariensis* also occur in Somalia/Ethiopia and possibly Egypt. Bristowe and Hoffstetter (1977) record *B.* cf. *sapucariensis* from the Late Cretaceous Napo Formation of Ecuador.

Cytherella gigantosulcata Rosenfeld, 1981 (Pl. 5, figs. 14, 15): Recorded as ostracod U-10 from Tunisia and Algeria (Glintzboeckel and Magne, 1959) and from Iran (Grosdidier, 1973), and as *Cytherella sulcata* by Rosenfeld and Raab (1974) and Al-Abdul-Razzaq (1979a; 1981) from Israel and Kuwait, respectively.

Cytherella khalidrazzaqi Al-Abdul-Razzaq, 1981 (Pl. 5, figs. 12, 13): Synonymous with the manuscript name "*Cytherella acropleura*" Al-Abdul-Razzaq (1977).

Cytherella kuwaitensis Al-Abdul-Razsaq, 1981 (Pl. 5, figs. 3, 4): Sayyab (1956) also illustrated this species from the Middle Cretaceous of the Arabian Gulf Coast, under the name *Cytherella ovata* (Roemer).

PLATE 3—Figs. 1, 2. *Veeniacythereis streblolophata schista* Al-Abdul-Razzaq and Grosdidier. Natih 'a+b' Fm. (? = A-2 juvenile of *V. jeezineensis*) Figs. 3, 4. *Veeniacythereis streblolophata streblolophata* Al-Abdul-Razzaq and Grosdidier. Natih Fm. (? = A-1 juvenile of *V. jeezineensis*) Figs. 5, 6. *Cythereis* cf. *fahrioni* Bischoff. Natih 'e' Fm. Figs. 7, 8. *Veeniacythereis maghrebensis* (Bassoullet and Damotte). Natih 'a+b' Fm. (?♀ of *V. jeezineensis*) Fig. 9. *Ovocytheridea* cf. *producta* Grekoff. Natih 'a+b' Fm. Figs. 10, 11. *Veeniacythereis jezzineensis* (Bischoff). Nahr Umr Fm. Figs. 12, 13. *Cythereis algeriana* Bassoullet and Damotte. Natih 'a+b' Fm. Fig. 14. *Veenia* sp. [OMN12]. Natih 'e' Fm. Fig. 15. *Hornibrookella divergens* Al-Furaih. Simsima Fm. Figs. 16, 17. *Paragrenocythere gravis* Al-Furaih. Simsima Fm. (scale bar = 500 μm). Fm.=Formation.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Cytherella sp. [OMN 10] (Pl. 5, figs. 7, 8): Similar to *Cytherella* [OMN 11], but differs in having a protuberance on the posteroventral margin of the right valve.

Cytherella sp. [OMN 11] (Pl. 5, figs. 5, 6): Very similar to *C. khalidrazzaqi* Al-Abdul-Razzaq, (q.v.) from the Cenomanian Ahmadi Formtion of Kuwait.

Eocytheropteron retroversicardinatum Al-Abdul-Razzaq, 1980 (Pl. 1, fig. 11): Similar to *Eocytheropteron* IRK13 Grosdidier (1973) from the Albian of Iran (see Al-Abdul-Razzaq, 1980). Also from Somalia/Ethiopia, Tunisia and Algeria (unpublished data).

Glenocythere bahreinensis Al-Abdul-Razzaq, 1979 (Pl. 4, figs. 3, 4): Sayyab's (1956) "*Amphicythereis bahreinensis*" from the lower part of the Middle Cretaceous (?Albian) of Qatar, Saudi Arabia, Kuwait and Iraq includes specimens identical to this species; other illustrated specimens belong to *G. triangularis*. "*Cythereis bahreini*" of old Middle East Oil Company reports includes this species, probably together with other species of *Glenocythere*. In Saudi Arabia it occurs in the lower part of the Ahmadi Formation and, according to Sayyab (1956), is used to mark a zone just above the Burgan Formation throughout the Arabian Gulf Coast area including Bahrein. Recorded by Grosdidier (1973) as *Cythereis* IRC2 from the Mauddud and Nahr Umr Fms of Iran (Early Cenomanian-Late Albian). Also from Somalia/Ethiopia (unpublished data).

Glenocythere reticulata Al-Abdul-Razzaq, 1979 (Pl. 4, figs. 7, 8): First described under the name "*Amphicythereis hasaensis*" by Sayyab (1956) from the lower part of the Middle Cretaceous in the Arabian Gulf Coastal area from Qatar to Iraq. ?*Nigeria* IRJ14 of Grosdidier from the Early Cenomanian to Albian Mauddud and Nahr Umr Formations of Iran is identical to *G. reticulata*. Also known from the Ahmadi Formation of Iraq (unpublished data).

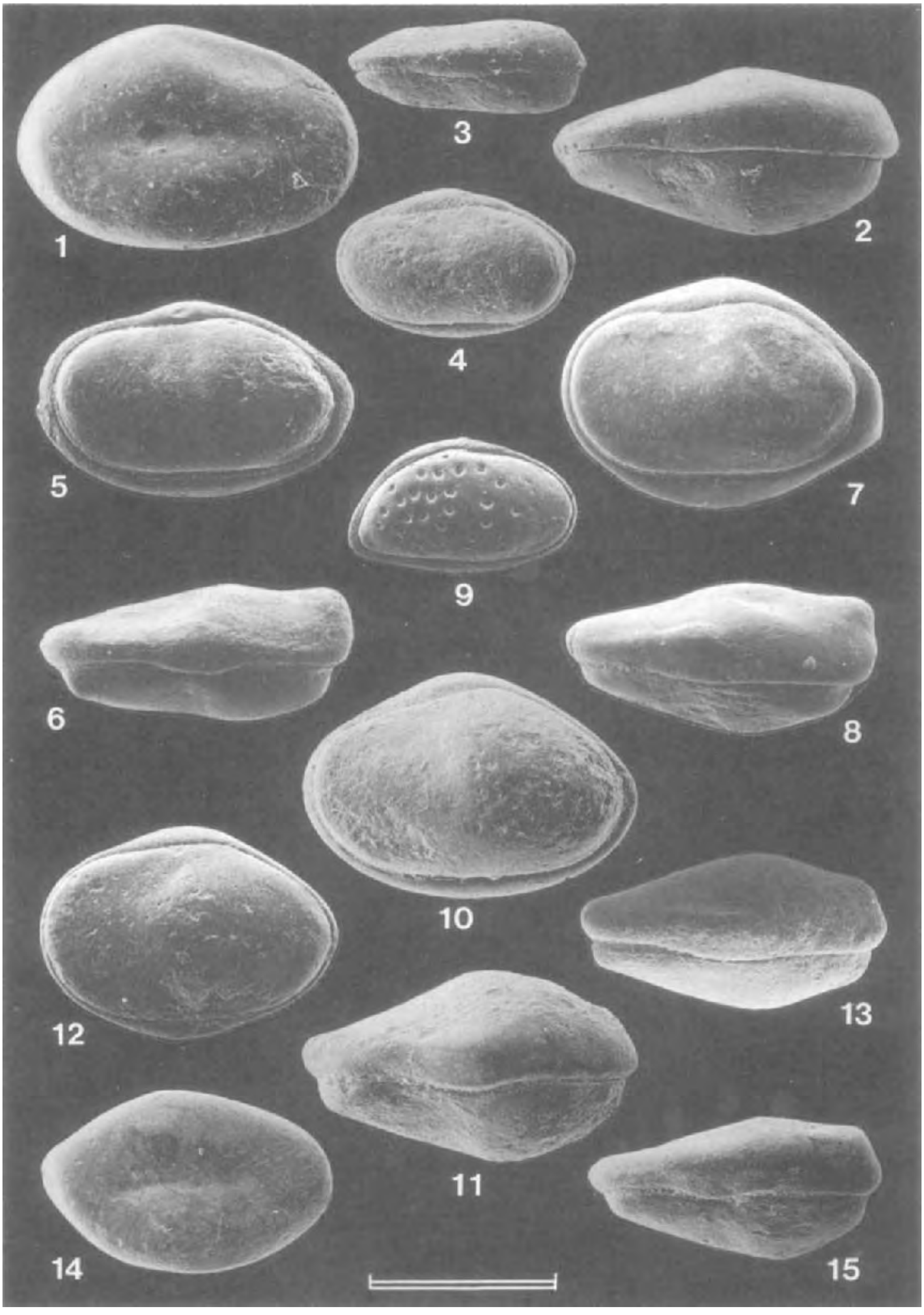
Glenocythere triangularis Al-Abdul-Razzaq, 1979 (Pl. 4, figs. 1, 2, 5, 6): Included in "*Amphicythereis bahreinensis*" by Sayyab (1956).

"*Louza amygdaloidea*" Al-Abdul-Razzaq, 1977 (Pl. 4, fig. 9): Recorded in Sayyab (1956) as "*Amphidentina nasri*" from the lower part of Middle Cretaceous (?Albian) of the Arabian Gulf Coast. According to Razzaq (1977), this species is synonymous with the *Brachycythere* sp. referred to by Jaber (1965) as being the marker for the upper zone of the Lower Ahmadi Limestone (=*Brachycythere* limestone).

Metacytheropteron berbericus (Bassoullet and Damotte), 1969 (Pl. 1, figs. 12, 13): Resembles "*Eocytherura striata* Sayyab" (1956) of probable Cenomanian age from the Arabian Gulf Coast between Iraq and Qatar. *Metacytheropteron striata* Razzaq (1977) is identical with this species and occurs in the Ahmadi and Mishrif Formations of Cenomanian to ?Turonian age in Kuwait. *Metacytheropteron pleura* Al-Furaih (1983) from the Cenomanian Wasia Formation of Saudia Arabia may also be assigned to this species. *Metacytheropteron parnesi* Sohn recorded by Grosdidier (1973) from the Albian to Cenomanian of Iran is probably also referrable to this species. *M. parnesi* Sohn (1967) from the ?Barremian of Israel is not regarded as synonymous (see Rosenfeld and Raab, 1974). Unpublished data confirm its presence in Egypt and Somalia/Ethiopia and also in the Ahmadi and Rumaila Formations of Iraq.

Metacytheropteron IRC10 Grosidier, 1973 (Pl. 1, figs. 8, 9): Specimens from the ?Ahmadi/Mauddud Formation of Iraq are also known (Unpublished data).

PLATE 4—Figs. 1, 2. *Glenocythere triangularis* Al-Abdul-Razzaq. Natih 'd' Fm. Figs. 3, 4. *Glenocythere bahreinensis* Al-Abdul-Razzaq. Natih 'e' Fm. Fig. 5—*Glenocythere* cf. *triangularis* Al-Abdul-Razzaq. Nahr Umr Fm. Fig. 6. *Glenocythere* cf. *triangularis* Al-Abdul-Razzaq. Natih 'f+g' Fm. Figs. 7, 8. *Glenocythere reticulata* Al-Abdul-Razzaq. Natih 'e' Fm. Fig. 9. "*Louza amygdaloidea* Al-Abdul-Razzaq". Natih 'd' Fm. Fig. 10. *Peleriops ulosa* Al-Abdul-Razzaq. Natih 'c' Fm. Fig. 11. *Peleriops ulosa* Al-Abdul-Razzaq. Natih 'd' Fm. Fig. 12. *Peleriops sphaerommata* Al-Abdul-Razzaq. Natih 'e' Fm. Fig. 13. *Peleriops elassiodictyota* Al-Abdul-Razzaq. Natih 'a+b' Fm. Fig. 14. *Aphrikanecythere phumatoides* Damotte and Oertli. Fiqa Fm. Fig. 15. "*Cythereis* cf. IRK26 Grosdidier". Kharaib Fm. Fig. 16. *Planileberis* cf. *malzi* (Bischoff). Kharaib Fm. Fig. 17. Indet. gen. *et.* sp. IRP6 Grosdidier. Shu'aiba Fm. (scale bar = 500 μm). Fm.=Formation.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Peleriops elasiodictyota Al-Abdul-Razzaq, 1979 (Pl. 4, fig. 13): Similar to *Cythereis malzi* Bischoff illustrated by Bischoff (1963) and Damotte and Saint-Marc (1972) from the Albian of the Lebanon.

Peleriops sphaerommata Al-Abdul-Razzaq, 1979 (Pl. 4, fig. 12): Ostracod E of Glintzboekel and Magne (1959) from the Vraconian to Cenomanian of Algeria and Tunisia may possibly be synonymous as may "*Anchycythereis compressa*" of Sayyab (1956) from the upper part of the Middle Cretaceous of the S. Arabian Gulf Coast. Similar to *Planileberis ziregensis* Bassoullet and Damotte (1969) and *P. pustulosa* Rosenfeld and Raab (1974) from Algeria and Israel, respectively.

Peleriop ulosa Al-Abdul-Razzaq, 1979 (Pl. 4, figs. 10, 11): There are further records of this species from Egypt, Somalia/Ethiopia and Lebanon and comparable specimens are also known from the Ahmadi Formation of Iràq (unpublished data). *Cythereis* gr. *malzi* Bischoff illustrated by Grosdidier (1973) from the Albian of Iran may be synonymous with *P. ulosa*. *Cythereis lindiensis* from the Cenomanian of Tanzania (Bate and Bayliss, 1969) and from the Albian of Iran (Grosdidier, 1973) is very similar to this species and may be conspecific.

Schuleridea baidarensis (Damotte and Saint-Marc), 1972 (Pl. 1, fig. 22): Originally recorded as ?*Dordoniella bairdarensis* from the Albian of Lebanon; Grosdidier (1973) illustrated similar specimens from the Late Albian of Iran. Also recorded by Rosenfeld and Raab (1974, 1984), and Hirsch *et al.* (1983) in Aptian to Early Cenomanian sediments in Israel and Sinai.

?*Schuleridea* sp. [OMN9] (Pl. 1, fig. 16): Identical with specimens from the Nahr Umr Formation of Iraq (unpublished data). Recorded by Grosdidier (1973) as *Dordoniella* IRJ15 from the Early Cenomanian of Iran.

Veeniacythereis jezzineensis (Bischoff), 1963 Group (Pl. 3, figs. 1–4, 7–10): This group includes forms referred to *V. jezzineensis, V. magrebensis* and *V. streblolophata* by various autors. Sayyab (1956) and Rosenfeld and Raab (1974) regarded *V. streblolophata* as juveniles of the other two species. Later, Colin and Dakkak (1975) and Rosenfeld and Raab (1983) concluded that these three forms were conspecific, with *V. magrebensis* being the female dimorph and *V. streblolophata strebolophata* and *V. streblolophata schista* being A-1 and A-2 juveniles, respectively. However, other authors (Al-Abdul-Razzaq and Grosdidier, 1981; Bismuth *et al.*, 1981) have recorded different stratigraphical ranges for these forms, a fact which suggests that their synonymy may not be justified. In this study, *V. streblolophata* subspp. occur at slightly lower stratigraphical levels in the 'a+b' member than *V. magrebensis* and *V. jeezineensis*. In order to retain the individual identity of these froms they appear separately in Text-figs. 2 and 4, in Plate 3 and in the following text.

The first available record of forms attributable to this group is '*Cythereis arabica*' Sayyab (1956) from the upper part of the Middle Cretaceous on the Arabian Gulf Coast between Iraq and Qatar. Sayyab commented that the '*Cythereis arabica*' zone was a useful marker interval widely recorded in Middle East oil company reports.

Cythereis jezzineensis was first described by Bischoff (1963) from the Albian to Middle Cenomanian of Lebanon. Subsequent records of this form under the name *Cythereis jezzineensis* are from the Early Cenomanian of Coastal Fars, Iran (Grosdidier, 1973), the Late Albian to Cenomanian of Israel (Rosenfeld and Raab, 1974) and the Early Cenomanian Ahmadi Limestone from Kuwait (Al-Abdul-Razzaq, 1977; Al-Abdul-Razzaq and Grosdidier, 1981). Koch (1968) and Hirsch *et al.* (1983) also mention this species from the Cenomanian of Jordan, and Late Albian/

PLATE 5—Figs. 1, 2. *Cytherella posterosulcata* Al-Abdul-Razzaq. Fiqa Fm. Figs. 3, 4. *Cytherella kuwaitensis* Al-Abdul-Razzaq. Natih 'c' Fm. Figs. 5, 6. *Cytherella* sp. [OMN11]. Nahr Umr Fm. Figs. 7, 8. *Cytherella* sp. [OMN 10]. Natih 'e' Fm. Fig. 9. "*Asciocythere* cf. *inpendula* Al-Abdul-Razzaq". Natih 'c' Fm. Figs. 10, 11. *Cytherella ahmadiensis* Al-Abdul-Razzaq. Natih 'd' Fm. Figs. 12, 13. *Cytherella khalidrazzaqi* Al-Abdul-Razzaq. Natih 'a+b' (base) Figs. 14, 15. *Cytherella gigantosulcata* Rosenfeld. Natih 'd' Fm. (base). (scale bar = 500 μm). Fm. = Formation.

Cenomanian of Israel, respectively, but in neither paper are specimens illustrated. Unpublished data suggest its further occurrence in Algeria, Tunisia, Egypt and Somalia/Ethiopia.

Veeniacythereis magrebensis was first recorded as Ostracod C, by Glintzboeckel and Magne (1959), and later as *Cythereis maghrebensis* by Bassoullet and Damotte (1969) from the Late Cenomanian of Tunisia and Algeria. This form is also known from Egypt and Somalia/Ethiopia (unpublished data).

Grosdidier (1973) recorded *V. streblolophata streblolophata* as *Cythereis* IRE3 from the Early Cenomanian to Albian of Iran. It appears under the name Ostracod C_2 and *Cythereis* C_2 in Glintzboeckel and Magne (1959) and Grekoff (1968), respectively from the Cenomanian of Tunisia and Algeria. *Phyrocythere streblolophata* described by Al-Furaih (1983) from the Cenomanian Wasia Formation of Saudi Arabia is identical with this sub-species. *Veeniacythereis streblolophata schista* was first recorded by Glintzboeckel and Magne (1959) as Ostracod C_3 from the Cenomanian of E. Algeria and Tunisia. Grosdidier (1973) also recorded this subspecies as *Cythereis* IRE4 from the Cenomanian of Iran.

ACKNOWLEDGEMENTS

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POSTSCRIPT

After this paper had been completed several further important publications became available, namely Bellion, Donze and Guiraud (1973), Viviere (1985), Honigstein (1984), Honigstein, Raab and Rosenfeld (1985), Bismuth (1984) and Al-Furaih (1984a, b). Full references are included in the References of this paper. Data from Al-Furaih (1984a, b) are included in the text, but not in the figures.

DISCUSSION

Colin: I have two comments to make on your palaeobiogeographical maps: 1) Your map on the Aptian and Albian shows no affinities with North Africa. This is misleading because almost no information has been published on Aptian ostracods from North Africa. 2) Your Campanian-Maasitichtian map shows a strong endemism for Middle East ostracods. A paper by Bellion, Donze and Guiraud on the Late Cretaceous ostracods from Algeria describes a few species that you report from Oman and especially your species of *Buntonia* (*Eobuntonia*).

Athersuch: 1) The map does not appear in my paper for that very reason. However, it does account for all of the records currently available. 2) It is interesting to know that "*Eobuntonia curta*" Sayyab MS. is found elsewhere. I am not familiar with Bellion *et al.* In future the affinities of all the faunas of the Tethyan Cretaceous should be more critically reviewed.

Reyment: It is gratifying to learn that these results for the Cretaceous of Oman are being made available, not the least for our work, as V. Emami of our department is in possession of considerable material from Iran, much of which also seems to be represented in the faunas you describe. As regards *Brachycythere sapucariensis* Krommelbein, I can mention that work in hand on ostracods of the Sapucari Formation (NE Brazil) may help in elucidating problems of identification (occasioned by the fact that the original description was accompanied by no more than schematic sketches). The "Turonian" Trans-Saharan seaway (the first of three) is now dated as latest Cenomanian, *birchbyi* zone on a mondial re-evaluation of the ammonite evidence, a by-product of IGCP project 58 Mid-Cretaceous events.

Athersuch: I am not surprised that Emami's material is similar to mine. In the Albian-Cenomanian at least, the similarities between the Oman and Iran faunas is very strong. It will be interesting to find out exactly what *B. sapucariensis* does look like.

Ostracods from Non-marine Early Cretaceous Sediments of the Campos Basin, Brazil

JOEL A. MOURA
Petrobrás Research Center, Rio de Janeiro, Brazil

ABSTRACT

Late Jurassic (?)–Early Cretaceous non-marine sequences of Brazil have been intensively investigated by means of their faunal content, mainly represented by a rich ostracod fauna.

It was possible to obtain an accurate biostratigraphical zonation for sediments based on ostracods which, in view of their endemism, led to the establishment of 6 local stages: Dom João stage (Late Jurassic ?), Rio da Serra, Aratu, Buracica, Jiquiá and Alagoas stages (Neocomian to Aptian).

This work deals with the study of ostracods from Petrobrás boreholes in the Campos Basin, NE Brazil, through the uppermost part of the Early Cretaceous, including both Jiquiá and Alagoas stages (probably Barremian to Aptian).

A biostratigraphical zonation is established and compared with those of the Sergipe/Alagoas and Recôncavo/Tucano basins.

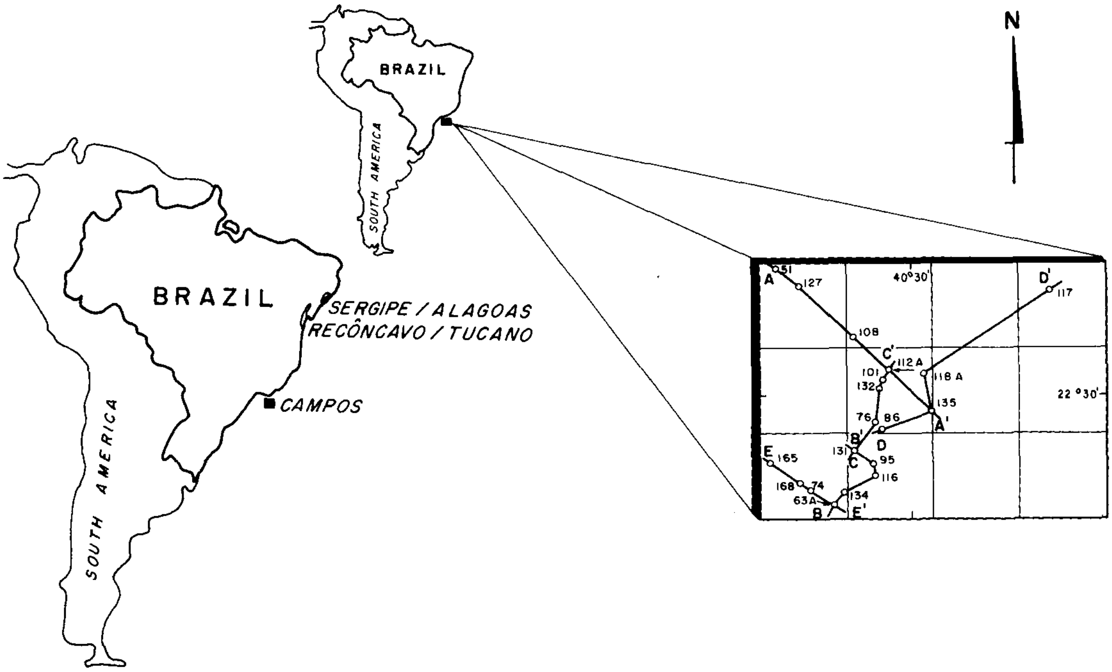
It was possible to recognise one undivided zone for the Alagoas stage, the Zone of *"Cytheridea"* spp. gr. 201/218, also found in the Sergipe/Alagoas basin, and two zones within the Jiquiá stage—the *Limnocythere troelseni* and *Petrobrasia diversicostata* zones, the latter being divided into the *Cypridea (S.) devexa* and *Bisulcocypris postangularis* subzones. All these three subzones were first identified in the Recôncavo/Tucano basin.

Based on uniformitarian principles and observations of morphofunctional characteristics of the ostracods, the sediments of the Alagoas stage are interpreted as being deposited under shallow, restrictive continental/transitional conditions and the Jiquiá stage, at least in its earlier part, in a deltaic-lacustrine environment as in the Recôncavo basin.

INTRODUCTION

The Campos basin (Text-fig. 1), located in the littoral of Rio de Janeiro State, Brazil, shows a tensional tectonic style and belongs to the Occidental province, according to the general classification of the world continental margins (Ponte and Asmus, 1976). Its oil potential has encouraged successful exploratory activity which generated a huge amount of data.

Wells drilled in the Campos basin, after passing through thick Cenozoic, Upper and Middle Cretaceous marine strata, commonly reach non-marine sediments of the Lower Cretaceous local stages Alagoas, Jiquiá and Buracica. They seldom reach older sediments, well known in the Recôncavo/Tucano and in the Sergipe/Alagoas basins (Text-fig. 1), which are the type-areas from which the type-sections of these sedimentary sequences were described.



Text-fig. 1—Study area and location of correlated sections, and location map of Campos, Recôncavo/Tucano and Sergipe/Alagoas Basins.

The biostratigraphical study of these non-marine sediments can be easily carried out by means of the ostracods, allowing a better comprehension of the geological history of Brazilian Cretaceous non-marine basins.

This paper represents the preliminary step in systematic biostratigraphical studies of this area based on ostracods. It is devoted to part of the lacustrine-deltaic clastic sequence of the Jiquiá local stage, also known as the "lake sequence", and to part of the evaporitic and clastic sequences of the Alagoas local stage, also called the "gulf sequence" (Pontes and Asmus, 1976).

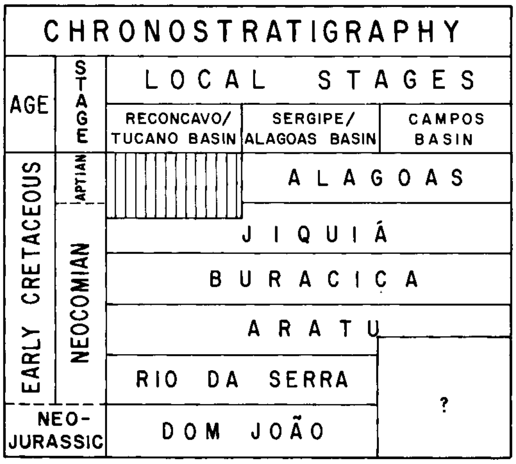
The ostracods of the Alagoas stage are almost the same as those found in the Sergipe/Alagoas basin, except for their bad preservation and lesser diversification. The Jiquiá stage is biostratigraphically better refined due to a more diversified ostracod fauna, mainly in its basal portion, which is comparable to a chronostratigraphically corresponding part of the Recôncavo/Tucano basin. The upper part of the Jiquiá stage is partly comparable to the Recôncavo/Tucano basin and completely comparable to the Sergipe/Alagoas basin in the corresponding sections.

A comparative chronostratigraphical table (Text-fig. 2) provides the local stage correlation and Text-fig. 3 shows the correlation of biostratigraphical units between the three basins (Campos, Recôncavo/Tucano and Sergipe/Alagoas) for the referred stages.

The units throughout the study area can be visualized by means of the stratigraphical correlative sections presented in Text-figs. 4 to 8.

Previous Work

Biochronostratigraphical studies in the Campos basin using ostracods have been carried out by Petrobrás personnel and are recorded in private reports existent in Petrobrás' files. Moura and



TEXT-FIG. 2—Local stage correlation among Recôncavo/Tucano, Sergipe/Alagoas and Campos Basins.

Praça (1985) carried out a biochronostratigraphical study of this interval in the Campos basin.

MATERIAL AND METHODS

Ditch and core samples from nineteen selected wells drilled by Petrobrás offshore in the Campos basin were the basic material for taxonomic, biostratigraphical, and correlative studies.

Recognition of the ostracod taxa was accomplished by consulting internal reports and the papers by Schaller (1969) and Vianna *et al.* (1971).

The two plates which illustrate this paper were produced using photomicrographs taken by the Petrobás Research Center's scanning electron microscope (S.E.M.).

BIOSTRATIGRAPHY

In the Campos basin three biostratigraphical zones have been recognized for the Alagoas and Jiquiá stages. The Alagoas stage is characterized by one single, undivided zone, the *"Cytheridea"*? spp. ex. group 201/218 zone, code 011, informally described by Schaller (1969, *op. cit.*) It is represented by a poor ostracod assemblage in which only some components are recognizable. Frequently, a thick sedimentary sequence is representative of this stage. Its upper part is commonly destitute of ostracods which is a reflection of the environmental restrictions.

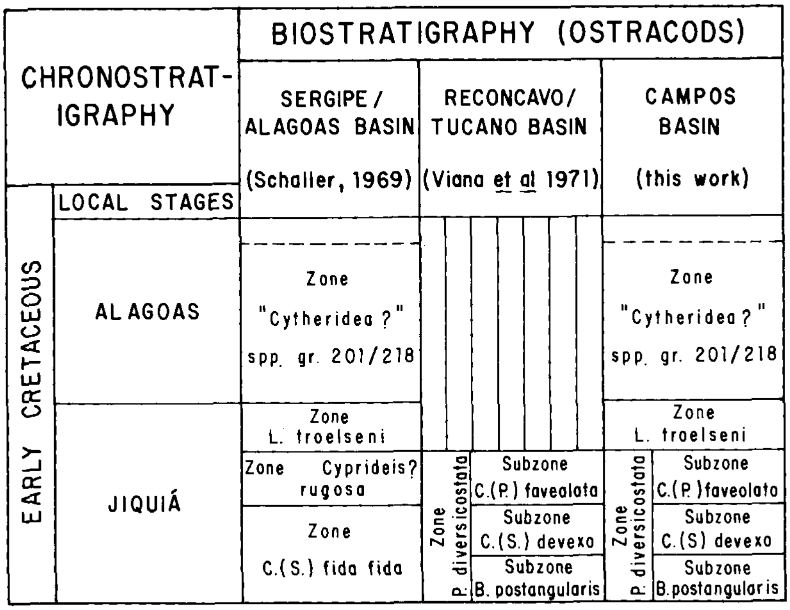
The other two zones, corresponding to the Jiquiá local stage, are distributed as follows from top of bottom: Zone *Limnocythere troelseni,* code 010, represented by a monospecific ostracod assemblage, occurs in some areas of the basin. This zone was also informally proposed by the same authors for the Sergipe/Alagoas basin, in the previously mentioned work (Schaller, 1969).

Zone *Petrobrasia diversicostata,* code 009, with three subzones, is represented by a richer and more diversified ostracod fauna. It was defined for the Recôncavo/Tucano basin (Viana *et al.,* 1971). This zone can be subdivided into three subzones:

Subzone *Cypridea* (*Pseudocypridina*) *faveolata,* code 009.3, which occurs more frequently,

Subzone *Cypridea* (*Sebastianites*) *devexa,* code 009.2,

Subzone *Bisulcocypris postangularis postangularis,* code 009.1, occurring less frequently in the basin.



CHRONOSTRATIGRAPHY		BIOSTRATIGRAPHY (OSTRACODS)				
		SERGIPE / ALAGOAS BASIN (Schaller, 1969)	RECONCAVO/ TUCANO BASIN (Viana et al 1971)		CAMPOS BASIN (this work)	
EARLY CRETACEOUS	LOCAL STAGES					
	ALAGOAS	Zone "Cytheridea ?" spp. gr. 201/218			Zone "Cytheridea ?" spp. gr. 201/218	
	JIQUIÁ	Zone L. troelseni			Zone L. troelseni	
		Zone Cyprideis? rugosa	Zone P. diversicostata	Subzone C.(P.) faveolata	Zone P. diversicostata	Subzone C.(P.)faveolata
		Zone C.(S.) fida fida		Subzone C.(S.) devexa		Subzone C.(S) devexa
				Subzone B. postangularis		Subzone B.postangularis

TEXT-FIG. 3—Biochronostratigraphical comparative table of Sergipe/Alagoas, Recôncavo/Tucano and Campos Basins for Alagoas and Jiquiá Stages.

CORRELATION SECTIONS

Biozones were used exclusively to construct the five sections which illustrate this paper. The choice of sea level as datum means that the biozones are shown as they occur at present, affected by all the tectonic disturbances in the basin. With respect to these sections, the following remarks can be made:

1) Zone 011, corresponding to the Alagoas stage, generally encompasses sedimentary sequences with regular thicknesses along the study area. A tendency for it to thin southward was observed and it is completely absent in the section E-E′.

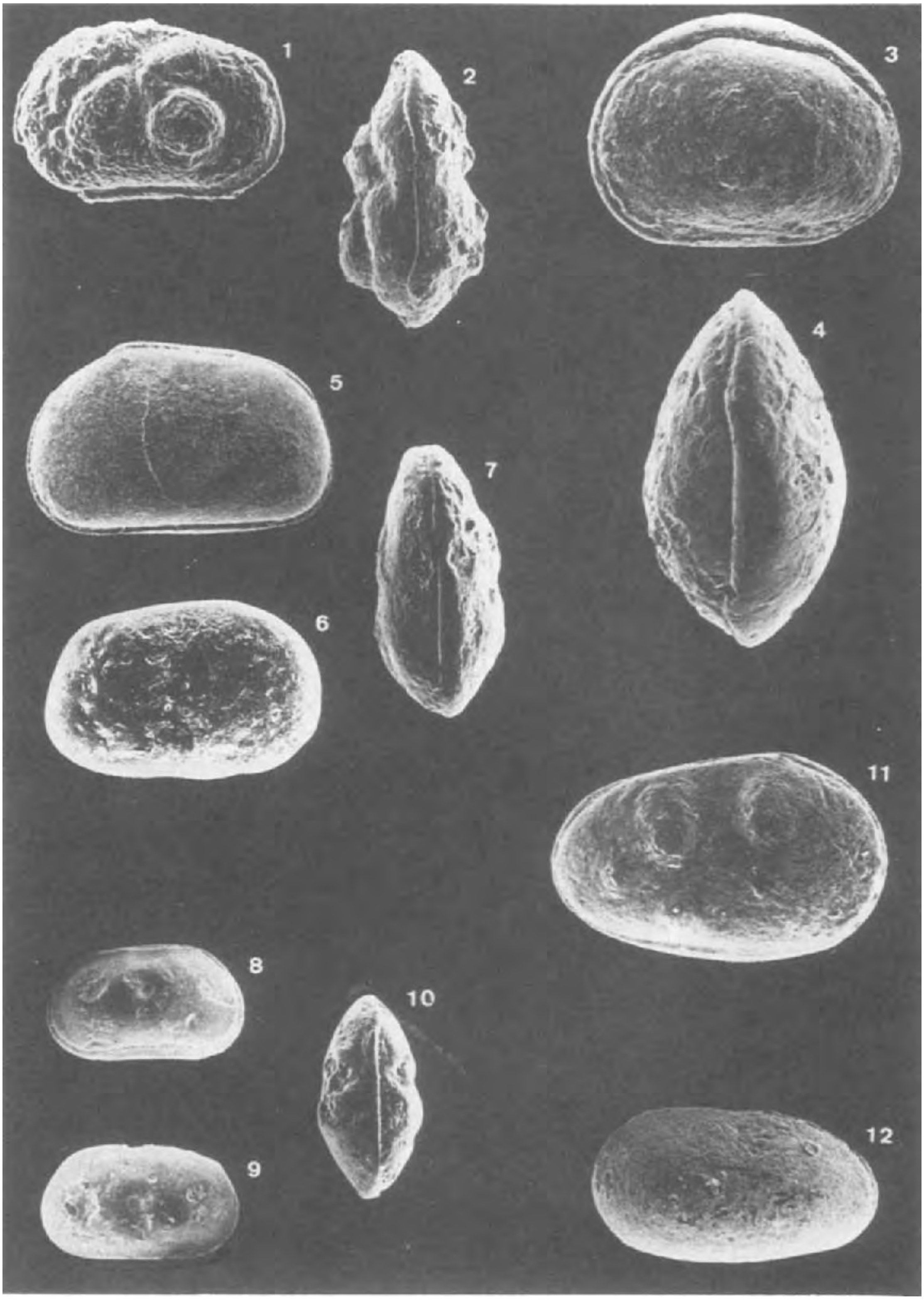
2) Zone 010 has an intermittent occurrence throughout the study area. It tends to disappear in the southernmost part of the basin.

3) Subzone 009.3 is geographically the most widely distributed biozone, encompassing the thickest sequences along the study area.

4) Subzone 009.2 occurs as the thinnest and most sporadic sequence in the Campos basin.

5) Subzone 009.1 is more regularly distributed in the southernmost portion of the study area, represented by the section E-E′.

PLATE 1—Figs. 1, 2. Ostracoda sp. 406. 1. left valve, 1-RJS-117A, 5100–5115m; 2, dorsal view, 1-RJS-119A, 5070–5085m. Figs. 3, 4. *Reconcavona* aff. *R. bateke*. 3, left valve, 1-RJS-65, 3065–3,075; 4, dorsal view, 1-RJS-135, 4,740-4,755m. Figs. 5–7. *Limnocypridea subquadrata*. 5, left valve, 1-RJS-102A, 4,860–4,875m; 6, right valve, 1-RJS-135, 4,440–4,445m; 7, dorsal view, 1-RJS-117A, 5100–5115m. Figs. 8–10. *Limnocythere troelseni*. 8, right valve, 1-RJS-102A, 4,710–4,725m; 9, left valve; 10, dorsal view, 1-RJS-102A, 4,650–4,665m. Fig. 11. *Cypridea* (*Sebastianites*) aff. *C.* (*S.*) *fida fida*, right valve, 1-RJS-131, 4,410–4,155m. Fig. 12. *Bisulcocypris postangularis postangularis*, right valve, 1-RJS-131, 4,140–4,155m. (magnification ×33).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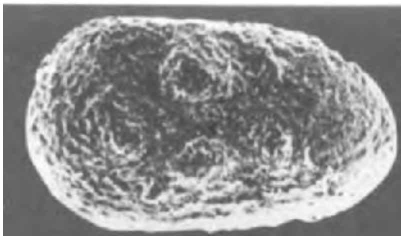
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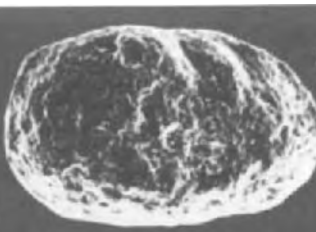
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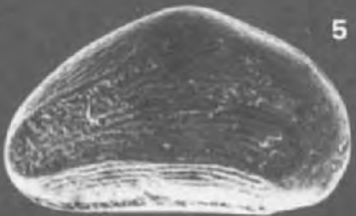
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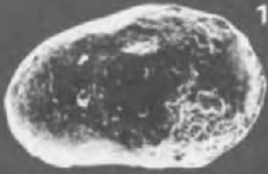
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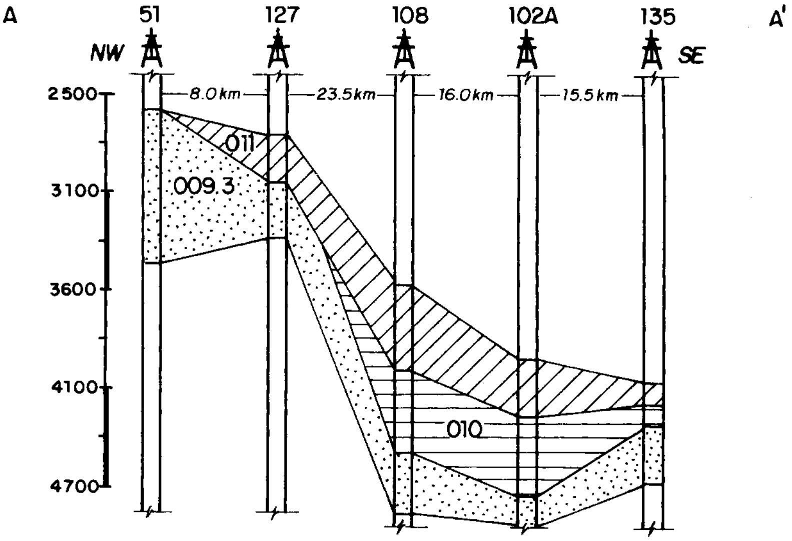
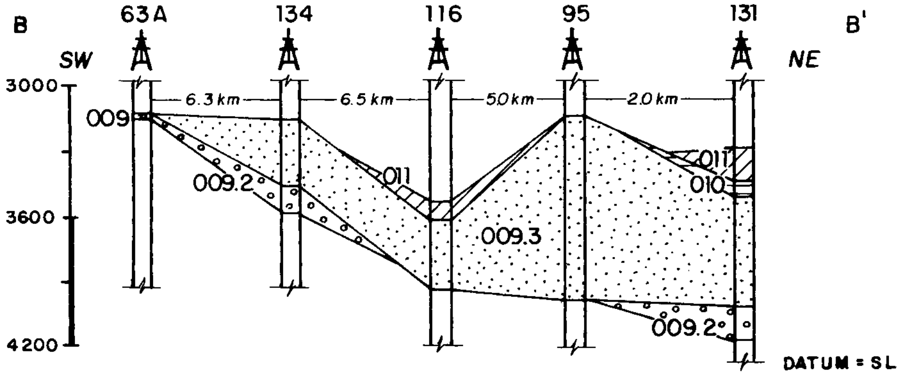


Text-fig. 4—Correlation section A-A′ (Biostratigraphical units, Campos Basin).

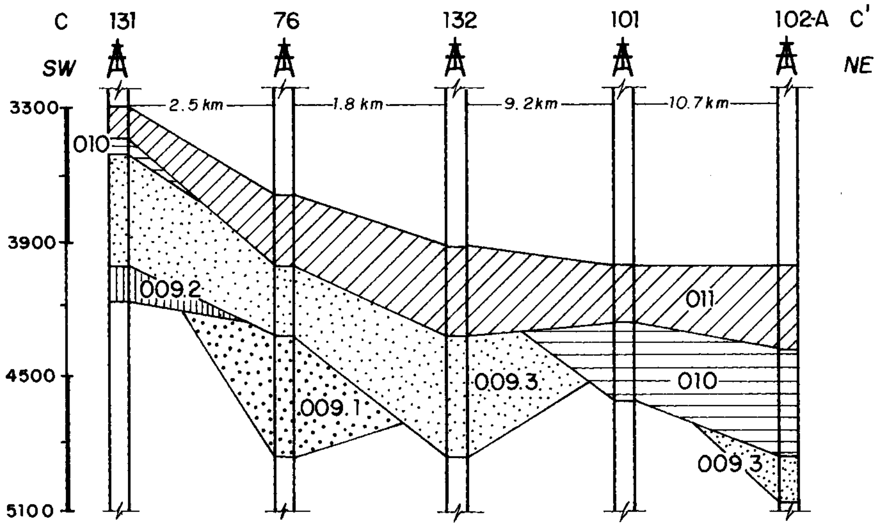


Text-fig. 5—Correlation section B-B′ (Biostratigraphical units, Campos Basin).

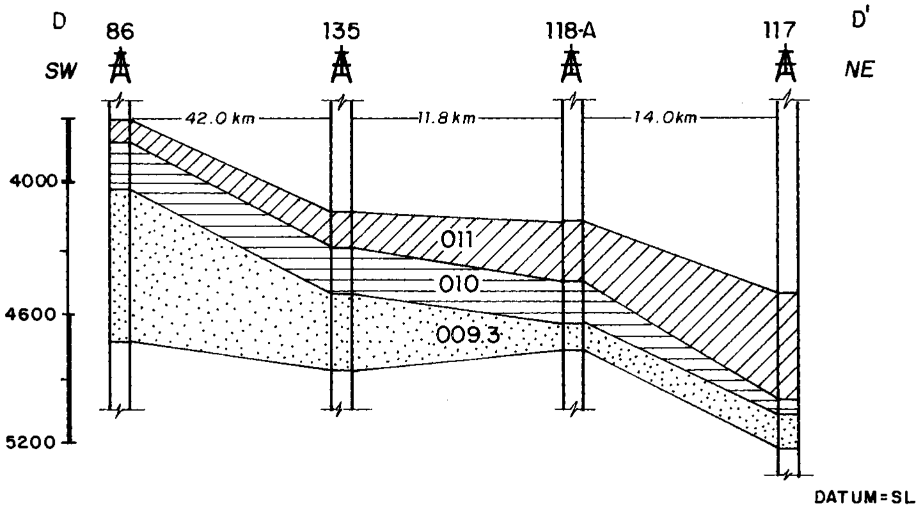
Age

Originally formalized in the Recôncavo/Tucano and Sergipe/Alagoas basins, the Alagoas and Jiquiá local stages have a problematical position in the international time scale, caused by the difficulties in correlating international stages. They are best represented in the Sergipe/Alagoas basin, but they occur in many other continental Brazilian basins, as well as in marginal ones. The best correlation in terms of a continental approach is with west African basins because of their common and peculiar origin.

Plate 2—Figs. 1, 2. *Theriosynoecum papillaris.* 1, right valve, 1-RJS-65, 3,270–3,285m; 2, dorsal view, 1-RJS-65, 3,150–3,165m. Figs. 3, 4. *Theriosynoecum dorsocallosum.* 3, right valve, 1-RJS-73B, 3,090–3,105m; 4, dorsal view, 1-RJS-65, 3,330–3,345m. Fig. 5. *Petrobrasia diversicostata,* right valve, 1-RJS-71, 3,495–3,510m. Figs. 6–14. "*Cypridea*" spp. ex. gr. 201/218. 6, left valve, 1-RJS-116, 3,570–3,585m; 7, left valve, 1-RJS-118A, 4,710–4,725m; 8, left valve, 1-RJS-125, 3,630–3,645m; 9, right valve, 1-RJS-101, 4,110–4,125m; 10, right valve, 1-RJS-118, 4,350–4,365m; 11, right valve, 1-RJS–101, 4,110–4,125m; 12, right, 1-RJS-118A, 4,710–4,725m; 13, right valve, 1-RJS-125m, 3,630–3,645m; 14, right valve, 1-RJS-118, 4,350–4,365m. (magnification ×33).



TEXT-FIG. 6—Correlation section C-C′ (Biostratigraphical units, Campos Basin).

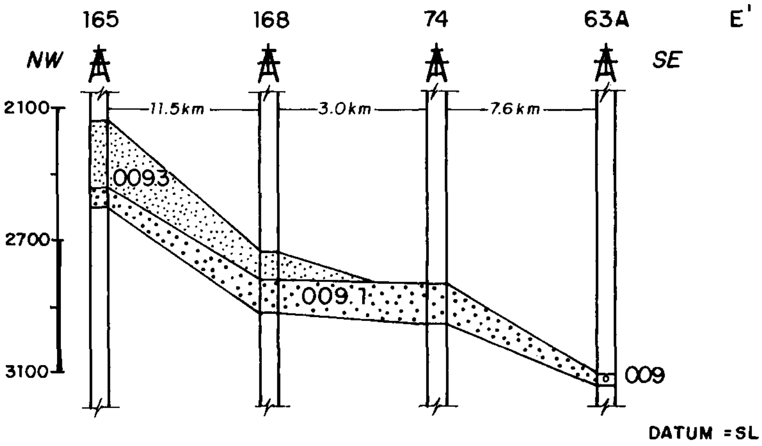


TEXT-FIG. 7—Correlation section D-D′ (Biostratigraphical units, Campos Basin).

The Alagoas stage is considered as at least partially equivalent to the Aptian, and the Jiquiá stage is considered as pertaining to the late Neocomian, more likely to the Barremian. Therefore, it is not out of the question that its youngest portion be accepted as belonging to the Aptian stage.

PALAEOECOLOGY

Using uniformitarian concepts, which must be taken as proposals for interpretation, some palaeoenvironmental inferences were drawn in this work concerning to the faunal content of the biozones of the Alagoas and Jiquiá stages. Caution is needed in adopting those premises, especially when applied to ancient ecosystems such as the ones analysed in this paper. The inferences drawn may be summarised as follows: the Alagoas stage ostracod fauna in the Campos



TEXT-FIG. 8—Correlation section E-E′ (Biostratigraphical units, Campos Basin).

basin consists of a low diversity, and fairly poor, assemblage. Exclusively smooth ostracods, questionably attributed to the genus *"Cytheridea"*, are found in the unique zone (011) of the stage. Associated with them, gastropod and pelecypod shells are recovered at some levels. Marine fossils are absent. This faunal content disappears upward towards the top of the stage, where the palinomorphs persist. Evaporitic beds are found just above this interval, ending a sedimentary evaporitic cycle common to the Brazilian and African Atlantic marginal basins. In view of these data, a transitional lacustrine to lagoonal environment is supposed to have been governing the sedimentary deposition of the Alagoas stage.

The Jiquiá stage, represented by five biozones, shows a different environmental pattern with a tendency for conditions to become brackish to freshwater in the earlier part. Analysing this sequence from top to bottom, zones 010 and 009 are found.

Zone 010, the youngest of the stage, is represented by a monospecific biota, made up of *Limnocythere troelseni*, a small and weakly ornamented species, which indicates an ecosystem where conditions of high stress prevailed, probably as a result of strong variations in the physico-chemical factors. Besides this fact, the intermittent occurrence of this biozone in the study area is observed. The preceding older zone 009, in its youngest subzone 009.3, bears ostracods among which are found some fairly ornamented forms. These ostracods generally possess strong carapaces and are absent in the Recôncavo/Tucaco basin, as is the fauna of the Alagoas stage. Both these faunas represent a sedimentary cycle inhibited in the Recôncavo/Tucano, but present in the Campos, Sergipe/Alagoas and in many other Brazilian and West-African coastal basins.

The lower part of the Jiquiá stage, dated by the oldest part of subzone 009.3 and by the entire 009.2 and 009.1 biozones, contains ostracods which are also found in the Recôncavo/Tucano basin and whose morphological characteristics are the same. These forms indicate a lacustrine-deltaic environment and species of the genera *Cypridea, Bisulcocypris, Theriosynoecum* and *Petrobrasia* are recognized among them.

REMARKS AND CONCLUSIONS

The aim of this work of refining the biostratigraphical zonation in the Campos basin for this interval is justified because of the presence of the best source and reservoir rocks within its boundaries (Estrella *et al.,* 1983).

Work on the recognition of the ostracod biozones established in Recôncavo/Tucano and Sergipe/Alagoas basins has been continuous in almost all the basins of the Brazilian continental margins. This has contributed to the understanding of its geological evolutionary history and improved the stratigraphical correlation of these basins.

ACKNOWLEDGEMENTS

The author expresses his gratitude to Petrobrás' management for permitting the presentation and publication of this work and acknowledges the suggestions and comments of his colleagues Diams Dias-Brito, Jorge Carlos Della Fávera and Jonas dos Reis Fonseca. He is grateful to Hélio Sá Brito and the photographic laboratory personnel for technical work in connection with the plates. The author also gratefully acknowledges the help of all those colleagues who have contributed to this paper.

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DISCUSSION

Athersuch: Do you consider your biozones to be truly chronostratigraphical or are they strongly influenced by facies? Do you have a good correlation between your biozones and seismic markers?

Moura: We have recently been concerned with this question. I would say that it depends on the observed time scale. Great events reflect changes in the environment and the ostracods mark time lines in this case. The several extinction levels are time lines and the recurrence of species was never observed. In response to your second question, ostracods are certainly well correlated with electric markers. I believe that good seismic reflectors are well correlated with ostracod time lines.

Ostracod Evolution and Depositional Characteristics of the Cretaceous Nenjiang Formation in the Songliao Basin, China

DE-QUAN YE
Research Institute of Exploration and Development, Daqing Petroleum Administration, P. R. China

ABSTRACT

In the Cretaceous Songliao Basin, the Nenjiang Formation is the best-developed and is overlain by the Sifangtai Formation and underlain by the Yaojia Formation. The Nenjiang Formation is more than 1000 m thick and forms a great area of dark mudstone and sandstone, where the oil-bearing beds of the Heidimiao and Shaertu reservoirs Sa-1-Zu and Sa-O-Zu are located. The formation changes little both in lithology and thickness and mainly consists of grey-dark mudstones, shales and oil-shales, grey-green mudstones, intercalating grey, grey-white fine silt sandstones and red mudstones at the upper part of the formation. Upwards, the Nenjiang Formation becomes finer in grain size and richer in fossils. Overall, the Nenjiang Formation can be divided into five successive members based on the vertical changes in lithology and fossil ostracods.

During recent years, secondary exploration in the Songliao Basin has taken place. The Hiedimiao reservoir of the Nenjiang Formation is of great interest to the oil industry and as a result, palaeontologists have also done a great deal of work on it, especially detailed work on ostracods.

OSTRACOD ZONATION OF THE NENJIANG FORMATION

Ostracods are common in the Nenjiang Formation. Their vertical and horizontal distribution has been understood through identification and statistics based on more than 2,800 specimens. According to the regular ostracod distribution, diversity and abundance, the ostracods from the Nenjiang Formation have been divided into sixteen fossil zones and correspondingly placed in seventeen beds (Table 1). The fossil ostracod zones can be used for comparison over the whole basin, and consequently, provide a palaeontological basis for further studies on the sedimentary facies of the Nenjiang Formation and for the subdivision of the Heidimiao oil-bearing reservoir.

From the characteristics of the fossil zonation, not only have the ostracod bearing strata been divided into seventeen beds, but it has also been established that the range of the ostracod species in most of the zones is very short. Some genera and species are limited to one fossil zone where they pass through all the different evolutionary stages—first appearance, development acme and extinction.

TABLE 1—THE STRATIFICATION OF FOSSIL OSTRACOD ZONES IN THE NENJIANG FORMATION.

Member		Reservoir	Oil-bearing Zu (bed)	sub-bed	Fossil ostracod zonation
Fifth	2			2	*Cypridea spongvosa* *Cypridea magna*
	1			1	*Harbinia hapla*
Fourth	2	Heidimiao oil-reservoir	Hei-1-Zu	2	*Ilyocyprimorpha inandita*
	1			1	*Cypridea augusta*
Third	4		Hei-2-Zu	4	*Cypridea arca*
	3			3	*Cypridea liaukhenensis* *Limnocypridea datongzhenensis*
	2			2	*Ilyocyprimorpha salebrosa*
	1			1	*Limnocypridea nova*
Second	3			3	*Ilyocyprimorpha portentosa* *Cypridea ordinata*
	2			2	*Ilyocyprimorpha netchaevae* *Cypridea bella*
	1			1	
First	6	Shaertu oil-reservoir	So	Upper	*Cypridea gunsulinensis, Cypridea Gunsulinensis* var. *carinata*
	5			Lower	*Cypridea gracila* *Cypridea ardua*
	4		Intercalation of So/S1		*Lycopterocypris mediocris* *Lycopterocypris vatida*
	3		S_1		*Cypridea anonyma*
	2		Intercalation of S1/S2	Upper	*Cypridea spiniferusa* *Cypridea turita*
	1			Lower	*Cypridea squalida* *Advenocy prisdeltoideus*

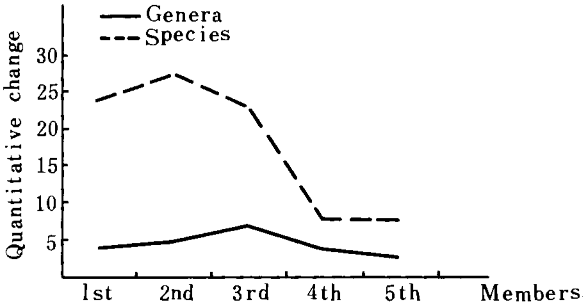
EVOLUTIONARY CHARACTERISTICS OF FOSSIL OSTRACODS IN THE NENJIANG FORMATION

After the transgression seen in the Qingshankou Formation and the regression of the Yaojia Formation, the Nenjiang Formation represents a new transgression in the Cretaceous Songliao basin. With the changing environment, the ostracod ecology of the Nenjiang Formation also changed considerably. Evolution clearly occurred in such features as the number of genera and species, the abundance of individuals, the development of ornamentation, etc.

Characteristics of the Evolution of Genera and Species

With the new transgression during the period of deposition of the Nenjiang Formation following the Yaojia regression, great changes happened in the variety and number of ostracod genera and species, of which there are more than in the Yaojia Formation, deposited at a time of regression.

The basin transgression began with the deposition of the 1st member of the Nenjiang Formation, when the ostracod fauna consisted of 24 species and 4 main genera: *Cypridea, Lycoptero-*



TEXT-FIG. 1—Showing the quantitative change in ostracod genera and species of the Nenjiang Formation.

cypris, Advenocypris, Kaitunia. Generally, these ostracods had relatively thick shells and occurred abundantly. Their shells were often concentrated in layers and preserved as oolitic-biostromal limestones.

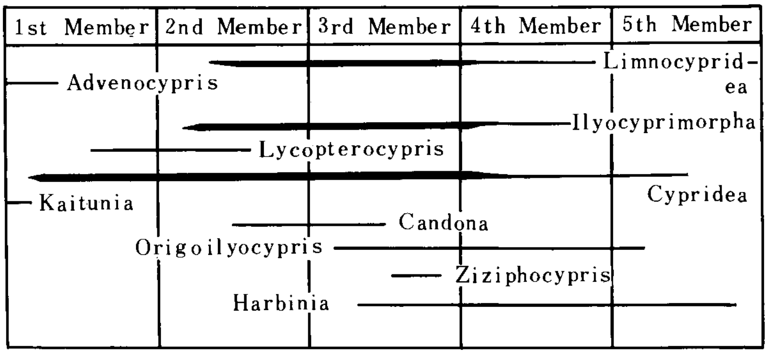
During deposition of the 2nd member of the Nenjiang Formation, the transgression reached its maximum extent. Ostracod genera and species quickly increased to 27 species and 5 main genera—*Cypridea, Limnocypridea, Ilyocyprimorpha, Lycopterocypris* and *Candona,* most of which have thin shells and the often preserved as single valves.

During deposition of the 3rd member of the Nenjiang Formation, the water in the basin began to decrease while the ostracods continued to prosper with an increasing number of genera. There are seven main genera—*Cypridea, Ilyocyprimorpha, Limnocypridea, Origoilyocypris, Candona, Ziziphocypris* and *Harbinia*—which include 23 species. These ostracods are often preserved as single valves of different sizes with thick walls and varied surface ornamentation.

In the period of deposition of the 4–5th members of the Nenjiang Formation, the basin entered its main contraction stage when it gradually became narrower with an obvious decrease both in the number of ostracod genera and species and in the number of individuals. In the 4th member, the four main genera are *Cypridea, Oligoilyocypris, Ilyocyprimorpha* and *Harbinia.* The total number of species from the two members is more than eight. The ostracods are preserved as complete, thick-walled carapaces with clear ornamentation.

From the changing variety and quantity of the ostracod genera and species, the Nenjiang Formation ostracods clearly passed through a complete evolutionary cycle from first appearance developing-prospering to declining (Text-fig. 1).

There is a correspondingly changing relationship between the variety and quantity of ostracods and the depositional cycle of the basin from developing to shrinking. The greatest development of the basin coincides with the most favourable time for expansion of ostracods; and the beginning and end of the basin correspond with ostracod origin and decline respectively. The evolution of the Nenjiang Formation ostracods followed the developing process of the basin through generation to development to decline. With the basin transgression beginning during deposition of the 1st member of the Nenjiang Formation, the ostracods started to develop. With the beginning of deposition of the 2nd member of the Nenjiang Formation, the basin transgression reached its maximum extent. At that time, the basin was quiet with relatively deep water where the ostracods developed and prospered. With deposition of the 3rd member of Nenjiang Formation, the basin regression began, but the ostracods were still numerous. During deposition of the 4–5th members, the basin contracted and the ostracods declined correspondingly, being very limited in distribution. The number of ostracods decreased greatly, especially in the 5th member of the Nenjiang Formation (Text-fig. 2).



TEXT-FIG. 2—Diagram showing the vertical evolution of the ostracods from the Nenjiang Formation.

Evolutionary Characteristics of Ostracod Ornamentation

Ecological characteristics of an organism can sometimes be shown by its fossils and can also indicate the environment where the organism lived. Different environments have different inhabitants. Different states and features of an organism, such as its development, acme, decline and extinction, its ornamentation and preservation, etc., are more or less controlled by such factors as the basin size, the water depth, temperature, turbulence, oxidation-reduction conditions, basin floor deposits, and the organic richness of the sediments, etc. Therefore, the sedimentary facies, the reconstruction of the palaeogeographical environment and the fossil evolution can be indicated by studies on the ornamentation of fossil ostracods.

One of the characteristics of the Nenjiang Formation is its richness in various fossil ostracods with complex ornamentation. Thus, the ostracods from the Nenjiang Formation are well-developed. To summarise, the ostracod ornamentation of the Nenjiang Formation evolves in two patterns: one is from punctate to reticulate; the other is from nodular to spinose to nodose.

Punctate—reticulate pattern

During the period of deposition of the 1st member of the Nenjiang Formation, with the beginning of the basin transgression, the ostracods of the Nenjiang Formation began to appear. At that time, only a few genera and species existed, such as *Advenocypris definita, Cypridea turita*, etc. These ostracods mainly belong to the type with smooth or fine punctate ornamentation.

In the 2nd member of the Nenjiang Formation, with the extension of the basin, the ostracods entered their most flourishing period when a large number of punctate ostracods such as *Cypridea liaukhenensis*, *Cypridea spongvosa*, etc. existed. Their carapaces were large and thin with coarse punctae, and they are well-preserved, but mainly as single valves.

The environment of deposition of the 3rd member of the Nenjiang Formation was basically similar to that of the 2nd member. Some of the punctate ostracods of the 2nd member also continued during deposition of the 3rd member, although the ostracods of the 3rd member were fewer in number with smaller punctae than those of the 2nd member. These facts indicate that the 3rd member was deposited at a time when the basin was contracting.

During deposition of the 4th member, the punctate ostracods became much fewer and their punctae were much smaller and clearer than before. The coarsely punctate species such as *Cypridea liaukhenensis* disappeared.

By the time of deposition of the 5th member, the ostracods had evolved from the puncta-ornamented into the puncta-reticulate or striate forms. This variation indicates that the ostracod living environment was becoming shallower. Because of the limited occurrence of the reticulate ostracods, it is assumed that the basin bottom was undulating and separated.

Nodose—spiny-nodose—nodose pattern

This evolutionary pattern of ostracod ornamentation is from nodose to spiny-nodose to nodose. It is inferred that this is due to the change in the ostracod living environment.

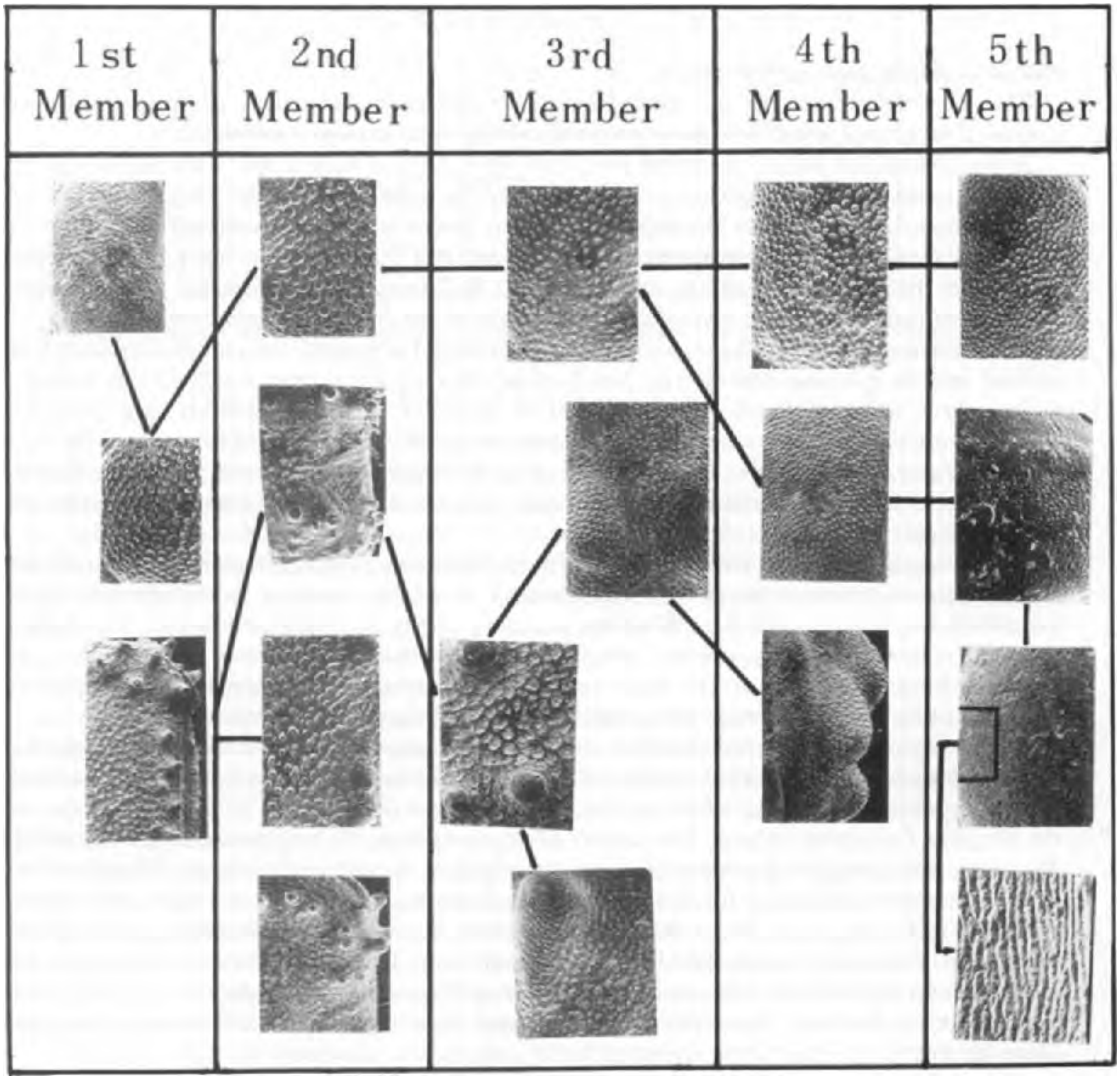
In the intercalated beds in the upper part of the Sa-1 and Sa-2 beds of the Nenjiang Formation, a nodose species, *Cypridea spiniferus,* is ornamented by nodes only on the marginal surface of the shell, occurs. The fact that the population of this species is low and its vertical distribution is very short shows that the basin transgression extended and that the basin water became deeper than before the period of deposition of the Sa-1 and Sa-2 beds. The development of the nodose-ornamented ostracods was caused by their adaptation to the deep water environment.

During deposition of the 2nd member of the Nenjiang Formation, the nodose ostracods had evolved into the spine-like nodose type. This kind of ostracod was characterised by many varieties and numbers, with well-developed ornamentation. Some of them had relatively long spine-like nodes at an oblique angle to the anterior or posterior end of the carapace. These ostracods, such as *Ilyocyprimorpha netchaevae, Cypridea bella, Ilyocyprimopha portentosa* and *Cypridea ordinata,* etc. are rather large with thin shells. Their existence indicates a calm and deep water environment in a large basin.

During deposition of the third member, the spine-like nodose ostracods generally evolved into nodose types of ostracods which were characterised by a large carapace, preservation as single valves and a different morphology of nodes, including circular, ridged and flowered. The species include *Ilyocyprimorpha sungarinensis, Ilyocyprimorpha salebrosa, Ilyocyprimorpha magnifica* etc. Their occurrence indicates that the basin was a shallow water environment and the develop ment from spine-like nodes to nodose ornamentation resulted because of the environment.

During deposition of the 4th member, the ostracod nodose ornamentation became simpler than that found in the 2nd and 3rd members. Only simple nodose ostracods such as *Cypridea augusta* and *Ilyocyprimorpha inandita,* which survived from the time of deposition of the 3rd member of the Nenjiang Formation, existed. The number of ostracods from the two members was very small. The water-body available for ostracods was rather shallow, narrow and turbulent. Therefore, the environment was unfavorable for ostracods to flourish. By the time of the 5th member, the nodose ostracods had disappeared. Their absence indicates that the water had become much shallower than before. Only simply ornamented ostracods could exist. Thus, the evolution of the nodes on the surface of the ostracod valve during the Nenjiang Formation was regular: the complex node ornamentation developed from the simple type and then regressed to the simple type again (Text-fig. 3).

The relationship between shell ornamentation and the environment is close. Generally speaking, most of the ostracods were smooth at the beginning of the basin transgression. The nodose-spiny type of ostracods were well developed in the depositional period of a lacustrine delta. For a comparatively deep basin, the nodose-ornamented type of ostracod, such as *Ilyocyprimorpha inandita* of the 3rd–4th members, existed in the relatively shallow region, while the spinose type, such as *Ilyocyprimorpha netchaevae* and *Ilyocyprimorpha protentosa* of the 2nd member occurred in the deeper area and the punctate ostracods such as *Cypridea spongvosa, Cypridea kerioformis,* etc. of the 5th member dominated in the period of rapid basin contraction.



TEXT–FIG. 3—Diagram showing the ornamental evolution of the fossil ostracods from the Nenjiang Formation.

DEPOSITIONAL CHARACTERISTICS OF THE NENJIANG FORMATION

There are three depositional characteristics for the Nenjiang Formation.

The depositional cycle

The Nenjiang Formation was deposited on the Yaojia Formation which belonged to a shallow water littoral facies. At the early-mid stage of basin subsidence, the sediments were dark mudstones of a deep to semi-deep water facies. Entering the mid-late stage, the basin was gradually

TABLE 2—OSTRACOD ORNAMENTATION AND DEPOSITIONAL CHARACTERISTICS OF THE NENJIANG FORMATION.

Horizon	1st Member	2nd Member	3rd Member	4th Member	5th Member
Species quantity	24	27	23		8
Ornamental feature	mainly smooth and punctate	developing various nodes and spines	mainly nodose	mainly punctate, less nodose	punctate and reticulate
Type of organism	planktonic and benthonic	planktonic	benthos and plant	a few organisms–plankton and plant	
Mudstone colours	dark-grey and green	dark	dark and grey	grey–green	green–red
Depositional environment	sub-deep water	deep water	subdeep, shallow and littoral water	littoral-shallow lacustrine and river	
Geochemical environment	reduction-heavy oxrdation	heavy reduction	reduction–weak reduction	weak reduction-oxidation	oxidation

uplifted and became a shallow to littoral lacustrine and river bank facies. This comprised a complete depositional cycle (Table 2).

During the deposition of the 1st member of the Nenjiang Formation, the basin entered its transgressive period when the sediments were dark grey mudstones intercalating with grey-green sandstones, mudstones and siltstones, with horizontal stratification and plenty of fossils which were highly diversified and well-preserved. Except for a few species, such as *Cypridea spiniferusa* and *Cypridea ardua,* the ostracods did not have spiny-nodose ornamentation. Well-preserved ostracods with inflated venters and thick walls indicate that the basin was a deep and stable environment with an abundant fauna and flora where the ostracods flourished.

During the deposition of the 2nd member of the Nenjiang Formation, the basin transgression reached its maximum extent and deposited dark grey mudstones and shales, of which the upper part has thin intercalated beds of grey to grey-white argillaceous sandstones and siltstones; in these strata, 5–15 metres from the bottom of the member there were oil-shales, usually 150–250 metres thick, with well-developed lamination. The 2nd member was rich in fossils such as ostracods, conchostracans, molluscs and plants (Table 3).

A special fossil ostracod assemblage occurred in the 2nd member. This assemblage was characterised by a great number of species high in diversity and of varied morphology. The species had small spines, nodes, ridges, depressions and pits on the shell surface. They were *Cypridea*? *dissona, Ilyocyprimorpha netchaevae, Cypridea ordinata,* etc. In the 2nd member, the ostracod morphology shows that there was a certain change in the ostracod habitat after the 1st member of the Nenjiang Formation had been deposited. A relatively quiet, deep water environment was suitable for the ostracods to flourish. The ostracods of the 2nd member amount to 16% of the total species from the Cretaceous.

Overlying the transgressive sediments of the 2nd Member of the Nenjiang Formation is the 3rd member which consists of three inverse grading layers and covers a vast ranging area. The lithology varies greatly. From bottom to top the sediments become coarser and include dark grey mudstones and grey to grey-white argillaceous sandstones and sandstones. They reach 60–100 m in thickness and contain a great number of ostracod fossils. This 3rd member of the Nenjiang Formation contains such species as: *Cypridea bella, Cypridea liauhenensis, Cypridea*? *dissona, Ilyocyprimorpha magnifica, Ilyocyprimorpha datongzenensis, Limnocypridea harbinensis,* etc. Characteristically, they are similar to those of the 2nd member. As regards palaeoecology, the ostracod habitats of the

TABLE 3—STATISTICS ON MAINLY AQUATIC GENERA FROM THE CRETACEOUS IN THE SONGLIAO BASIN.

Classification Horizon	Ostracods	Conchostracans	Gastropods	Bivalves	Fishes	Charaphytes
			Number of Genera			
Mingshui Formation	7	1	2	3		17
Sifangtai Formation	9		2			22
Nenjiang Formation	14	22	17	10	4	13
Yaojia Formation	5	4		2	1	8
Qingshankou Formation	8	14	1	4	1	8
Quantou Formation	6	1		2		12

3rd and 2nd members were similar to each other. Presumably, during the deposition of the 3rd member, the basin was still a fairly large and stable environment. The ostracods had a wide distribution, were abundant and highly diverse. They were ornamented by various nodes, ridges and spines. Compared with those of the 2nd member, the ostracods of the 3rd member had more nodes and less spines. This fact indicates that the 3rd member was deposited in a period of slow regression following the maximum transgression during the 2nd member.

During the period of deposition of the 4–5th members, the waters were still regressing and the sediments mainly consisted of grey–green sandstone and interbeded mudstone of which the lower part had more dark mudstone; red and variegated mudstones increased upwards. The sandstones and mudstones of the two members are positively graded with a maximum thickness of 613 metres. From the 4–5th members, only a few fossils have been obtained with a limited distribution. The ostracod species and genera are simple and relatively poorly preserved. A few fossils are

TABLE 4—RELATIONSHIP BETWEEN BASIN SIZE AND OSTRACOD MORPHOLOGY IN THE NENJIANG FORMATION.

Basin change Characteristic	Large Deep	Basin ········> ········>	Small Shallow
Node-spine	Thickening Spine ········>	Bar-like node	Thickening ········> Node
Puncta	Deep Large	········> ········>	Shallow Small
Shell thickness	Thin	········>	Thick
Diversity	Low ········>	High········>	Low
Morphology	Trapezoic ······ Quadrate ······ ··>	Elliptic········>	Subtriangular
Ratio of length to thickness of the carapace	Large	········>	Small
Preservation	Poor ········>	Good ········>	Poor
Quantity	Less ········>	More ········>	Less

ornamented by nodes and spines and are small in size. All of these features indicate that the ostracod environment changed greatly during deposition of the 4–5th members, the basin water becoming shallow, turbid and unsuitable for the organisms to thrive. Because of their limited distribution and low diversity, it is assumed that the depositional area became smaller and more separated. The sediments belong to shallow littoral-lacustrine and river sedimentary facies.

Based on the depositional characteristics and ostracod features mentioned above, the depositional environments of the Nenjiang Formation are thought to be as follows: a sub-deep water lacustrine facies for the 1st member; a deep water facies for the 2nd member; a sub-deep-littoral shallow water facies for the 3rd member; and a littoral lacustrine-river facies for the 4–5th members. With the change in the depositional environments of the different members and the basin expanding and contracting, the ostracod morphology changed greatly (Table 4).

Relative rates of deposition

The rate of deposition of the Nenjiang Formation was rapid, since more than 1000m of strata were deposited in a short geological time. The main bases for this conclusion are:

1) The number of ostracod fossils in one gram of sample is generally as follows (details are shown in Table 5):

2nd and 3rd members of the Qingshankou Formation	8–250/g
2nd–3rd members of the Yaojia Formation	4–120/g
1st member of the Nenjiang Formation	0.2–70/g
2nd–5th members of the Nenjiang Formation	0.1–10/g

The above statistics show that the number of ostracods from the Nenjiang Formation is less than one tenth of that from the Qingshankou and Yaojia Formations. What may have caused this could be that during the depositional periods of the Qingshankou and Yaojia Formations, no subaqueous deposition occurred when a great number of ostracod carapaces were cemented by carbonate and formed nearly pure biostromal limestones or calcareous beds. This is a feature of lacustrine deposition.

2) As for the vertical stratigraphical distribution of the main species of ostracods, those in the Qingshakou and Yaojia Formations generally range over some 10–80m, while those in the Nenjiang Formation have ranges from 20–450 m. For example, *Cypridea liaukhenensis* lasted from the 2nd member to the 3rd member, while *Cypridea kerioformis* and *Cypridea magna* existed from the upper part of the 2nd member to the 5th member of the Nenjiang Formation. The individual vertical stratigraphical distribution of these ostracods occupied a relatively thick sequence of deposits.

TABLE 5—STATISTICS ON THE NUMBER OF OSTRACODS FROM THE QINGSHANKOU, NENJIANG AND YAOJIA FORMATIONS.

Horizon		Number of fossils in one gram of sample	Statistical sampling number
Formation	Number		
Nenjiang	5th	0.2–8	4
	4th	2–10	12
	3rd	2–18	20
	2nd	2–10	10
	1st	0.2–70	30
Yaojia	2nd–3rd	4–100	20
	1st	1–20	4
Qingshankou	2nd–3rd	8–250	40
	1st	2–10	3

TABLE 6—STATISTICS OF THE LIMESTONES IN THE MID-PART OF THE CRETACEOUS.

	Classification Thickness	Thickness of the limestones (metre)	Stratigraphic thickness (metre)	Thickness ratio of limestones to strata (%)	Limestone developing area
Horizon	Nenjiang Formation	7.1	662	1.1	Taiyuan
	Yaojia Formation	10.4	171	6.1	Gulong
	Qingshankou Formation	61	307	19.9	Yingtai

3) Fewer subaqueous deposition gaps are an indicator of rapid deposition. During the period of deposition of the Nenjiang Formation, only a few layers of calcareous algae and stromatolites occurred at the top of the 2nd member, in the 3rd member and at the bottom of the 4th member. The stromatolites exhibit cone in cone structure 5–10 cm thick, and muddy crystal state with 30% calcium and much argillo-arenaceous matter. There are also a few thin beds of marlstone. Few chemical sediments and biolimestones have been found in the 2nd–5th members, and the oil-bearing assemblage of the mid-part of the Cretaceous is missing. These facts indicate that few subaqueous deposition gaps occurred during deposition of the Nenjiang Formation (Table 6).

Flourishing of organisms other than ostracods

During the period represented by the Nenjiang Formation, all the faunas were well-developed, especially the ostracods and conchostracans which were very common and widely distributed. Conchostraca were preserved in a concentrated layers in the 1st and 2nd members of the Nenjiang Formation. Such a combination of large numbers, wide variety, good preservation and rapid evolution is rarely found anywhere in the world.

A) The absolute-dominance of endemic conchastraca:

The endemic species of the conchostracans, which are only found in this area, account for up to 99% of the total number of specimens. This fact indicates that at that time the basin was not connected with the outside.

B) The distribution of the conchostra-bearing strata, which are relatively concentrated:

The conchostracan fossils of the 2nd and 3rd members of the Qingshankou Formation and the 1st and 2nd members of the Nenjiang Formation, amount to 90% of the total number, while, among them, those of the 2nd member of the Nenjiang Formation comprise 40% of the total.

C) The conchostracan have a short existence, rapid evolution and clear zonation:

Most of the conchostracan species and genera only occur within one fossil zone, *i.e.*, within the period of one fossil zone a species or genus often passes through a complete cycle of origination-development-acme-decline-extinction.

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DISCUSSION

De Deckker: I really enjoyed listening to Mr. Ye's presentation because his observations are similar to those that we have made in Australia. That is, when ostracod shells are thin and spinose and finely reticulated they are formed in deep water. On the other hand, when shells are thick and smooth the ostracods grew in a shallow environment. In the latter environment, charophytes (meaning shallow water) occur too. All these shell architectural differences relate to the PCO_2 in the water and this therefore controls the level of calcite saturation which itself affects ostracod shell building. The availability of calcium carbonate certainly affects ostracod shell building and architecture.

Mr. Ye's remarks are most useful for oil exploration because he has demonstrated the possibility of relating ostracod shell architecture to a particular facies which may be a potential source rock.

Ostracoda Across the Albian/Cenomanian Boundary in Cambridgeshire and Western Suffolk, Eastern England

IAN P. WILKINSON
British Geological Survey, Keyworth, England

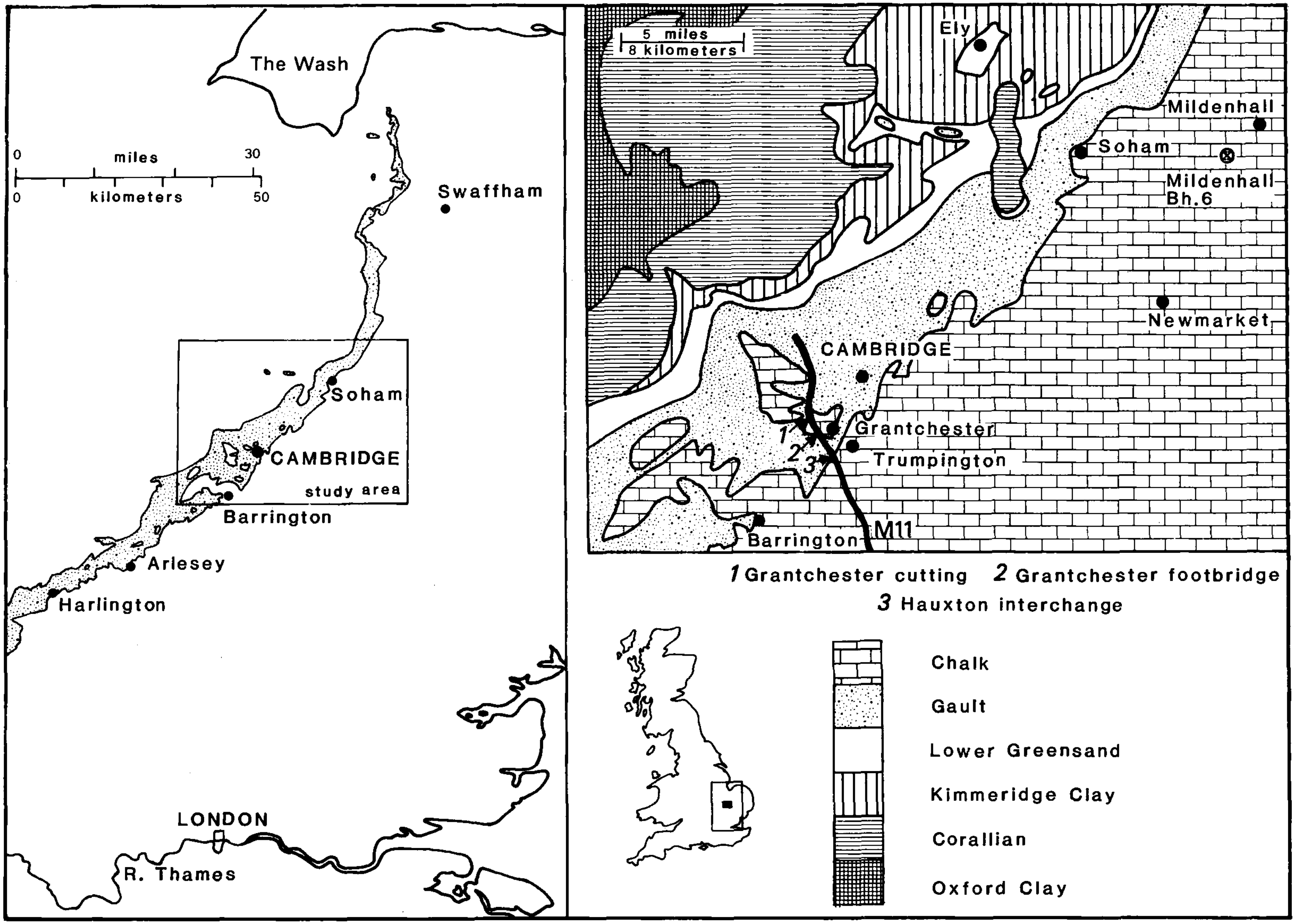
ABSTRACT

Ostracoda from the Upper Gault (late Albian, Lower Cretaceous) and Cambridge Greensand (early Cenomanian, Upper Cretaceous) near Cambridge and Mildenhall, eastern England, are discussed. One genus (*Phthanoloxoconcha*) and one species (*Patellacythere bicostata*) are new. An age of late *Callihoplites auritus–Mortoniceras rostratum* subzones for the highest part of the Gault and early to mid *Neostlingoceras carcitanense* subzone for the Cambridge Greensand is indicated. There is some evidence, however, that the lower part of the Cambridge Greensand in the Mildenhall No. 6 borehole, Suffolk, may fall within the highest part of the Albian.

INTRODUCTION

Towards the close of the Albian, a period of regression initiated erosion of the Gault. Reworking of the top part of the Gault took place and the Cambridge Greensand, a glauconitic sand with phosphatic nodules, was deposited onto the irregular erosion surface. The Cambridge Greensand, which grades upwards into a chalky marl, crops out between Harlington, Bedfordshire, and the Fens of Cambridgeshire and western Norfolk (Text-fig. 1), although exposure is limited. It is rarely more than 0.3–0.6 m thick, but Worssam and Taylor (1969) recorded thicknesses up to about 1.5 m in boreholes.

The stratigraphic age of the Cambridge Greensand has been a matter of contention for over a century. Early work was purely descriptive (Seeley, 1865; Davidson, 1869; Bonney, 1875) and it was not until 1875 that palaeontological work was begun (Jukes-Browne, 1875; Sollas, 1876; Vine, 1888, 1889; Chapman, 1898, 1899). Penning and Jukes-Browne (1881), after mapping the Cambridge area for the Geological Survey of Great Britain, concluded that the Cambridge Greensand was Cenomanian in age and this was later confirmed by Reed (1897). Spath (1923–1943) disagreed with the conclusions of the nineteenth century workers and, on the basis of the ammonites, believed the deposit to be of Upper Albian age, with faunal elements from the *Mortoniceras aequatorialis, Arrhaphoceras substuderi* and *Mortoniceras perinflatum* subzones (in modern terms the highest part of the *Callihoplites auritus, Mortoniceras rostratum* and *M. perinflatum* subzones). Breistroffer (1940, 1947), however, placed the deposit into the lower Vraconian, a view supported by Casey (in Edmonds and Dinham, 1965) who was sceptical about the provenance of the specimens of *Schloenbachia* which Cookson and Hughes (1964) used to suggest a basal Cenomanian age. He also considered that the conclusions of Peake and Hancock (1961), who regarded the brachiopod fauna as also indicative of that age, required further investigation.



TEXT-FIG. 1—Sample localities and geological sketch map of the study area.

Foraminiferal assemblages from the Upper Gault and Cambridge Greensand of Barrington and Arlesey were examined by Hart (1973a), Primarily on the basis of the lack of planktonic foraminifera in the 250–500 micron sieve fraction, Hart argued that the highest Gault at Barrington and Arlesey is of the *C. auritus* Subzone, confirming Casey's (1965) reinterpretation of Fearnside's (1904) material. This age determination was later modified by Carter and Hart (1977, p. 75) who placed the top of the Gault in the area within the *A. substuderi* Subzone (*i.e.* the *M. rostratum* Subzone of Owen, 1976). These same authors assigned the top of the Gault to benthonic foraminifera zone 6i on figure 18 (p. 72, 73), but did not define the zone (they refer only to zones 6 and 6a in the text). However, Hart's (1973b) concept of benthonic foraminifera zone 6i would place it in the upper part of the *C. auritus* Subzone. The cause of this apparent anomaly appears to be due to the incomplete succession at Folkestone, the section on which Hart relied heavily for his benthonic foraminifera zonal scheme. The first occurrence of certain index species (*e.g. Globigerinelloides bentonensis*) is at a higher stratigraphical level at that locality compared to other sequences in southern England (*e.g.* Glyndebourne Borehole) as a result of the non-sequence below Bed XII. Hart (1973a) recovered a mixed late Albian and Lower and early Middle Cenomanian foraminiferal assemblage from the Cambridge Greensand at Barrington. The faunas were not sufficiently diagnostic to provide a restricted age determination for the deposit, but he suggested that the absence of benthonic foraminifera zone 7, which is restricted to the Glauconitic Marl in southern England, and the reduced thickness of zone 8, compared to the Lower Cenomanian Chalk of Kent, indicated that the earliest part of the *Neostlingoceras carcitanense* ammonite Subzone was missing. The upper boundary of the Cambridge Greensand was placed within benthonic foraminifera zone 8 by Hart on the basis of the similarity of planktonic to benthonic ratios of the Lower Chalk at Dover and Barrington.

THE OSTRACODA

The Ostracoda from the Cambridge Greensand of Swaffham were first examined in detail by Chapman (1898), who expanded on and revised the species lists which had been published previously (Sollas, 1872; Vine, 1889; Jones and Hinde, 1890). Kaye (1964) re-examined as many of Chapman's original specimens as were available and, together with additional material from Barrington, systematically described the ostracod assemblage.

Until now there has been no attempt at biostratigraphical analyses using Ostracoda, but investigations into the Albian (Wilkinson and Morter, 1981; unpublished data) and Cenomanian (Weaver, 1982) faunas of southern and eastern England prove distributions which are used as the basis for the present discussion. The significant biostratigraphical events of the interval are illustrated in Text-fig. 2.

Grantchester Cutting (National Grid Reference TL 4200 5626)

Within a drainage trench at this locality, 1.7 m of Gault were seen to be overlain by 0.25 m of Cambridge Greensand which graded up into the Chalk Marl. The clay/greensand junction is an irregular erosion surface and pockets of glauconitic siltstone had accumulated in the hollows (Text-fig. 3.1).

The Gault was sampled approximately 0.6 m below the base of the Cambridge Greensand at which level 22 species and subspecies of ostracod were recovered including *Cythereis* (*Rehacythereis*) *luermannae hannoverana* Bertram and Kemper, *Eucythere* (*Phodeucythere*) *trigonalis* (Jones and Hinde), *Neocythere* (*Neocythere*) *vanveeni* Mertens and *Planileberis scrobicularis* Weaver. The assemblage is typically late Albian and the association of *Cythereis* (*Rehacythereis*) *luermannae* *hannoverana* together with *Planileberis scrobicularis* and the absence of *Cythereis* (*Cythereis*) *folkestonensis* Kaye is indicative of the upper part of the *C. auritus* and the *M. rostratum* subzones, *i.e.* the upper part of the *hannoverana* ostracod Zone (Bertram and Kemper, 1971; Wilkinson and Morter, 1981).

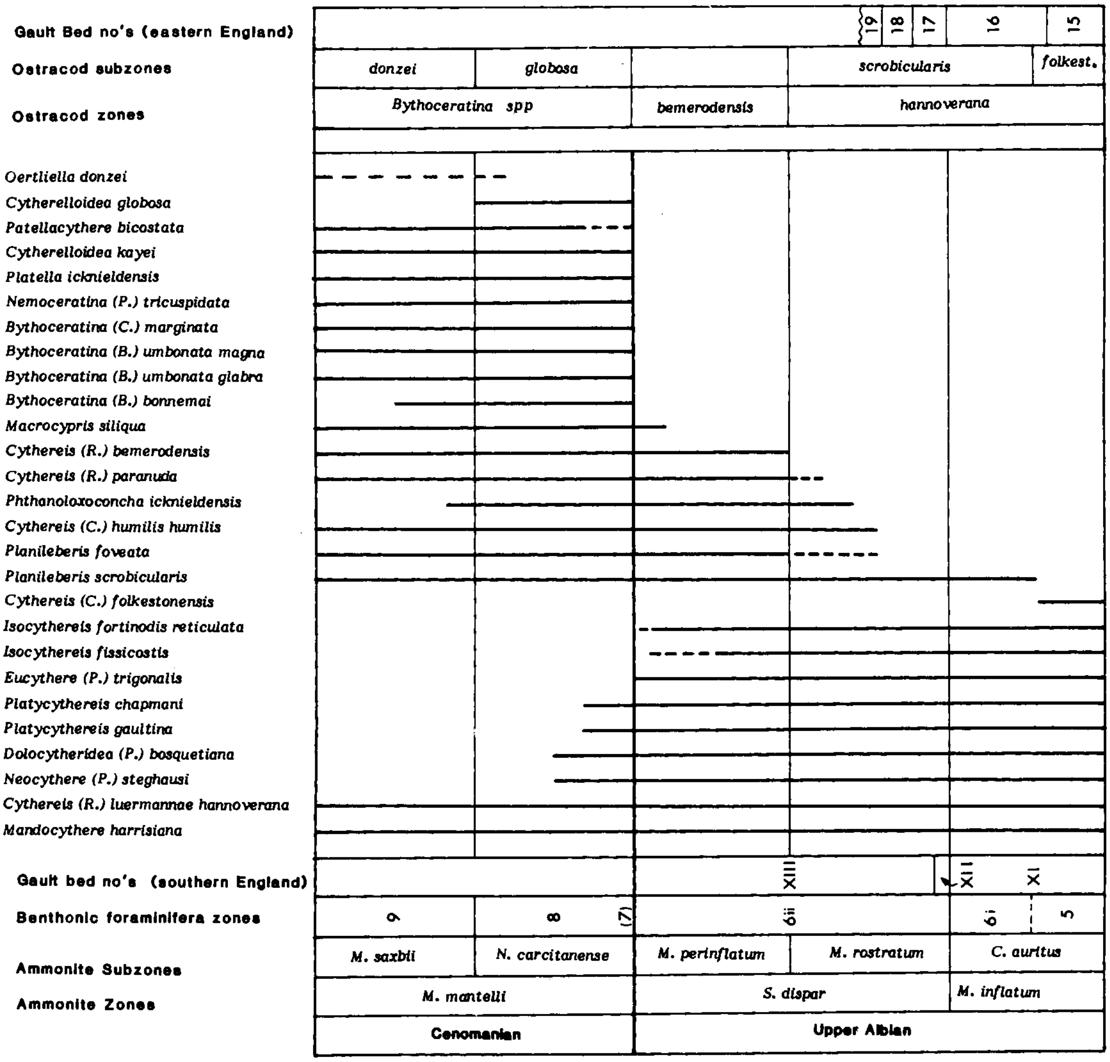
The basal glauconitic siltstone of the Cambridge Greensand contains 11 species in common with the Gault, but 10 further forms are present. Amongst these are *Cythereis* (*Cythereis*) *humilis humilis* Weaver, *Cythereis* (*Rehacythereis*) *paranuda* Weaver, *Cytherelloidea globosa* Kaye, *Bythoceratina umbonata glabra* Weaver and *Planileberis foveata* Weaver. *Cythereis* (*Rehacythereis*) *bemerodensis* was found in small numbers. Bertram and Kemper (1971) used this latter form as an index for the ostracod zone, equating it with the upper part of the *M. rostratum* and *M. perinflatum* subzones in Germany, but later on (Kemper, 1984) this was modified to (?)*M. perinflatum* and *N. carsitanense* subzones. In southern England, it has been found only in the *M. perinflatum* Subzone (at Borrow Pit, near Godstone, Surrey; N.G.R. TO3408 5315) and Cenomanian (Weaver, 1982), but it is not present in the Gault of East Anglia (Wilkinson and Morter, 1981). *Eucythere* (*Phodeucythere*) *trigonalis* becomes extinct within the topmost Albian, but other forms which first develop in the *S. dispar* Zone and cross the Albian/Cenomanian boundary to become extinct within the lower part of the *N. carcitenense* Subzone, were recovered. The extinction level of *Platycythereis chapmani* Kaye and *Neocythere* (*Physocythere*) *steghausi* (Mertens), for example, is in the lower part of benthonic foraminifera zone 8 and that for *Phthanoloxoconcha icknieldensis* (Weaver) is within the lower part of zone 9.

The ostracod fauna from the overlying greensand with phosphatic nodules and the chalky marl is similar to that of the basal siltstone. The presence of *Bythoceratina* (*Bythoceratina*) *umbonata magna* Weaver, *Bythoceratina* (*Bythoceratina*) *bonnemai* (Kaye), *Cytherelloidea globosa* and *Planileberis foveata* Weaver is characteristic of the basal Cenomanian in eastern England. Although *Planileberis foveata* has been recorded from the uppermost *Stoliczkaia dispar* Zone of Kent, that horizon is absent in East Anglia and the species is unknown below the Cambridge Greensand.

Grantchester footbridge (N.G.R. TL 4255 5506)

Overlying 1.22 m of Gault in the footbridge foundations excavation near Trumpington, 0.18 m of glauconitic silt with phosphatic nodules was present (Text-fig. 3.2). A sample of Gault was taken above a phosphatic nodule band 1.2 m below the contact with the Cambridge Greensand. The ostracod assemblage is essentially identical to that found in the Gault of the Grantchester Cutting and the presence of *Cythereis* (*Rehacythereis*) *luermannae hannoverana* and *Planileberis scrobiculata* indicates the upper part of the *C. hannoverana* ostracod Zone and the upper part of the *C. auritus* and *M. rostratum* ammonite subzones. This sample also contains the coccolith *Eiffelithus turriseiffeli* s.s. which extends from Gault Bed 16 (upper *C. auritus* subzone) up into the Cenomanian (A.W. Medd, pers. comm.). The ostracod assemblage recovered from the phosphatic nodule bed that overlies the Gault is also similar to that of the Cambridge Greensand of the Grantchester cutting. *Cythereis* (*Cythereis*) *humilis humilis*, *Cythereis* (*Rehacythereis*) *paranuda*, *Cytherelloidea globosa*, *Planileberis foveata* and *Bythoceratina umbonata glabra* form a characteristic assemblage.

Overlying the Cambridge Greensand is 0.23 m of disturbed sandy clay containing a mixed fauna of Albian and Albo-Cenomanian forms together with rare species restricted to the early Cenomanian. The most likely explanation for the presence of this sandy clay is that it is Gault thrown up during the last century by "coprolite" diggers (A. A. Morter, pers. comm.). This would account for the disturbed nature of the deposit and the intense reworking of the ostracod fauna.



TEXT-FIG. 2—The stratigraphical distribution of some of the more important species of Albian and Cenomanian Ostracoda.

Hauxton Interchange (N.G.R. TL 4363 5348)

Within the cutting dug during the construction of the interchange with the A10, 0.25–0.30 m of Cambridge Greensand was exposed. It overlies pale grey Gault and grades upward into Chalk Marl. The Gault was not examined at this locality, but an assemblage of 25 species of Ostracoda was recovered from the Cambridge Greensand (Text-fig. 3.3). *Planileberis scrobicularis, P. foveata, Cytherelloidea globosa* and *Cythereis* (*Cythereis*) *humilis humilis* are present, but in this locality species of *Bythoceratina* were not recorded. The age of the Cambridge Greensand at this site is no younger than the lower part of the *N. carcitanense* Subzone (lower part of benthonic foraminifera zone 8) as *Platycythereis chapmani, P. gaultina, Neocythere* (*Physocythere*) *steghausi* and *Phthanoloxoconcha icknieldensis* were all recovered.

Mildenhall Borehole No. 6 (N.G.R. TL 6928 7307)

The borehole penetrated the Cambridge Greensand between 51.78 and 52.50 m before entering the Gault, which is 20.04 m thick at this locality. The Cambridge Greensand is thicker here compared to the other localities examined and could be subdivided into a series of beds bounded by erosion levels (as indicated in Text-fig. 3.4).

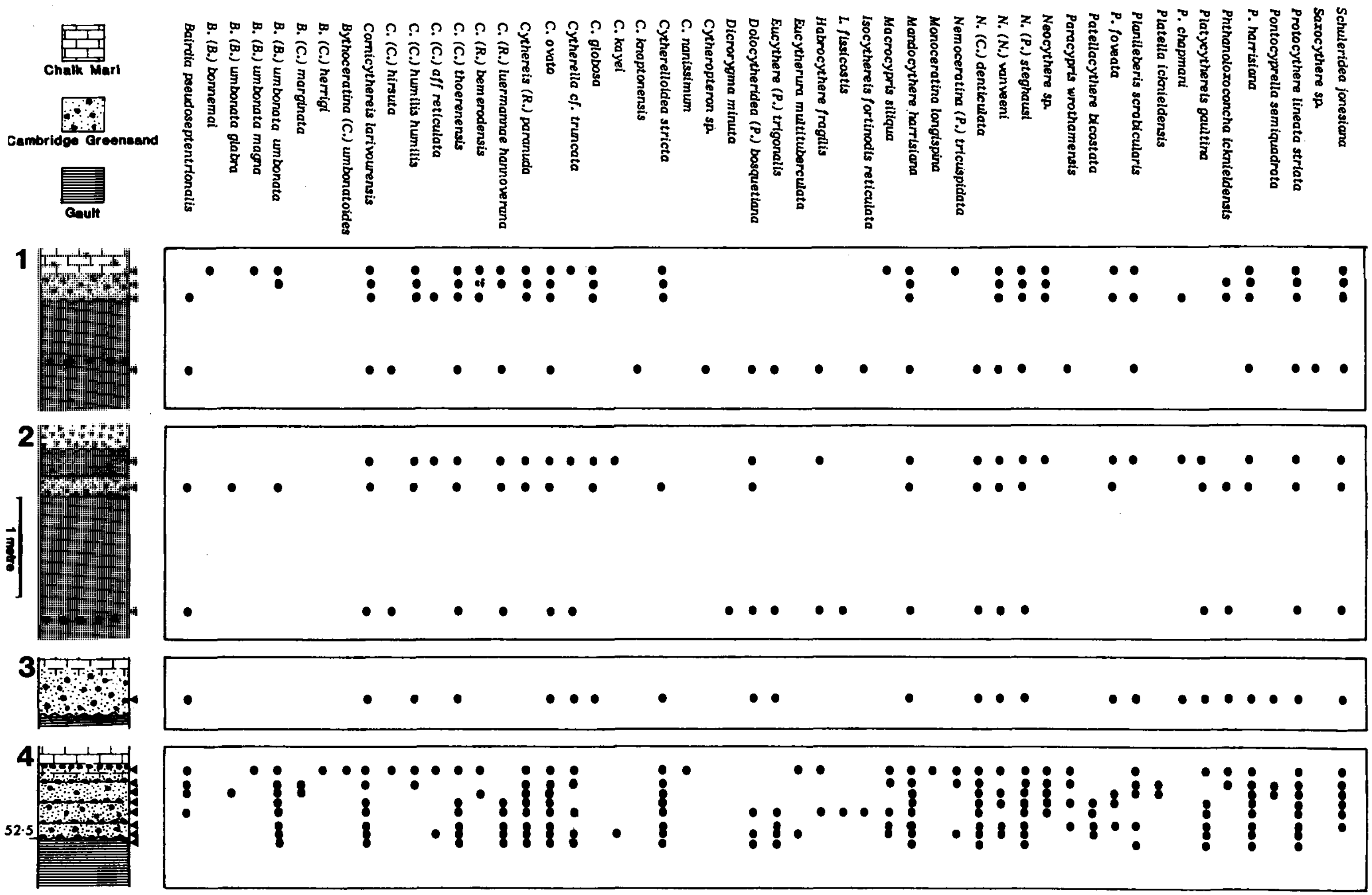
The faunas from the upper part of the Gault and lower part of the Cambridge Greensand (below the erosion surface at 52.12 m) are essentially identical. *Cythereis* (*Rehacythereis*) *luermannae hannoverana, Eucythere* (*Phodeucythere*) *trigonalis* and *Isocythereis fissicostis* are present together with *Planileberis scrobicularis,* but *Cythereis* (*Rehacythereis*) *bemerodensis* is not present. This fauna is indicative of the higher part of the *hannoverana* ostracod Zone, *i.e.* stratigraphically no younger than the *M. rostratum* Subzone of the *S. dispar* Zone. Above the erosion surface at 52.12 m, *Cythereis* (*Rehacythereis*) *bemerodensis* Bertram and Kemper was found associated with several species occuring for the first time, notably *Platella icknieldensis* Weaver and numerous members of Bythocytheridae—*Bythoceratina* (*Bythoceratina*) *umbonata umbonata* (Williamson), *B.* (*B.*) *umbonata glabra* Weaver, *B.* (*B.*) *umbonata magna* Weaver, *B.* (*B.*) *umbonatoides* Kaye, *B.* (*Cuneoceratina*) *herrigi* Weaver, *B.* (*C.*) *marginata* Weaver, '*Monoceratina*' *longispina* (Bosquet) and *Nemoceratina* (*Pariceratina*) *tricuspidata* (Jones and Hinde). This association is very characteristic of the basal Cenomanian.

It would appear, therefore, that in the Mildenhall Borehole 6, where the Cambridge Greensand is more fully developed, the lower part may be of *M. rostratum* Subzone age (Upper Albian). It is interesting to note that *Neohibolites praeultimus* Spath and common oysters are present at the base of the Cambridge Greensand at this locality (Morter and Wood, 1983), as they are in the base of Gault Bed 19 (of Gallois and Morter, 1982) in the Gayton Borehole (N.G.R. TF7280, 1974) (A. A. Morter, personal communication). The presence of ostracod species such as *Platycythereis gaultina* and *Neocythere* (*Physocythere*) *steghausi* suggests that the highest sample examined is no younger than the middle part of benthonic foraminifera zone 8 (middle *N. carcitanense* Subzone). It seems likely that where the deposit is not fully developed, it is the earliest part which is cut out.

BIOSTRATIGRAPHICAL CONCLUSIONS

The *Cythereis* (*Rehacythereis*) *luermannae hannoverana* Ostracod Zone (Upper Albian) of Bertram and Kemper (1971) was defined for eastern England by Wilkinson and Morter (1981). It can be subdivided into two subzones, the earlier one being recognised by the presence of *Cythereis* (*Cythereis*) *folkestonensis* when associated with the zone fossil (equivalent to the lower part of the *C. auritus* ammonite Subzone) and the base of the higher subzone being defined by the first occurrence of *Planileberis scrobicularis* (equating with the upper part of the *C. auritus* and *M. rostratum* subzones) (see Text-fig. 2).

The succeeding ostracod zone was recognised in the upper part of the *M. rostratum* and the *M. perinflatum* ammonite subzones in Germany by Bertram and Kemper (1971). The exact stratigraphical position of the base of the *bemerodensis* ostracod Zone, in terms of the ammonite zonal scheme is, however, uncertain and, as indicated by Morter and Wood (1983), may be approximately equivalent to the *M. rostratum*/*M. perinflatum* boundary. This conclusion was accepted by Kemper (1984) who redefined the zone as earliest Cenomanian and questionably highest Albian (*M. perin-*



TEXT-FIG. 3—The distribution of Ostracoda across the Albian/Cenomanian boundary in Cambridgeshire and western Suffolk (Eastern England). 1, Grantchester Cutting; 2, Grantchester Footbridge; 3, Hauxton Interchange; 4, Mildenhall Borehole no. 6.

flatum Subzone). Wilkinson and Morter (1981) and Morter and Wood (1983) noted that the highest Gault (Bed 19) of the Gayton Borhole contained forms transitional between *C.* (*R.*) *luermannae hannoverana* and *C.* (*R.*) *bemerodensis*, but these were not found elsewhere in eastern England and the interval cannot be placed in the *bemerodensis* ostracod Zone, although it must be very high within the *hannoverana* ostracod Zone. Although the zone is recognisable in the *M. perinflatum* Subzone of Godstone, Surrey (unpublished data), it has not been recognised in the Gault of eastern England, the stratigraphically oldest record being from the Cambridge Greensand.

In the Cenomanian, the association of numerous species of *Bythoceratina* together with *Cytherelloidea globosa* can be used to define an ostracod zone equivalent to the *N. carcitanense* ammonite Subzone and benthonic foraminifera zone 8 of Carter and Hart (1977). In the lower part of the ostracod zone (lower part of the *N. carcitanense* Subzone), *Platycythereis gaultina, P. chapmani, Dolocythereidea* (*Puracytheridea*) *bosquetiana* and *Neocythere* (*Physocythere*) *steghausi,* all of which have their origins in the Albian, become extinct.

The problem in assessing the stratigraphical position of the Cambridge Greensand results from the reworking of faunas from the top of the Gault and, particularly in the case of the Ostracoda, the indifferent preservation. Just below the Cambridge Greensand in Cambridgeshire and western Suffolk, the Gault is of the *C.* (*R.*) *luermannae hannoverana* ostracod Zone, *i.e.* the upper part of the *C. auritus* and *H. rostratum* subzones. Species characteristic of this zone are present in the lower part of the Cambridge Greensand in the Mildenhall Borehole No. 6, but in the upper part of the sequence and in the samples from the M11 Motorway sections, the Ostracoda are indicative of the early and mid part of the *N. carcitanense* ammonite Subzone (basal part of benthonic foraminifera zone 8). It may be that the entire ostracod assemblage in the lower part of the Mildenhall Borehole No. 6 is re-worked into deposits of Cenomanian age, but if this was the case one would expect to find a mixed assemblage. The lack of Cenomanian species can only be explained by invoking a situation where the Albian assemblages were reworked in an interval barren of an indigenous ostracod population.

The base of the Lower Chalk at Grantchester Cutting is also of mid *N. carcitanense* age on the basis of the ostracod assemblage, and the *O. donzei* ostracod zone was not recognised.

PLATE 1—Bythocytheridae and Cytherellidae from the Cenomanian of eastern England. Left valve: lateral views except where stated. Fig. 1. *Monoceratina longispina* (Bosquet, 1854), MPK 4981, Mildenhall Borehole no. 6, Cambridge Greensand, depth 51.85 m, length 600 μm, height 270 μm. Fig. 2. *Bythoceratina* (*Bythoceratina*) *umbonatoides* (Kaye, 1964), MPK 4982, Mildenhall Borehole no. 6, Cambridge Greensand, depth 51.85 m, length 1000 μm, heigh 480 μm. Fig. 3. *Bythoceratina* (*B.*) *umbonata* (Williamson, 1847), MPK 4983, Mildenhall Borehole no. 6, Cambridge Greensand, depth 51.85 m, length 820 μm, height 370 μm. Fig. 4. *Bythoceratina* (*B.*) *umbonata magna* Weaver, 1982, MPK 4984, Mildenhall Borehole no. 6, Cambridge Greensand, depth 51.94 m, length 860 μm, height 420 μm. Fig. 5. *Bythoceratina* (*B.*) *bonnemai* (Kaye, 1964), MPK 4985, Grantchester Cutting, Chalk Marl, 0.3 m above base of Cambridge Greensand, length 700 μm, height 320 μm, Fig. 6. *Bythoceratina* (*Cuneoceratina*) *herrigi* Weaver, 1982, MPK 4986, Grantchester Cutting, Chalk Marl, 0.3 m above base of Cambridge Greensand, length 710 μm, height 350 μm. Fig. 7. *Patellacythere bicostata* n. sp., Right valve, lateral view, MPK 4987, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.44 m, length 520 μm, height 230 um. Fig. 8. *Nemoceratina* (*Pariceratina*) *tricuspidata* (Jones and Hinde, 1890), MPK 4988, Mildenhall Borehole no. 6, Cambridge Greensand, depth 51.85 m, length 670 μm, height 280 μm. Fig. 9. *Cytherelloidea kayei* Weaver, 1982, Right valve, lateral view, MPK 4989, Grantchester Cutting, Chalk Marl, 0.3 m above base of Cambridge Greensand, length 550 μm, height 330 μm. Fig. 10. *Cytherelloidea stricta* (Jones and Hinde, 1890), Right valve, lateral view, MPK4990, Grantchester Cutting, Chalk Marl, 0.3 m above base of Cambridge Greensand, length 690 μm height 390 μm, Figs. 11, 12. *Cytherelloidea globosa* Kaye, 1964, Grantchester cutting, Chalk Marl, 0.3 m above base of Cambridge Greensand. 11, Right valve, lateral view, MPK4991, length 580 μm, height 340 μm; 12, Dorsal view; MPK4992, length 610 μm width 310 μm. Fig. 13. *Platella icknieldensis* Weaver, 1982, MPK4993, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.0 m, length 710 μm, height 360 μm.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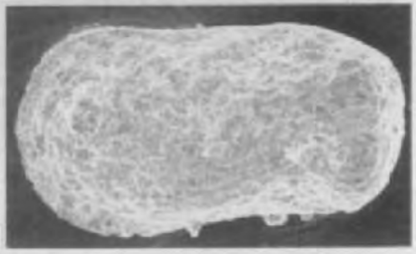
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PALAEOECOLOGICAL CONCLUSIONS

During much of the Late Albian in eastern England, deposition of the Gault and Hunstanton Chalk took place in quiet, shallow, but gradually deepening marine conditions. The regressive regime, which began in the highest (*M. dispar*) zone, led to erosion and the highest subzones are wholly or partly removed (Gallois and Morter, 1982). Accumulation of the Greensand facies began in the *M. rostratum* subzone and continued intermittently into the Cenomanian. The rapid transgression which took place in the Early Cenomanian resulted in the Cambridge Greensand facies rapidly passing up into the Chalk Marl.

Water temperature also increased with the transgressive regimes, the warmer water entering the area from the south when the effect of the London-Ardennes Massif was reduced and the Anglo-Paris Basin was widened (Owen, 1979). It increased slowly through the Upper Albian, but it was not until after the 'Mid-Cenomanian Break' that major temperature increases took place. Other parameters which affected the community (*e.g.* food supply, light, oxygen levels etc.), the physiological stress of Sanders (1969) and Slobodkin and Sanders (1969) and the spatial variability of Valentine (1971, 1973) were such that the community diversity remained high throughout much of the period in question.

The ostracod population responded to the variations in the environment in several ways. Depth related parameters (*e.g.* thermocline, oxygen minima, hydrodynamism or light penetration and related plant life) appear to be important in the case of *Platycythereis, Dolocytheridea* and *Neocythere* (*Centrocythere*) which are considered to be shallow water indicators (Bassoullet and Damotte, 1969; Rosenfeld and Raab, 1974; Babinot and Colin, 1983). Species of *Platycythereis* (*P. gaultina* and *P. chapmani*) are frequently found in the *S. dispar* Zone of the Gault in eastern and southern England, but become rather rare in the basal Cenomanian and extinct in the middle part of the *N. carcitanense* Subzone. *Dolocytheridea* (*P.*) *bosquetiana* is commonly found in the Middle Albian, is somewhat rarer in the Upper Albian and becomes extinct towards the top of the *N. carcitanense* Subzone. Finally, the subgenus *Neocythere* (*Centrocythere*) occurs in large numbers in the Albian, but becomes rare towards the top of the stage, and disappears from the British record in the early part of the *M. saxbii* Subzone (Weaver, 1981, 1982).

Although rare specimens of *Bythoceratina* (*B.*) *umbonata umbonata*, '*Monoceratina*' *longispina* and *Nemoceratina* (*P.*) *tricuspidata* are found scattered throughout the Gault, Bythocytheridae, and particularly *Bythoceratina,* become more diverse in the early Cenomanian. Of the 13 species

PLATE 2—Trachyleberididae from the Albian and Cenomanian of eastern England. Left valve; lateral views except where stated. Fig. 1. *Cythereis* (*Rehacythereis*) *luermannae hannoverana* Bertram and Kemper, 1971, MPK4994, Grantchester Cutting, Gault, 0.61 m below base of Cambridge Greensand, length 1080 μm, height 590 μm. Fig. 2. *Cythereis* (*R.*) *bemerodensis* Bertram and Kemper, 1971, MPK4995, Grantchester Cutting, Chalk Marl, 0.3 m above base of Cambridge Greensand, length 480 μm, height 620 μm. Fig. 3. *Cythereis* (*Cythereis*) *humilis humilis* Weaver, 1982, MPK 4996, Grantchester Cutting, basal Cambridge Greensand, length 580 μm, height 350 μm. Fig. 4. *Cythereis* (*R.*) *paranuda* Weaver, 1982, MPK 4997, Grantchester Cutting, basal Cambridge Greensand, length 840 μm, height 490um. Fig. 5. *Planileberis scrobicularis* Weaver, 1982, MPK 4998, Grantchester Cutting, Gault, 0.61 m below base of Cambridge Greensand, length 1040 μm, height 600 μm. Fig. 6. *Planileberis foveata* Weaver, 1982, MPK4499, Grantchester Footbridge, Cambridge Greensand, length 700 μm, height 400 μm. Fig. 7. *Isocythereis fissicostis fissicostis* Triebel 1940, MPK5000, Grantchester Footbridge, Gault, 1.22 m below base of Cambridge Greensand, length 530 μm, height 280 μm. Fig. 8. *Isocythereis fortinodis reticulata* Gründel, 1964, MPK5001, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.25 m, length 630 μm, height 280 μm. Fig. 9. *Platycythereis gaultina* (Jones, 1849), MPK5002, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.44 m, length 640 μm, height 280μm. Fig. 10. *Platycythereis champani* Kaye, 1964, MPK 5003, Grantchester Cutting, basal Cambridge Greensand, length 1000 μm, height 500 μm.


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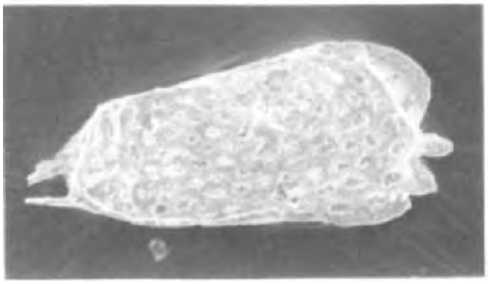
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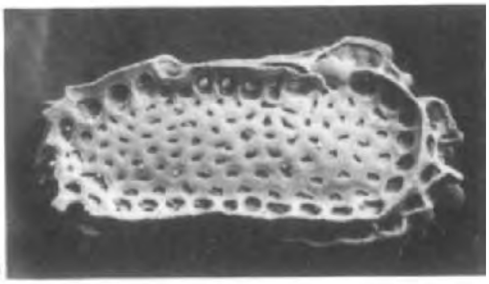
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and subspecies recorded in the Cenomanian (Weaver, 1982), ten were recovered from the Cambridge Greensand and Chalk Marl, examined by the present author, and seven are members of the genus *Bythoceratina*. This latter genus is associated with present day deeper water (middle and outer shelf down to bathyal regions). Off southeastern USA, for example, it has an upper depth limit of 220 m (but extends down to 1034 m) where temperature oscilates a few degrees on either side of 10° C (but goes as low as 5° C in the bathyal areas) (Cronin 1983a, b). Their presence in small numbers in the basal Cenomanian of eastern England probably indicates that they were close to their upper depth limit; they become more common higher in the Upper Cretaceous where water depths are greater.

Although Neale (1964) considered salinity a primary factor in controlling ostracod distribution, he regarded hydrogen ion concentration in seas of open circulation almost certainly insignificant, but did not consider water chemistry further. Peypouquet (1979, 1980) and Peypouquet *et al.* (1980), however, showed that the ionic relationship of Mg/Ca or that of other ions could affect the ostracod carapace and it seems likely that the ionic balance can considerably affect the population also. There was certainly a change from argillaceous Gault to carbonate Chalk Marl, but this does not necessarily mean that sea bed conditions were saturated with $CaCO_3$ (see Hancock, 1976, for a summary). The effect of carbonate sedimentation on the ostracod population has, however, not been fully studied. Babinot and Colin (1983) showed the effect of the ionic balance on the ornament of *Platycythereis* (their *Chapmanicythereis*). This effect is also seen in Britain where the circular to sub-ovate punctations of Albian *P. gaultina* become distinctly elongate in the Cenomanian chalk (see Weaver, 1982, Pl. 14, figs. 16, 18). Specimens from the Cambridge Greensand are intermediate between the two, but closer to the Gault form. The genera's preference for the middle and inner areas of the carbonate platform where there is an input of argillaceous material and organic matter (Babinot and Colin, 1983) is a reflection of food supply and, to some extent, water chemistry. It is interesting to note that the only record of a British Cenomanian species of *Dolocytheridea*, above the mid part of the *N. carcitanense* Subzone, is near the top of the *M. dixoni* Zone (Weaver, 1982) where there is a reduction in calcimetry (Destombes and Shephard-Thorne, 1971; Weaver; 1981).

It would appear, therefore, that the important changes in the structure of the ostracod population were not entirely due to evolutionary trends, but also a response to environmental parameters. The faunal changes do not coincide with lithological boundaries as might be expected if the forms were facies controlled, but there is a gradual change beginning in the latest Albian and continuing in the earliest Cenomanian. It appears to be depth related, but water chemistry probably also played a part.

SYSTEMATIC PALAEONTOLOGY

All specimens are housed with the British Geological Survey, Keyworth, Nottinghamshire, England.

Family BYTHOCYTHERIDAE Sars, 1926

Genus PATELLACYTHERE Gründel and Kozur, 1971

Type species.—Monoceratina williamsi Stephenson, 1946.

PATELLACYTHERE BICOSTATA n. sp.

(Pl. 1, fig. 7)

Patellacythere sp. A. Weaver, 1982: p. 45, Pl. 7, figs. 11–13.

Derivation of name.—After the two ventral ribs anterior of the spine.

Holotype.—MPK 4987.

Diagnosis.—A species of *Patellacythere* with two ventral ribs extending from the postero-ventral spine to mid height and at approximately 1/10th of the length, where they unite.

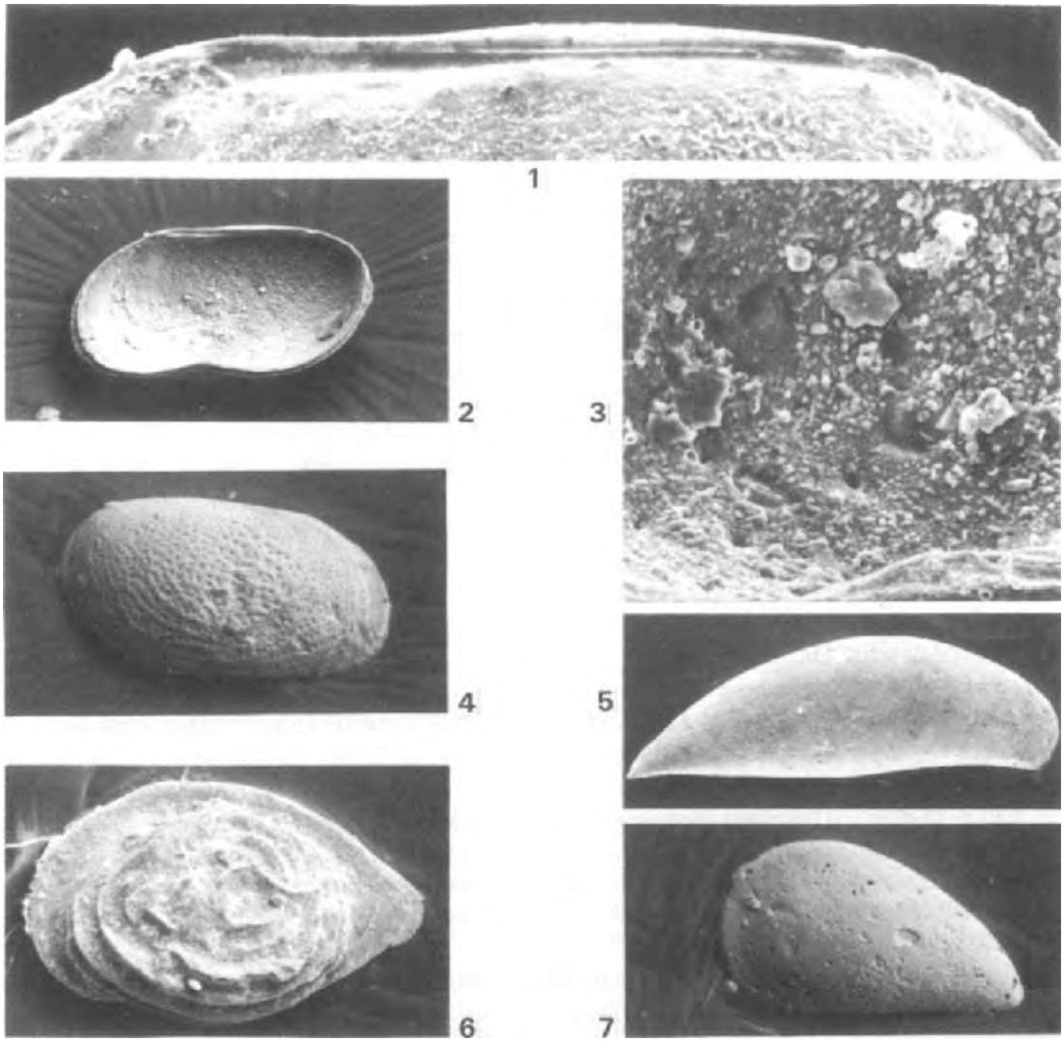

Plate 3—Ostracoda from the Albian and Cenomanian of eastern England. Figs. 1–4. ***Phthanoloxoconcha*** **n. gen.** 1, ***Phthanoloxoconcha icknieldensis*** (Weaver, 1982), hinge, right valve, male, MPK5004, Grantchester Footbridge, Gault, 1.22 m below base of Cambridge Greensand, length 180 μm; 2, Internal view of the same specimen; 3, Muscle scars of the same specimen, width 140 μm; 4, External lateral view, male, MPK5005, Hauxton Interchange, Cambridge Greensand, length 730 μm, height 390 μm. Fig. 5. ***Macrocypris siliqua*** (Jones, 1849), MPK5006, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.36 m, length 1440 μm, height 440 μm. Fig. 6. ***Neocythere (Physocythere) steghausi*** (Mertens, 1956), MPK5007, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.36 m, length 910 μm, height 510 μm. Fig. 7. ***Eucythere (Phodeucythere) trigonalis*** (Jones and Hinde, 1890), MPK5008, Mildenhall Borehole no. 6, Cambridge Greensand, depth 52.36 m, length 570 μm, height 320 μm.

Description.—Carapace elongate and caudate. Dorsal and ventral margins straight and subparallel; anterior margin broadly rounded; posterior acute and level with the dorsal margin. Dorsal rib extends from the anterodorsal margin to anterior of the caudal process. Two ventral ribs extend from the broad base of the posteroventral spine, the more dorsal being straight and the more ventral arcuate. They unite at mid-height and at approximately 1/10th length. A broad, shallow sulcus extends between the dorsal and ventral ribs at mid-length. Anterior of the sulcus is a low swelling. Intercostal area smooth. Internally as for the genus.

Remarks.—This rare, thin shelled species, was frequently found fragmented. Weaver (1982) figured three broken specimens from the Cenomanian Chalk Marl and Grey Chalk of southeastern England, leaving them in *nomenclatura aperta* due to the poor preservation. The species appears to be restricted to the *N. carcitanense* to *C. naviculare* macrofaunal subzones in southern and eastern England.

Family LOXOCONCHIDAE Sars, 1925
Subfamily LOXOCONCHINAE Sars, 1925
Genus PHTHANOLOXOCONCHA n. gen.

Type species.—*Loxoconcha icknieldensis* Weaver, 1982.

Derivation of name.—*φθανω* Greek, anticipate, plus *Loxoconcha.*

Diagnosis.—Ovate-rhombic carapace. Dorsal margin straight, ventral margin convex, anterior margin obliquely rounded, posterior margin round, but obliquely upturned posteroventrally. Ventral margin hidden by ventral inflation. Left valve overlaps right. Lateral surface pitted or punctate.

Inner margin broad; list prominent; anterior and posteroventral vestibules narrow; marginal pore canals few, straight, simple. Hinge lophodont; in the right valve consisting of elongate terminal teeth and straight smooth groove and in the left valve elongate sockets and smooth median bar. Muscle scars consist of a kidney-shaped frontal scar, four ovate adductor scars and an elongate mandibular scar. Dimorphic.

Remarks.—*Phthanoloxoconcha* evolved in the highest Albian and ranges up into the Upper Cretaceous. The genus is similar to *Loxoconcha,* but differs in being more ovate in outline and in possessing a lophodont hinge. It evolved into *Loxoconcha* in the late Cretaceous (? Campanian). Two species of *Phthanoloxoconcha* are known in Britain, by original designation: *Loxoconcha*? *bluebellensis* Weaver, 1982 and *Loxoconcha*? *icknieldensis* Weaver, 1982. *Phthanoloxoconcha icknieldensis* (Weaver, 1982) (Pl. 3, figs. 1–4), the type species of the genus, differs from *P. bluebellensis* (Weaver, 1982), in being less arched dorsally and in having a coarser ornament. When viewed dorsally, *P. icknieldensis* can be seen to be compressed, whereas *P. bluebellensis* is inflated laterally.

P. icknieldensis first evolved in the highest Albian and has been found in the highest part of the *S. dispar* Zone of Kent. It has not been found in the Late Albian Gault or Hunstanton Chalk Member ("Red Chalk") of eastern England, the highest parts of which fall within the *M. rostratum* Subzone of the *S. dispar* Zone. The present author has, however, recovered the species from the Cambridge Greensand (early Cenomanian) of Cambridge and Mildenhall Borehole no. 6, western Suffolk, where it is a useful index. It becomes extinct in the basal part of the *M. saxbii* Zone (early Cenomanian) according to Weaver (1982) and evolves into *Phthanoloxoconcha bluebellensis* (Weaver) in the *M. saxbii* or *M. dixoni* zones.

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DISCUSSION

Neale: Work over the last thirty years has shown that it is possible to use a number of genera such as *Cytherelloidea, Neocythere. Rehacythereis* etc. as biostratigraphical guides. On the other hand, it is difficult to construct continuous evolutionary sequences in *Neocythere* and *Rehacythereis* because of gaps in our knowledge. Has Mr. Wilkinson managed to fill in any of these gaps and recognise a continuously evolving series of species which would add to the value of what promises to be an extremely interesting paper?

Wilkinson: *Neocythere* is a useful genus in biostratigraphical work, although there are taxonomic problems as indicated by Weaver (1982). The *Cythereis (Rehacythereis) luermannae/bemerodensis* lineage is particularly useful as it evolves quickly and is commonly found. The ostracod zones work well for Britain and Germany, but further south in the Paris Basin work by Damotte indicates that they are difficult to recognise, presumably due to "Tethyan" influences.

The Application of Ostracoda to the Location of the Non-marine Jurassic–Cretaceous Boundary in the Sichuan Basin of China

YU-WEN LI
Chengdu Institute of Geology and Mineral Resources, Chengdu, China

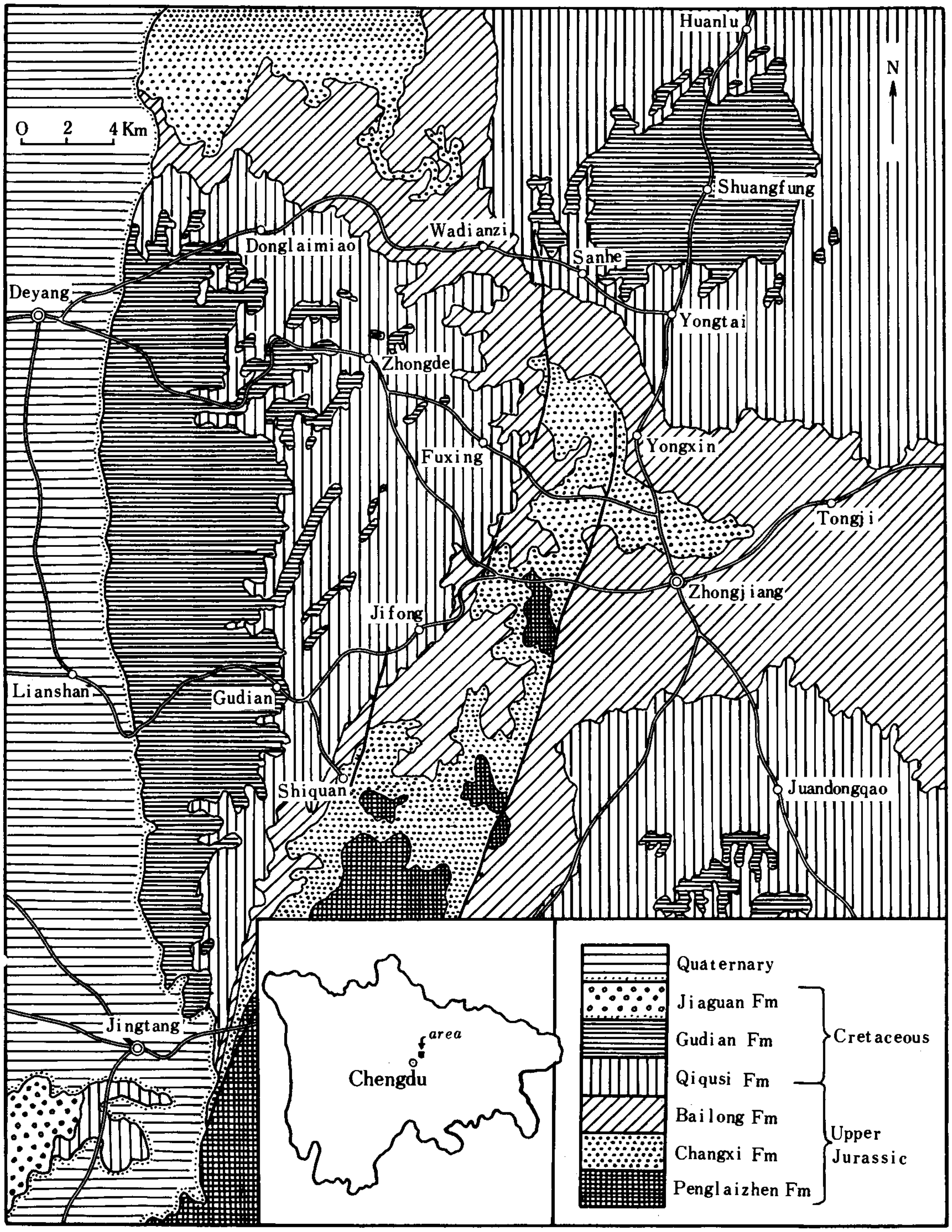
ABSTRACT

This paper discusses the non-marine Jurassic–Cretaceous boundary in the Sichuan Basin in terms of the subidivsions of ostracod biostratigraphical units. The writer considers that the whole of the non-marine Jurassic–Cretaceous transitional beds should be regarded as a superconcurrent range zone which comprises two concurrent range zones and six assemblage zones. On the basis of careful correlation with the international type section in Europe, the boundary is placed at the *Pinnocypridea–Jingguella* Concurrent range zone, *i.e.* between the *Jingguella* (*J.*) *acutura* –*J.* (*Minheella*) *minheensis* Assemblage zone and the *Cypridea dayaoensis–Qingjiania* Assemblage zone, and correspondingly between the Lower and Upper Members of the Qiqusi Formation in the Chengqiangyan Group. Their type section is situated at Jingjisi, Shiquan, Zhongjiang County, Sichuan Province.

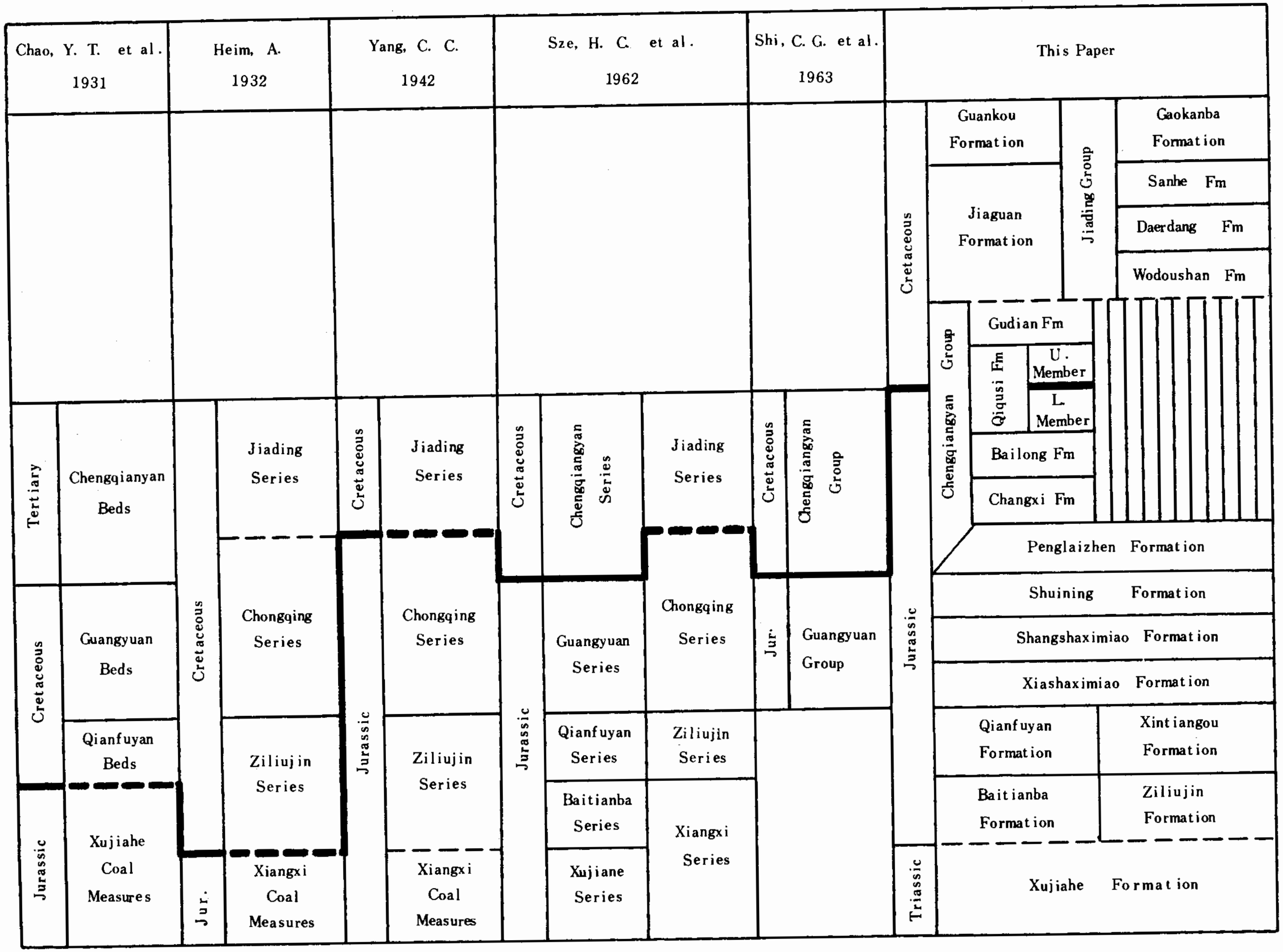
INTRODUCTION

The non-marine Jurassic and Cretaceous sediments in China are well-developed in the Sichuan Basin and can be found throughout the basin. However, the transitional beds occur mainly in the central part of the basin, for example in Zhongjiang, Deyang and Jingtang County (see Text-fig. 1).

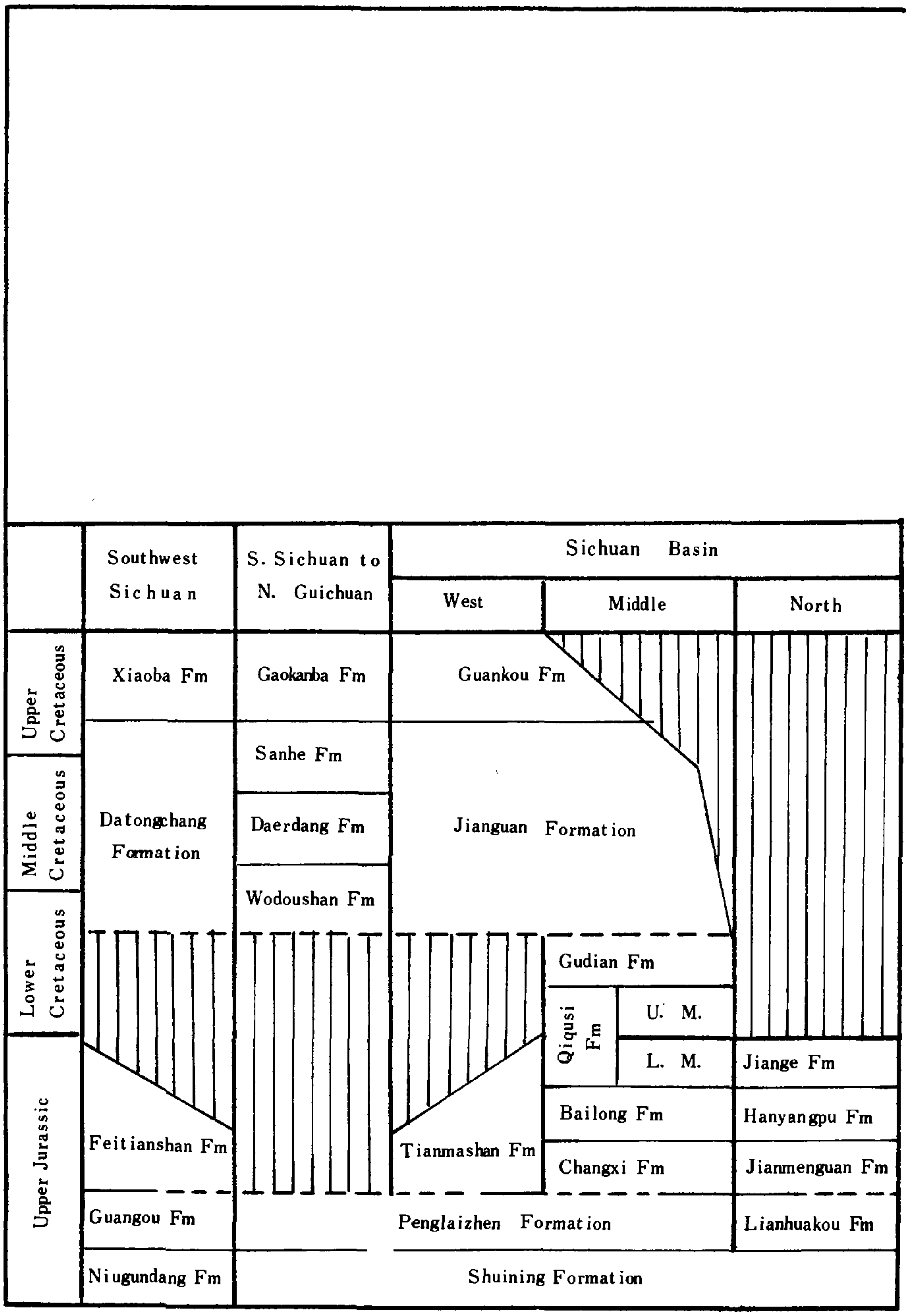
Text-figure 1 illustrates the region northeast of Chengdu City, where the outcropping strata range from the Penglaizhen Formation to the Guankou Formation of lower Jiading Group. Here I consider that the Jurassic–Cretaceous boundary is located in the upper part of the Chengqiangyan Group, an opinion different from that of previous workers. As illustrated in Text-fig. 2, there have been many opinions about the boundary, and they can be divided into three kinds: the first one, proposed by Richthofen (1882), placed the boundary at the top of the Xujiahe Coal Series, a boundary also adopted by Chao and Huang (1931), Hou and Wang (1939) and Chao *et al.* (1945). This is a relatively low boundary, but is not the lowest one, because the Xujiahe Coal Series actually contains the Baitianba Formation. The second boundary is the lowest and is placed at the bottom of the Ziliujing Series by Heim (1930, 1932) and Tan *et al.* (1931). Thirdly, since 1940 many geologists have placed the boundary at the bottom of the Chengqiangyan Group and also at the bottom of the Jiading Series *i. e.* between the Chongqing Series and the Jiading Series, or between the Guangyuan Group and the Chengqiangyan Group. This third view was held by Young (1942), Sze *et al.* (1962), Shi and Ho (1963) and Gu (1964). As opinions vary on the boundary



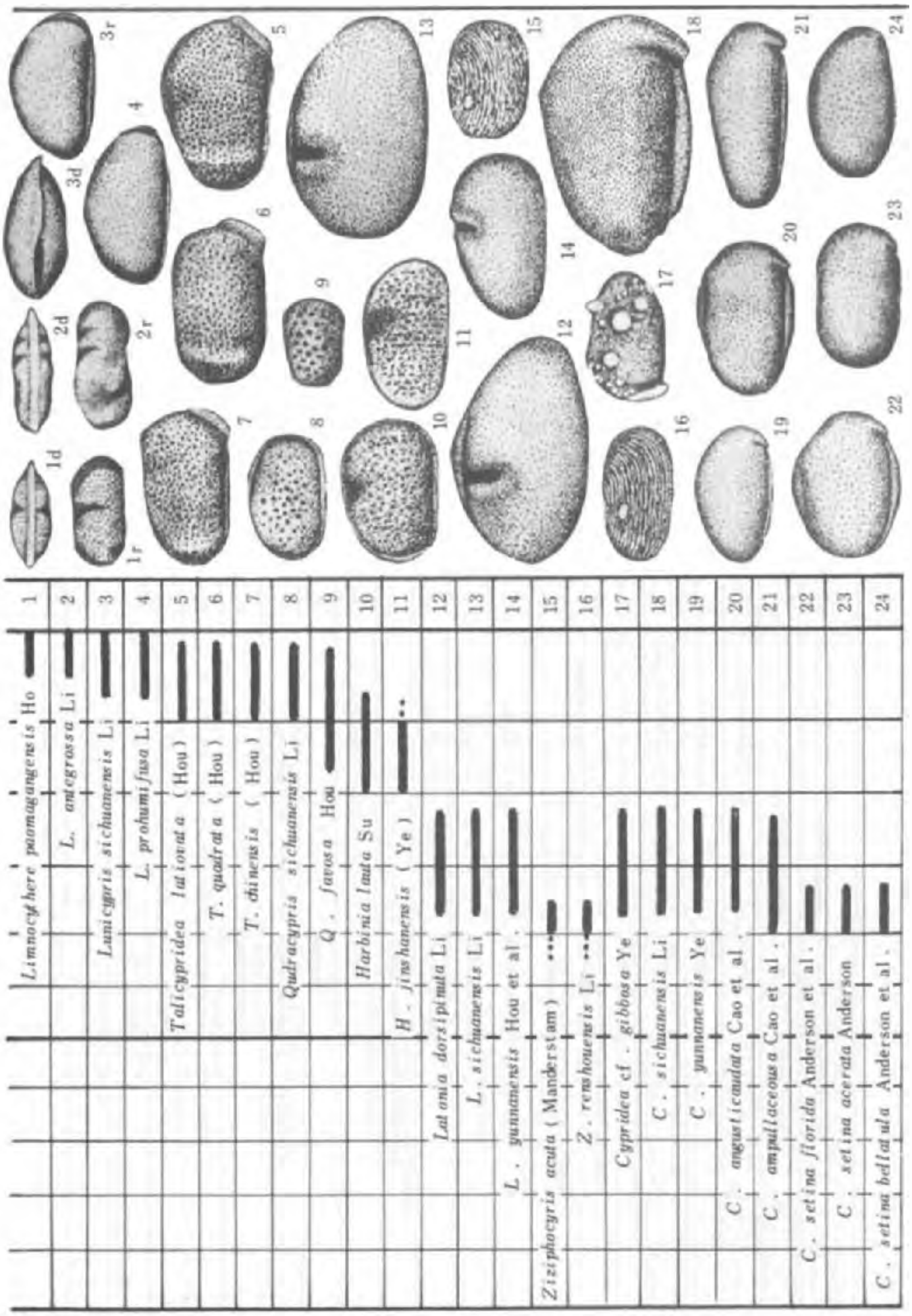
TEXT-FIG. 1—Upper Jurassic–Lower Cretaceous distribution map of the district around the Deyang-Zhongjiang, Sichuan Province.



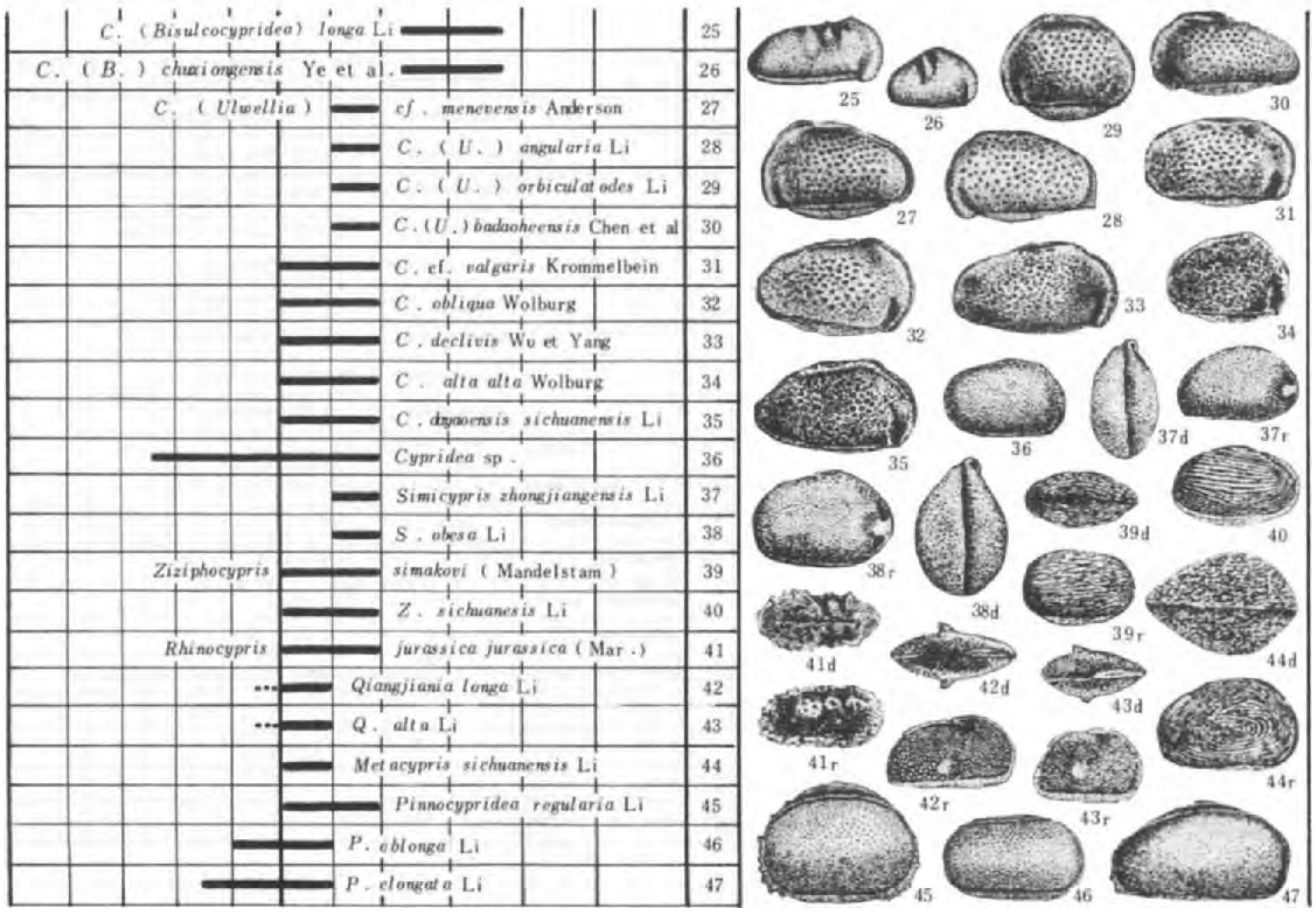
TEXT–FIG. 2—Evolution of the placement of the Jurassic–Cretaceous boundary in the Sichuan Basin.



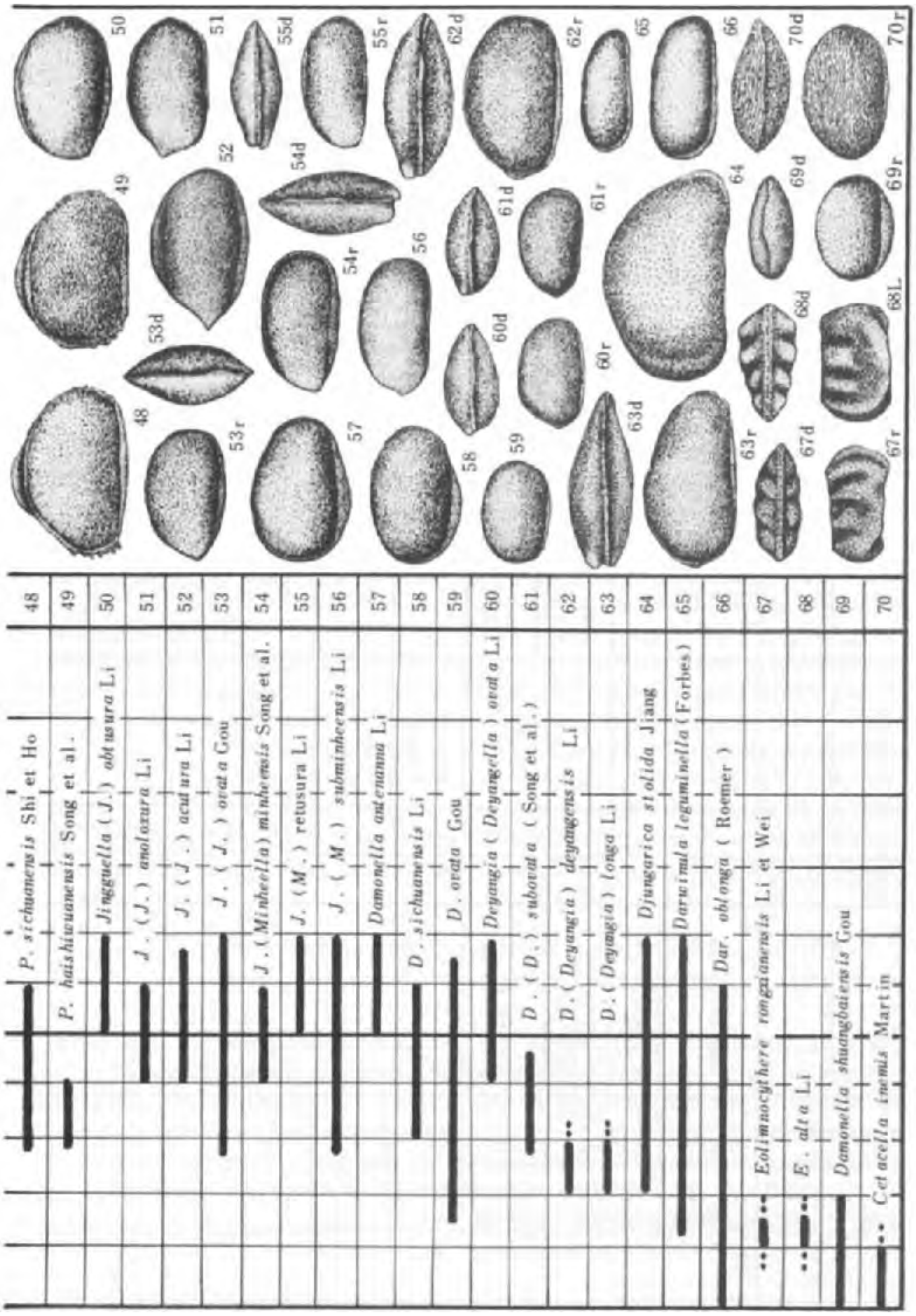
TEXT-FIG. 3—The chief ostracods of the non-marine Upper Jurassic and Cretaceous deposits in Sichuan, China.



TEXT-FIG. 3—*Continued.*



TEXT-FIG. 3—*Continued.*



TEXT-FIG. 3—*Continued.*

<table>
<tr><th colspan="3">Chronostratic units (Hinte, 1976)</th><th colspan="5">England (Anderson, 1971)</th><th colspan="8">Sichuan Basin (This paper)</th></tr>
<tr><th rowspan="2">Series</th><th rowspan="2">Stage</th><th rowspan="2">Time M.Y.</th><th rowspan="2" colspan="2">Stage</th><th rowspan="2" colspan="2">Lithostratic units</th><th>Biostratic units</th><th rowspan="2">Chronostratic units</th><th colspan="3">Lithostratic units</th><th colspan="4">Biostratic units (Ostracoda –zone)</th></tr>
<tr><th>Ostracoda–zone</th><th>Group</th><th>Formation</th><th>Memder</th><th>Sc.–r.–zone</th><th>C.–r.–zone</th><th>Subconcurrent –range–zone</th><th>Assemblage –zone</th></tr>
<tr><td rowspan="4">L. Cret. (part)</td><td rowspan="4">Berriasian</td><td>131</td><td>Upper</td><td rowspan="5">erriasian”</td><td>Upper</td><td rowspan="5">Purbeck Bed</td><td><i>Cypridea setina</i></td><td rowspan="4">L. Cret. (part)</td><td rowspan="7">Chengqiangyan Group</td><td rowspan="2">Gudian Formation</td><td rowspan="2"></td><td rowspan="9"><i>Damonella–Darwinula oblonga</i> Superconcurrent –range –zone</td><td rowspan="7"><i>Pinnocypridea–Jingguella</i> Concurrent –range –zone</td><td rowspan="4"><i>Cypridea dayaoensis –Pinnocypridea</i> Subconcurrent –range –zone</td><td rowspan="2">C. (<i>Ulwellia</i>) –<i>Simicypris</i> Assemblage –zone</td></tr>
<tr><td></td><td rowspan="3">Middle</td><td rowspan="3">Middle</td><td><i>C. vidrana</i></td></tr>
<tr><td></td><td><i>C. fasciculata</i></td><td rowspan="3">Qiqusi Formation</td><td rowspan="2">Upper Member</td><td rowspan="2"><i>C. dayaoensis – Qingjiania</i> Assemblage –zone</td></tr>
<tr><td></td><td><i>C. granulosa</i></td></tr>
<tr><td rowspan="5">Upper Jurassic</td><td rowspan="3">Portlandian</td><td>135</td><td>Lower</td><td>Lower</td><td><i>C. dunkeri</i></td><td rowspan="5">Upper Jurassic</td><td>Lower Member</td><td rowspan="3"><i>D.</i> (<i>Deyangella</i>) <i>prona–Jingguella</i> Subconcurrent –range–zone</td><td rowspan="2"><i>Jingguella</i> (<i>J.</i>) <i>acutura</i> –<i>J.</i> (<i>Minheella</i>) <i>minheesis</i> Assemblage –zone</td></tr>
<tr><td></td><td rowspan="2" colspan="4">Portlandian</td><td rowspan="4"></td><td>Bailong Formation</td><td></td></tr>
<tr><td></td><td>Changxi Formation</td><td></td><td><i>Deyangia</i> (<i>Deyangia</i>)–<i>Jingguella</i> (<i>J.</i>) Assemblage –zone</td></tr>
<tr><td rowspan="2">Kimmeridgian</td><td>138.5</td><td rowspan="2" colspan="4">Kimmeridgian</td><td rowspan="2">Chongqing Group (U. part)</td><td>Penglaizhen Formation</td><td></td><td rowspan="2" colspan="2"><i>Damonella shuangbaiensis –Darwinula oblonga</i> Concurrent –range –zone</td><td><i>Eolimnocythere –Damonella shuanbaiensis</i> Assemblage –zone</td></tr>
<tr><td>141.5</td><td>Shuining Formation</td><td></td><td><i>Cetacella –Damonella shuangbaiensis</i> Assemblage –zone</td></tr>
</table>

Text–fig. 4—The subdivision of the non-marine Jurassic–Cretaceous transitional strata in Sichuan and its correlabetween the two systems, and because of the lack of fossils and the absence of a combined study on the biostratigraphy, lithostratigraphy and chronostratigraphy, no unanimous conclusion can be drawn.

THE SEQUENCE OF STRATA

The strata involved in the discussion of the Jurassic–Cretaceous boundary are the Chongqing Series, the Guangyuan Group, the Chengqiangyan Group and the Jiading Series. One of the reasons for the endless debate in the past is that people did not recognize the normal sequence of the above-mentioned four groups. At first sight, the Chengqiangyan Group overlies the Guangyuan Group in North Sichuan and the "Chengqiangyan Group" overlies the Chongqing Series in Central Sichuan, which leads people to consider that the upper two groups correspond to each other and that the same applies in the case of the lower two groups. This is not, in fact, the case because the lower part of the Chengqiangyan Group in North Sichuan is older than the lower part of the "Chengqiangyan Group" in Central Sichuan, and this is the first point in the argument against placing the boundary at the bottom of Chengqiangyan Group (in its broad sense). Secondly, the Chongqing Series is overlain by different strata in different regions; for example, by the "Chengqiangyan Group" in Central Sichuan and by the Jiading Series in South Sichuan. The uppermost part of the Chonqing Series is older than the lowest part of the Chengqiangyan Group and the Chengqiangyan Group lies above the Chongqing Series in the transitional region (Li, 1981). Thus it is self-contradictory if the boundary is put both at the bottom of the Chengqiangyan Group and at the bottom of the Jiading Series. The third point is that according to systematic study of the ostracod fossils, not only the Chengqiangyan Group in North Sichuan, but also the "Chengqiangyan Group" in Central Sichuan, are not all Cretaceous; on the contrary, they are mainly Jurassic (see Text-fig. 3). At the same time, the overlying Jiading Series contains none of the oldest Cretaceous rocks but only late Early Cretaceous to Eocene sediments. So, the opinions putting the boundary at the bottom of the Chengqiangyan Group and the Jiading Series or within the latter are all groundless. Text-figure 3 illustrates the ranges of the ostracods on which subdivision of the Jurassic–Cretaceous in the Sichuan Basin into biostratigraphical units is made.

THE BIOSTRATIGRAPHICAL UNITS AND THE RELATIONSHIPS BETWEEN THEM AND THE LITHOSTRATIGRAPHICAL UNITS

The Jurassic–Cretaceous transitional beds may be referred to a superconcurrent range zone, namely the *Damonella–Darwinula oblonga* Superconcurrent Range Zone, including both *Damonella shuangbaiensis–Darwinula oblonga* Concurrent Range Zone and the *Pinnocypridea–Jingguella* Concurrent Range Zone. The former is subdivided from bottom to top into the *Cetacella–Damonella shuangbaiensis* Assemblage Zone and the *Eolimnocythere–Damonella shuangbaiensis* Assemblage Zone, and the latter into the *Deyangia–Jingguella* Assemblage Zone, the *Jingguella* (*J.*) *acutura–J.* (*Minheella*) *minhheensis* Assemblage Zone, the *Cypridea dayaoensis-Qingjiania* Assemblage Zone and the *Cypridea* (*Ulwellia*)*–Simicypris* Assemblage Zone (see Text-fig. 4).

Damonella–Darwinula oblonga Superconcurrent Range Zone

The genus *Damonella* Anderson, 1966 and *Darwinula oblonga* (Roemer, 1839) are taken as indicative of this zone. The appearance of *Damonella shuangbaiensis* Gou, 1977 heralds the beginning of this zone, and the extinction of *Damonella ovata* Gou, 1977 is taken as its end. The zone corresponds to the lithostratigraphical units Shuining Formation to Chengqiangyan Group, and is more or less distriubted all over the Sichuan Basin. The type section runs from Shuining County to Zhongjiang County and is about 1,823 m in thickness. In the Guangyuan section in the northwest margin of the basin, the zone is very thick reaching 3,423 m in thickness. The fossils, which range from Kimmeridgian to Berriasian in terms of European stages, are found in this zone. The zone may be subdivided into two concurrent range zones as follows:

Damonella shuangbaiensis–Darwinula oblonga Concurrent Range Zone

The appearance of *Damonella shuangbaiensis* Gou, 1977 and the absence of the genera *Jingguella* Gou, 1977, *Pinnocypridea* Shi and Ho, 1963, and *Deyangia* Li, 1983 are diagnostic of this zone. It corresponds to the lithostratigraphical units Shuining Formation and Penglaizhen Formation. The type section and distribution are the same as for the superconcurrent range zone, reaching a thickness of about 1,125 m in Shuining County and 2,130 m in Guangyuan County. It contains *Cetacella inermis* Martin, 1958 which comes from the Kimmeridgian in England (Anderson *et al.*, 1971) and Spain (Brenner, 1976). This concurrent range zone includes 2 assemblage zones which are as follows:

1) *Cetacella inermis–Damonella shuangbaiensis* Assemblage Zone

This is an assemblage zone that takes *Cetacella inermis* Martin, 1958 and *Damonella shuangbaiensis* Gou, 1977 as representative, with many associated species of *Darwinula* Brady and Norman, 1889; it is found in the Shuining Formation in Sichuan. This zone corresponds to the Lower Kimmeridgian of the Upper Jurassic.

2) *Eolimnocythere–Damonella shuangbaiensis* Assemblage Zone

This zone takes *Eolimnocythere* Li and Wei, 1983 and *Damonella shuangbaiensis* Gou, 1977 as representative and is associated with many species of *Darwinula* Brady and Norman, 1889. It contains *Eolimnocythere rongxianensis* Li and Wei, 1983, *E. alta* Li, 1983, *Darwinula oblonga* (Roemer, 1836), *D. leguminella* (Foebes, 1855), *Damonella shuangbaiensis* Gou, 1977, *D. ovata* Gou, 1977 and *Djungarica yunnanensis* Ye, 1977 (Text-fig. 3). It corresponds to the Penglaizhen Formation in Central Sichuan and the Lianhuakou Formation in North Sichuan. The typical section in Pengxi, Zhongjiang County is 883 m thick. It is thin in South Sichuan where it is less than 200 m thick, but the thickness increases in North Sichuan to 1,720 m. It may be correlated with the Upper Kimmeridgian of the Upper Jurassic.

Pinnocypridea–Jingguella Concurrent Range Zone

This concurrent range zone is very rich in fossils. Not only do the genera *Pinnocypridea* Shi and Ho, 1963, *Jingguella* Gou, 1977, *Deyangia* (*Deyangella*) Li, 1984 and *Darwinula* Brady and Norman, 1889 coexist with the development of various species, but other genera (or subgenera) such as *Deyangia* (*Deyangia*) Li, 1983, *Djungarica* Jiang, 1976, *Metacypris* Brady, 1870, *Ziziphocypris* Chen, 1956, *Cypridea* Bosquet, 1852, *C.* (*Ulwellia*) Anderson, 1939, *Qingjiania* Li, 1983 and *Simicypris* Li, 1983 are also present. This zone corresponds mainly to the "Chengqiangyan Group" in the middle part of the basin, the middle–upper part of the Chengqiangyan Group in the northern part and the Tianmashan Formation in the western part of the basin. The main genus of the concurrent range zone is *Pinnocypridea* Shi and Ho, 1963 which was named in the present region by Shi and Ho (1963). The characteristic *Mantelliana cyrton* Anderson, 1971 which is reported from the Lower Purbeck Beds of England by Anderson (1971, p. 104, Pl. 23, figs. 4, 5) conforms to the generic diagnosis of *Pinnocypridea* Shi and Ho, 1963, because the former has a "flange" on its dorsal margin, *i. e.* so-called dorsal fin ridge of Shi and Ho, and there are a few pustules at the anterior end (called spines by Shi and Ho). Some other species also belong to this genus among which are: "*Cypris*" aff. *purbeckensis* Oertli, 1963 collected from the Lower Purbeckian of the Villemoyenne 2 borehole by Oertli (1963, Pl. 5, fig. 33); "*Bairdia*" sp. Klingler, 1955 of Wienholz (1968, Pl. 1, figs. 1a–c); *Mantelliana* cf. *purbeckensis* (Forbes, 1855) recorded from the Berriasian of Spain by Brenner (1976, p. 136, Pl. 10, fig. 8), from the Lower Berriasian by Wienholz (1968, p. 236, Pl. 1, figs. 4, 5), from Portlandian to Middle Purbeck Beds by Anderson (1966, p. 438, figs. 4–7, 11) and from "Purbeckian" by Oertli (1963, p. 18, Pl. 5, figs. 28–32). Therefore, *Pinnocypridea* Shi and Ho, 1963 may be one piece of evidence that the *Pinnocypridea–Jingguella* concurrent range zone corresponds to the Portlandian–Berriasian of Europe. The zone contains two subzones as follows:

Deyangia (Deyangella) prona–Jingguella (J.) Subconcurrent Range Zone

This subconcurrent range zone is part of the *Pinnocypridea–Jingguella* concurrent range zone containing the characteristic *Deyangia* (*Deyangella*) *prona* (Wei, 1979). Its corresponding lithostratigraphical units range from the Changxi Formation to the Lower Member of the Qiqusi Formation in Central Sichuan and from the Jianmenguan Formation to the Jiange Formation in North Sichuan. Its changes of thickness are relatively large. It is 468 m thick in the type section of Shiquan, Zhongjiang County and it is more than 1,000 m thick towards the north in Jiange County. It may be roughly correlated with the Portlandian, and includes two assemblage zones as follows:

3) *Deyangia (D.)–Jingguella (J.)* Assemblage Zone

This zone is that part of the subconcurrent range zone which contains the typical subgenus *Deyangia* (*Deyangia*) Li, 1983 throughout. It ranges from the Changxi Formation to the lower part of the Bailong Formation in the central part of the basin, from the Jianmenguan Formation to the lower part of the Hanyangpu Formation in the northern part of the basin, and consists of the Tianmashan Formation in the western part of the basin. It is 300 m thick in the Baimaguan section of Deyang County, and in North Sichuan reaches more than 600 m. It may be roughly correlated with the Lower Portlandian.

4) *Jingguella (J.) acutura–J. (Minheella) minheensis* Assemblage Zone

This zone takes the existence of *Jingguella* (*Minheella*) *minheensis* Song and Cheng, 1982 and the abundant development of the genus *Pinnocypridea* Shi and Ho, 1963 as diagnostic. All the genera of the *Pinnocypridea–Jingguella* concurrent range zone are well-developed in the present assemblage zone, but *Cypridea* Bosquet, 1852 appears only rarely. Lithostratigraphically, the zone extends from the middle part of the Hangyangpu Formation to the Jiange Formation in the northern part of the basin, and from middle part of the Bailong Formation to the Lower Member of the Qiqusi Formation in the central part of the basin. Its thickness in the Shiquan section of Zhongjiang County is 220 m and towards the north in the Jiange section it reaches 600 m. It may be correlated with the Middle–Upper Portlandian.

Cypridea dayaoensis–Pinnocypridea Subconcurrent Range Zone

This subzone is that part of the *Pinnocypridea–Jingguella* Concurrent Range Zone which contains abundant *Cypridea* Bosquet, 1852, and ranges from the upper part of the Qiqusi Formation to the Gudian Formation. Its residual thickness is 287 m. It may be roughly correlated with the Berriasian, and includes two assemblage zones as follows:

5) *Cypridea dayaoensis–Qingjiania* Assemblage Zone

The diagnosis of this zone includes abundant *Cypridea* Bosquet, 1852 in association with *Qingjiania* Li, 1983, *Jingguella* Gou, 1977 and *Pinnocypridea* Shi and Ho, 1963 which are also abundant. It corresponds to the Upper Member of the Qiqusi Formation in the central part of the Sichuan Basin. In the type section of Shiquan, Zhongjiang County, it is 110 m thick and may be correlated with the Lower Berriasian.

6) *Cypridea* (*Ulwellia*)-*Simicypris* Assemblage Zone

The characteristic of this assemblage zone is the coexistence of abundant *Cypridea* (*Ulwellia*) Anderson, 1939 and *Simicypris* Li, 1983, and of relict *Jingguella* Gou, 1977 and *Pinnocypridea* Shi and Ho, 1963. It corresponds to the Gudian Formation in Central Sichuan, and is 117 m thick at the type section of Gudian in Zhongjiang County. It may be correlated with the Middle-Upper Berriasian.

THE JURASSIC–CRETACEOUS BOUNDARY IN SICHUAN

The Biostratigraphical Boundary

Judging from the above-mentioned division into biostratigraphical units, the *Damonella shuangbaiensis–Darwinula oblonga* Concurrent Range Zone undoubtedly belongs to the Jurassic Kimmeridgian, because it contains *Damonella shuangbaiensis* Gou, 1977 and *Cetacella inermis* Martin, 1958. The *Pinnocypridea–Jingguella* Concurrent Range Zone should be the biostratigraphical zone in which we search for the Jurassic–Cretaceous boundary, because some species of the genus *Pinnocypridea* Shi and Ho, 1963 in this zone are also found in the Portlandian–Berriasian of Europe.

The fossil features of the two subconcurrent range zones contained in the *Pinnocypridea–Jingguella* Concurrent Range Zone are notably different (Text-fig. 3). In the *Deyangia* (*Deyangella*) *prona–Jingguella* Subconcurrent Range Zone there are only are *Cypridea* Bosquet, 1852, and there are relatively new genera, such as *Deyangia* Li, 1983, *Pinnocypridea* Shi and Ho, 1963 and *Jingguella* Gou, 1977 which occur at higher or lower horizons, in addition to *Damonella* Anderson, 1966 and *Darwinula* Brady and Norman, 1889 which are a continuation of genera from the Kimmeridgian. In the *Cypridea dayaoensis–Pinnocypridea* Subconcurrent Range Zone, there are abundant *Cypridea* Bosquet, 1852, and in addition to *Darwinula* Brady and Norman, 1889, *Damonella* Anderson, 1966, *Deyangia* Li, 1983, *Jingguella* Gou, 1977, and *Pinnocypridea* Shi and Ho, 1963 which are a continuation from the underlying subconcurrent range zone, there appear new genera such as *Qingjiania* Li, 1983 and *Simicypris* Li, 1983. Thus there should be a mutation surface between the two subconcurrent range zones. In the *Cypridea dayaoensis–Qingjiania* Assemblage Zone of the lower part of the *Cypridea dayaoensis–Pinnocypridea* Subconcurrent Range Zone, a great many *Cypridea* Bosquet, 1852 such as *C. sowerbyi* Martin, 1940, *C. primeva* Anderson, 1941, *C. alta alta* Wolburg, 1959, *C. declivis* Wu and Yang, 1980, *C. obliqua* Wolburg, 1959, *Cypridea* cf. *C. vulgaris* Krömmelbein, 1962, *C. dayaoensis* Chen and Ye, 1977 and *C.* cf. *C. vidrana* Wolburg, 1959 are associated with some species of *Qingjiania* Li, 1983 (Text-fig. 3). Among them are some species which were first named by Wolburg (1959) from Upper Purbeck to Wealden Beds in NW-Germany and which are supposed by many palaeontologists to actually correspond to the Middle Purbeck Beds of England (Brenner, 1976). *C. vidrana* Wolburg is considered to be a zone fossil of the Middle Purbeck Beds of England by Anderson (1971). *C. obliqua* Wolburg ranges from the Middle Purbeck to Upper Purbeck Beds (Anderson *et al.*, 1971). *C. sowerbyi* Martin, 1940 is found abundantly in the *Cypridea dayaoensis–Qingjiania* Assemblage Zone. This species is named from the Serpulite Bed in North Germany, and is associated with *C. granulosa* (Sowerby, 1836) which is considered to be the first fossil zone of the Middle Purbeck Beds of England (Anderson *et al.*, 1971). The Serpulite Bed corresponds to the Middle Purbeck Beds of England (Brenner, 1976, p. 171). *C. vulgaris* Krömmelbein, 1962 is named from the Upper Teil Beds in Germany (Krömmelbein, 1962); the comparable species in Sichuan is very similar except for its larger size. Finally, *C. primeva* Anderson, 1941 is associated with *C. granulosa* in England. To sum up, the *Cypridea dayaoensis–Qingjiania*

Assemblage Zone in Sichuan corresponds to two ostracod zones of the middle-lower part of the Middle Purbeck Beds of Berriasian age in Europe. The Jurassic–Cretaceous Boundary should thus be placed at the bottom of the *Cypridea dayaoensis–Qingjiania* Assemblage Zone, *i.e.* the bottom of the Upper Member of the Qiqusi Formation of the lithostratigraphical units.

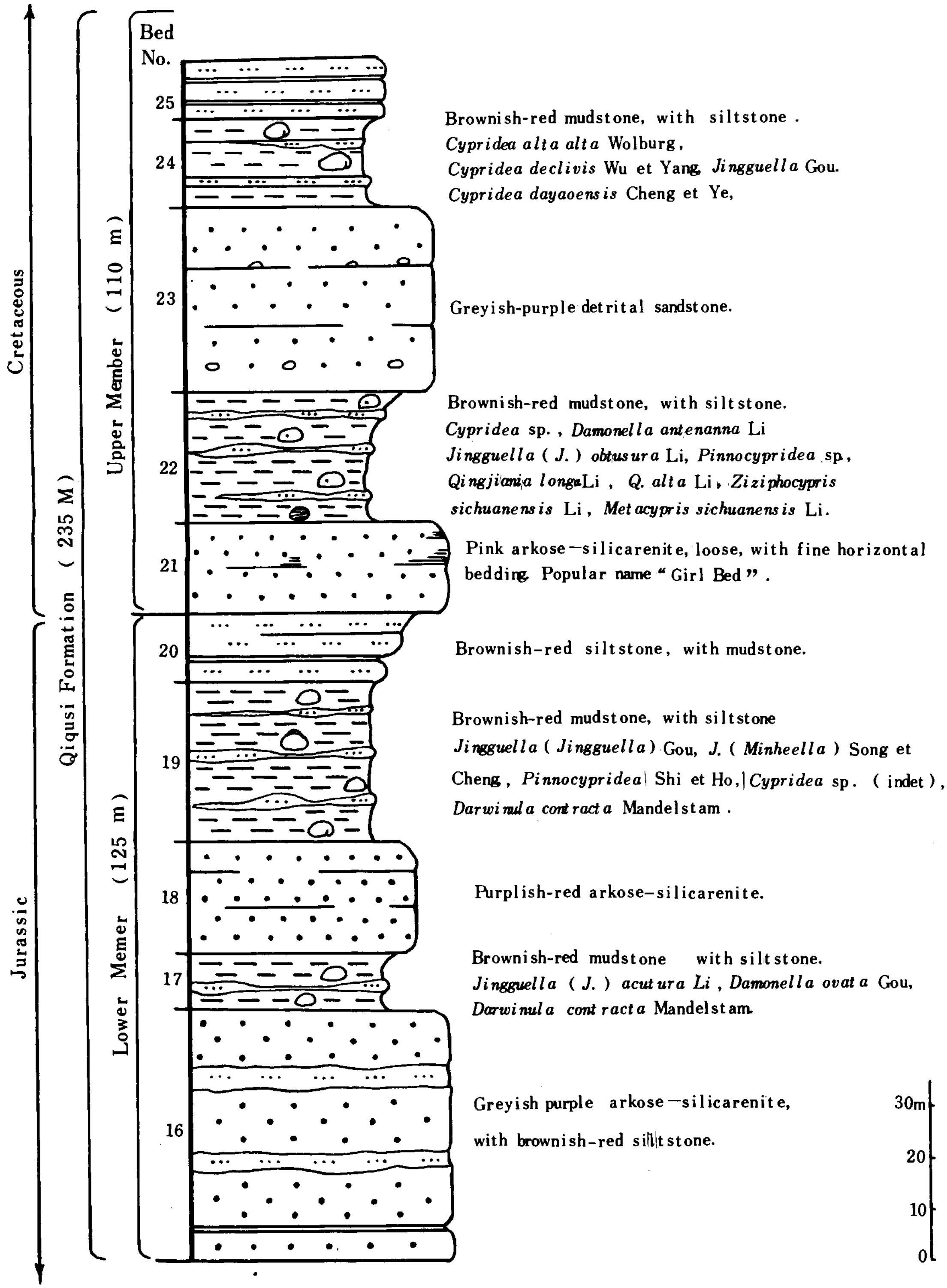
Upwards, the fossil features of the *Cypridea* (*Ulwellia*)*–Simicypris* Assemblage Zone exactly correspond to those of the ostracod zone of the upper part of the Middle Purbeck and Upper Purbeck Beds. In this zone, there are some species of *Cypridea* (*Ulwellia*) Anderson, 1939, forms with thickly punctate surfaces such as *C.* (*U.*) *angularia* Li, 1983, *C.* (*U.*) *subacuminata* Hou, Ye and Cao, 1977, *C.* (*U.*) *badaoheensis* Chen and Ye, 1977, *C.* (*U.*) *orbiculatodes* Li, 1983, *C.* (*U.*) *darvelensis* Anderson, 1971 and *C.* cf. *C.* (*U.*) *menevensis* Anderson, 1939. They are associated with species with carpaces smooth or sparsely punctate, such as *C.* (*U.*) *penshurstensis* Anderson, 1971, *C.* (*U.*) *breviorstrata* Martin, 1940 and *C.* (*U.*) *paulsgrovensis* Anderson, 1939 (Text-fig. 3). *C.* (*U.*) *badaoheensis* Chen and Ye, 1977 differs from *C.* (*U.*) *paulsgrovensis* Anderson, 1939 in its punctate carapace. Anderson (1939, 1971) found that *C.* (*U.*) *paulsgrovensis* ranged from the Upper Purbeck to Lower Wealden Beds in England. Both species occur in the Sichuan Basin, but. *C.* (*U.*) *badaoheensis* is the more abundant. *C.* (*U.*) *angularia* Li, 1983 differs in its punctate surface from *C.* (*U.*) *penshurstensis* Anderson, 1971 which occors in the *C. setina* zone of the upper part of the Middle Purbeck to Upper Purbeck of England (Anderson *et al.*, 1971). They are both found in the Sichuan Basin and the former is the more abundant. There is a species comparable to *C.* (*U.*) *menevensis* Anderson, 1939 which is usually seen in younger strata and is recorded from Wealden Beds. *C.* (*U.*) *darvelensis* Anderson, 1971, which comes from the *Cypridea vidrana* zone of the Middle Purbeck Beds of England (Anderson *et al.*, 1971), appears abundantly in the *Cypridea* (*Ulwellia*)*–Simicypris* Assemblage Zone of Sichuan. *C.* (*U.*) *brevirostrata* Martin, 1940, which is found from upper Middle Purbeck to Upper Purbeck Beds (Anderson *et al.*, 1971, Pl. 5), generally occurs in the assemblage zone. To sum up, the *Cypridea* (*U.*)*–Simicypris* Assemblage Zone of Sichuan corresponds to the *Cypridea vidrana* zone and *C. setina* zones of England, and this further confirms our opinion of putting the Jurassic–Cretaceous boundary at the bottom of the *Cypridea dayaoensis–Qingjiania* Assemblage Zone.

The Lithostratigraphical Boundary

The non-marine Jurassic–Cretaceous transitional bed consists of red clastic sediments which form many sandstone mudstone cyclothems. According to the geological age as shown by the biostratigraphical units, the boundary between the two systems should be drawn in the Qiqusi Formation in Central Sichuan at the bottom of a marker bed, the first bed or "Girl Bed" of the Upper Member of the Qiqusi Formation. The "Girl Bed" consists of pink arkose-silicarenite with fine horizontal bedding, lying conformably on the underlying brownish-red siltstone and mudstone. The lithological similarity of the marker bed with its overlying sandstone of the *Cypridea dayaoensis–Qingjiania* Assemblage Zone and the lithological difference of the marker bed from the underlying sandstone of the *Jingguella* (*J.*) *acutura–J.* (*Minheella*) *minheensis* Assemblage Zone make it clear that the "Girl Bed" is similar to the *Cypridea dayaoensis–Qingjiania* Assemblage Zone in lithology and that the boundary should be put at the bottom of the "Girl Bed". The Jingjisi section of Shiquan, Zhongjiang County is the type section for this division (Text-fig. 5).

The Correlation of Strata

According to the combined study of the biostratigraphical and lithostratigraphical units, the Tianmashan Formation in West Sichuan belongs not to the Cretaceous but rather to the Jurassic, because it is an unstable lithostratigraphical unit in the basin corresponding more or less to the lower part of the "Chengqiangyan Group" in the central basin, but without the fossils



Brownish-red mudstone, with siltstone .
Cypridea alta alta Wolburg,
Cypridea declivis Wu et Yang, *Jingguella* Gou.
Cypridea dayaoensis Cheng et Ye,

Greyish-purple detrital sandstone.

Brownish-red mudstone, with siltstone.
Cypridea sp. , *Damonella antenanna* Li
Jingguella (*J.*) *obtusura* Li, *Pinnocypridea* sp,
Qingjiania longa Li , *Q. alta* Li, *Ziziphocypris sichuanensis* Li, *Metacypris sichuanensis* Li.

Pink arkose—silicarenite, loose, with fine horizontal bedding. Popular name " Girl Bed " .

Brownish-red siltstone, with mudstone.

Brownish-red mudstone, with siltstone
Jingguella (*Jingguella*) Gou, *J.* (*Minheella*) Song et Cheng, *Pinnocypridea* Shi et Ho, *Cypridea* sp. (indet), *Darwinula contracta* Mandelstam .

Purplish-red arkose–silicarenite.

Brownish-red mudstone with siltstone.
Jingguella (*J.*) *acutura Li* , *Damonella ovata* Gou,
Darwinula contracta Mandelstam.

Greyish purple arkose—silicarenite,
with brownish-red siltstone.

TEXT-FIG. 5—The Jurassic–Cretaceous boundary in Jingjishi, Shiquan, Zhongjiang, Sichuan.

of the *Cypridea dayaoensis–Qingjiania* Assemblage Zone and with some older species of the genera *Damonella* Anderson, 1966, *Pinnocypridea* Shi and Ho, 1963, *Jingguella* Gou, 1977 and *Deyangia* Li, 1983.

Cypridea setina bellatula Anderson, 1971, found in the Wealden Hastings, and *Ziziphocypris acuta* (=*Timiriasevea acuta* Mandelstam, 1955) from Berriasian to Valanginian in Mongolia are collected from the bottom part of the Jiading Group in South Sichuan, so the transitional beds of Jurassic–Cretaceous boundary are missing here, *i. e.* the boundary does not lie at the bottom or within the Jiading Group.

Fossils from the Puchanghe Formation in Central Yunnan confirm the presence there of early Early Cretaceous deposits (Ye *et al.*, 1977) and are similar to those of the *Cypridea dayaoensis–Pinnocypridea* Subconcurrent Range Zone of Sichuan. The underlying Gaofengsi Formation produces *Pinnocypricea* Shi and Ho, 1963, and so should belong to the *Pinnocypridea–Jingguella* Concurrent Range Zone. The writer thinks the Jurassic–Cretaceous boundary is either at the bottom of the Puchanghe Formation or in the upper part of the Gaofengsi Formation.

The Jinxing Formation in West Yunnan and the Datonghe Formation in Qunghai belong to the *Pinnocypridea–Jingguella* Concurrent Range Zone because there are abundant fossils of the genera *Damonella* Anderson, 1976, *Jingguella* Gou, 1977 and *Pinnocypridea* Shi and Ho, 1963, but up to the present *Cypridea* Bosquet, 1852 has not been found so they are presumably mainly Jurassic.

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Biostratigraphical Scale in the Toarcian of the Paris Basin (France) by Means of Ostracod Associations

ANNE-MARIE BODERGAT AND PIERRE DONZE
Université Claude Bernard, Lyon, France

ABSTRACT

Stratigraphical and paleontological studies on the edges of the Paris Basin enable us to recognize five ostracod species associations during the Toarcian. These associations, as a result of an evolutionary trend, allow us to propose a biostratigraphical scale.

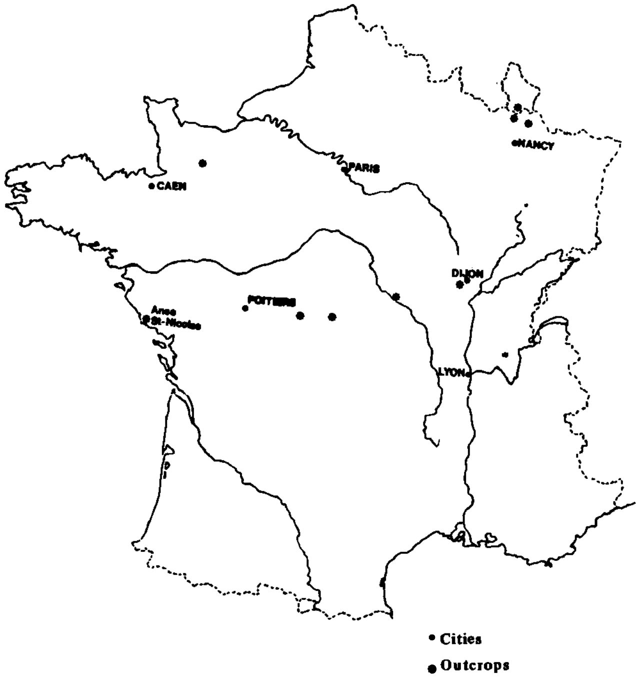
INTRODUCTION

During the last decades, the Liassic formation of the Paris Basin and its dependents have been studied by many geologists, in particular Mouterde (1953), Gabilly (1964) and Rioult (1968). Actually, the stratigraphy, based on ammonites, can be considered as pretty well known. Linked with this research, an abundant material has been collected from the main sections of the Lower, Middle and Upper Lias for micropalaeontological investigations. We express our deepest thanks to J. Gabilly, P. Maubeuge, R. Mouterde, M. Rioult and H. Tintant for their valuable collaboration.

As far as the ostracod biostratigraphy is concerned, the main results have been recently published concerning the Lower and Middle Lias (Donze, 1985). Taking into account the previous studies (Apostolescu, 1959; Apostolescu, Magné and Malmoustier, 1961; Bizon and Oertli, 1961; Viaud, 1963; Maupin, 1975; Depèche, 1985), the aim of this work is to extend the results to the Upper Lias, underlining the remarkable population break between the Middle and the Upper Lias.

THE PRE-TOARCIAN OSTRACOD POPULATIONS

In the Paris Basin, the Middle Lias yields generally rich populations of ostracods, characterized by the abundance of individuals, and high generic and specific diversity, indicating very good environmental conditions. These conditions seem to change and to become less favourable in the Domerian with a decreasing diversity and the predominance of Metacopina populations. Nevertheless, the appearance of several species easy to identify, sucn as *Gramannella apostolescui* (Gramann, 1952), *Cytherelloidea anningy* Lord, 1974, *Ektyphocythere* sp. A Lord, 1974, marks the base of the stage (*Stockesi* Zone). Unfortunately, inside the Domerian, a precise biostratigraphy based on ostracods is difficult, the evolutionary rate being very low (Donze, 1985).



Text-fig. 1—Location of outcrops.

There is no doubt that the spectacular microfaunistic renewal at the beginning of the Upper Lias is linked with important changes in palaeogeographic and ecologic conditions. It is noteworthy to remark here that the adaptive response to ecological changes is faster among ostracod populations than among benthonic foraminifers. While in the *Tenuicostatum* Zone the Middle Lias taxonomic stock is only represented by a few species of Metacopina, most of the Domerian foraminifer species persist in this zone (Ruget, 1983).

Ostracod Associations and Their Succession into the Toarcian Stage

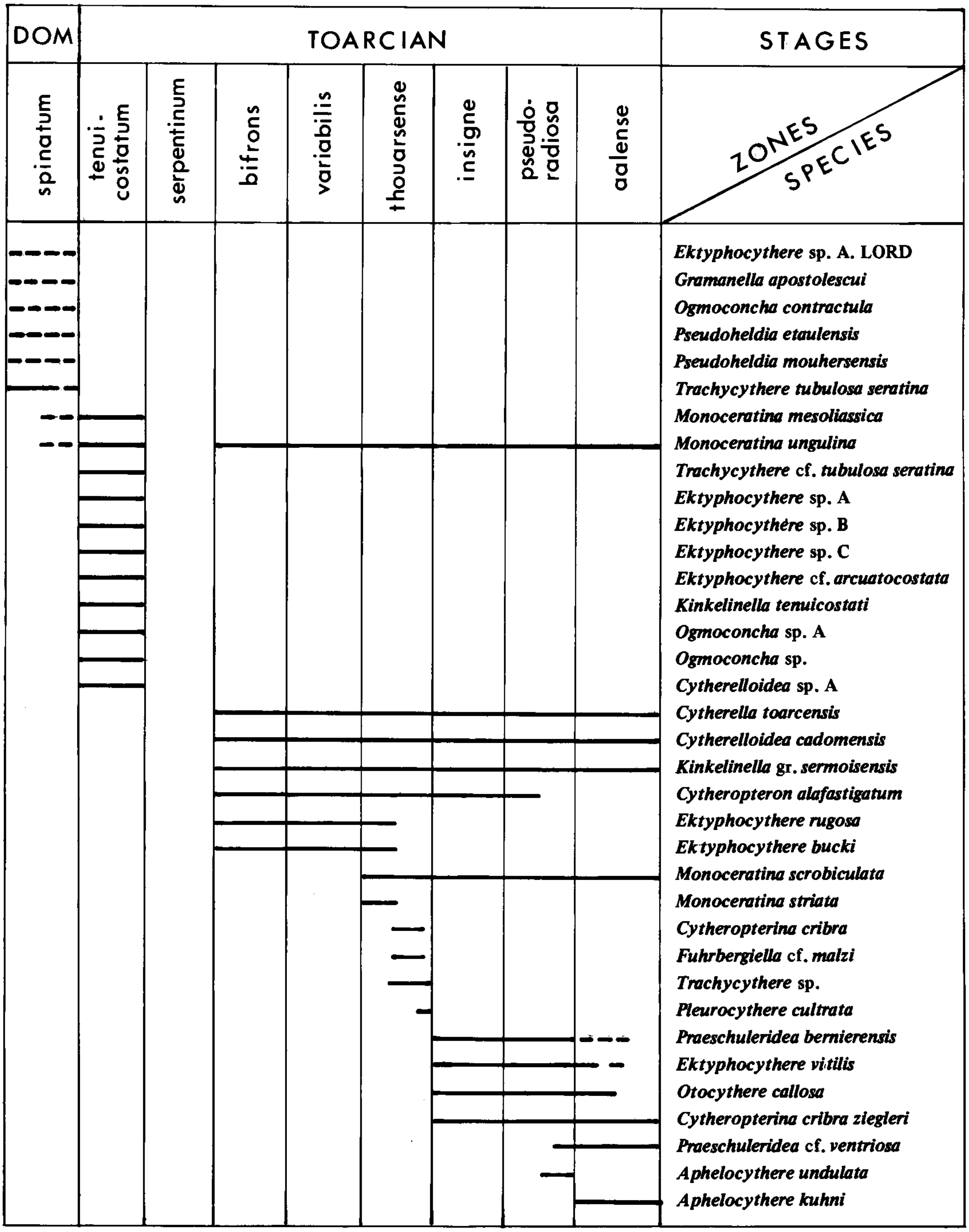
Association A (Text-fig. 2).

As already noted, most of the Domerian species are not found in the *Tenuicostatum* Zone which can be characterized by the appearance of several species and their disappearance at the top:

Kinkelinella tenuicostati Martin, 1960 (Pl. 1, fig. 4),
Ektyphocythere cf. *arcuatocostatum* (Martin, 1960) (Pl. 1, fig. 7).

and also by several probably new species, not yet described:

Ektyphocythere sp. A (Pl. 1, fig. 2), with five "chevron" costae arranged,
Ektyphocythere sp. B (Pl. 1, fig. 5), with reticulation between the ribs,
Ektyphocythere sp. C, with numerous fine ribs,
Ogmoconcha sp. A (Pl. 1, fig. 1), with a strong anterior pad,
Cytherelloidea sp. A (Pl. 1, fig. 3),
Trachycythere aff. *tubulosa seratina* Triebel and Klingler, 1959 (Pl. 1, fig. 6).



TEXT-FIG. 2—Repartition of the main Ostracod species.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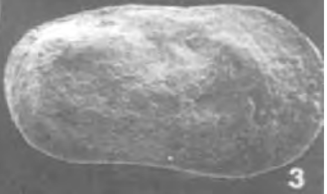
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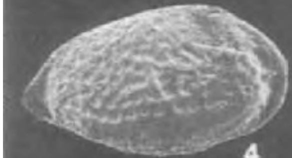
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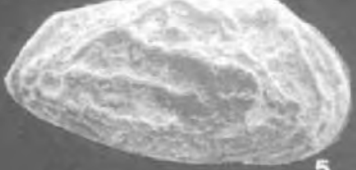
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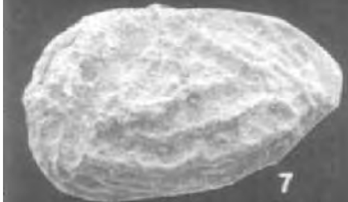
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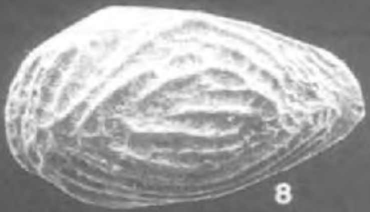
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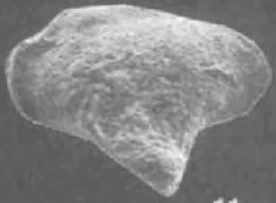
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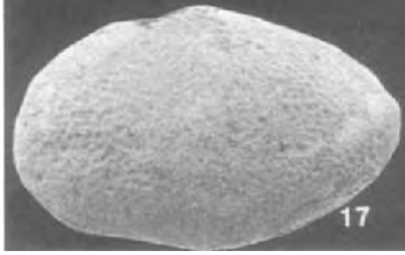
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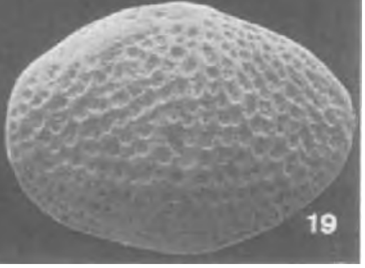
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We cannot mention any ostracods in the *Serpentinum* Zone (Text-fig. 2) because this stage is generally badly represented. So we do not know exactly when the above species become extinct. However that may be, except for *Monoceratina ungulina*, we have not found them in the *Bifrons* Zone.

Association B (Text-fig. 2).

At the base of the *Bifrons* Zone, we find three species which also occur in the *Aalense* Zone:

Cytherelloidea cadomensis Bizon, 1960 (Pl. 1, fig. 9),

Cytherella toarcensis Bizon, 1960 (Pl. 1, fig. 10),

Kinkelinella gr. *sermoisensis* (Apostolescu, 1959). Within this group, it is possible to distinguish several trends of evolution.

Inside the *Bifrons* and the *Variabilis* Zones, some other ostracods also occur:

Cytheropteron alafastigatum Fischer, 1962 (Pl. 1, fig. 11), still present in the *Pseudoradiosa* Zone,

Ektyphocythere rugosa (Bizon, 1960) and *E. bucki* (Bizon, 1960) (Pl. 1, fig. 8), which are present in the *Thouarsense* Zone.

The simultaneous occurence of these species enables us to recognize both the *Bifrons* and the *Variabilis* Zones.

Association C (Text-fig. 2).

The *Thouarsense* Zone is well characterized by the following species association:

Monoceratina scrobiculata Triebel and Bartenstein, 1938, which is also present in the above Zone,

Monoceratina striata Triebel and Bartenstein, 1938, which already exists at the beginning of the *Thouarsense* Zone,

Cytheropterina cf. *cribra* (Pl. 1, fig. 14), which is probably a precursor of *Cytheropterina cribra ziegleri* Wienholz, 1967,

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PLATE 1—Fig. 1. *Ogmoconcha* sp. A. RV, lateral view, FSL 171022. Plage de la Mine, Vendée, France. Lower Toarcian, *Tenuicostatum* Zone (×76). Fig. 2. *Ektyphocythere* sp. A. RV, lateral view, FSL 171019. Anse St-Nicolas, Vendee, France. Lower Toarcian, *Tenuicostatum* Zone (×68). Fig. 3. *Cytherelloidea* sp. A. RV, lateral view, FSL 171024. Plage de la Mine, Vendée, France. Lower Toarcian, *Tenuicostatum* Zone (×66). Fig. 4. *Kinkelinella tenuicostati* Martin, 1960. RV, lateral view, FSL 171023. Plage de la Mine, Vendée, France. Lower Toarcian, *Tenuicostatum* Zone (×66). Fig. 5. *Ektyphocythere* sp. B. RV, lateral view, FSL 171020. Anse St-Nicolas, Vendée, France. Lower Toarcian, *Tenuicostatum* Zone (×65). Fig. 6. *Trachycythere* cf. *tubulosa seratina* Triebel and Klingler, 1959. LV, lateral view, FSL 171026. Plage de la Mine, Vendée, France. Lower Toarcian, *Tenuicostatum* Zone (×67). Fig. 7. *Ektyphocythere* cf. *arcuatocostata* (Martin, 1960). LV, lateral view, FSL 171025. Plage de la Mine, Vendée, France. Lower Toarcian, *Tenuicostatum* Zone (×73). Fig. 8 .*Ektyphocythere bucki* (Bizon, 1960). LV, lateral view, FSL 17.028. St-Denis, Vendée, France. Middle Toarcian, *Bifrons* Zone (×67). Fig. 9. *Cytherelloidea cadomensis* Bizon, 1960. C, lateral view, FSL 171029. St-Denis, Vendée, France, Middle Toarcian, *Bifrons* Zone (×68). Fig. 10. *Cytherella toarcensis* Bizon, 1960. RV, lateral view, FSL 171032. St-Denis, Vendée, France. Middle Toarcian, *Bifrons* Zone (×67). Fig. 11. *Cytheropteron alafastigatum* Fischer, 1962. LV, lateral view, FSL 171031. St-Denis, Vendée, France. Middle Toarcian, *Bifrons* Zone (×68). Fig. 12. *Pleurocythere cultrata* Apostolescu, Magne and Malmoustier, 1961. LV, lateral view, FSL 171037. St-Denis, Vendée, France. Upper Toarcian, top of the *Thouarsense* Zone (×70). Fig. 13. *Trachycythere* sp. LV, lateral view, FSL 171040. St-Denis, Vendée, France. Upper Toarcian, top of the *Thouarsense* Zone (×68). Fig. 14. *Cytheropterina cribra* Wienholz, 1967. C, dorsal view, FSL 171039. St-Denis, Vendée, France. Upper Toarcian, top of the *Thouarsense* Zone (×68). Fig. 15. *Otocythere callosa* Triebel and Klingler, 1959. LV, lateral view, FSL 171044. St-Denis, Vendée, France. Upper Toarcian, lower part of the *Pseudoradiosa* Zone (×69). Fig. 16. *Ektyphocythere vitilis* Apostolescu, Magne and Malmoustier, 1961. RV, lateral view, FSL 171043. St-Denis, Vendée, France. Upper Toarcian, *Insigne* Zone (×68). Fig. 17. *Praeschuleridea bernierensis* (Apostolescu, 1959). LV, lateral view, FSL 171045. St-Denis, Vendée, France Upper Toarcian, lower part of the *Pseudoradiosa* Zone (×68). Fig. 18. *Cytheropterina cribra ziegleri* Wienholz, 1967. RV, lateral view, FSL 171048 St-Denis, Vendee, France. Upper Toarcian, *Thouarsense* Zone (×68). Fig. 19. *Praeschuleridea ventriosa* (Plumhoff, 1963). LV, lateral view, FSL 171046. Vergisson, Saône-et-Loire, France, Upper Toarcian, *Pseudoradiosa* Zone (×69).

Furhbergiella cf. *malzi* Wienholz, 1967,
Trachycythere sp. (Pl. 1, fig. 13), close to *T. tubulosa seratina* Triebel and Klingler, 1959, but smaller and with a dorsal margin more sloping.

Association D (Text-fig. 2).

Several species occur at the beginning of the *Insigne* Zone:
Praeschuleridea bernierensis (Apostolescu, 1959) (Pl. 1, fig. 17),
Ektyphocythere vitilis (Apostolescu, Magne and Malmoustier, 1961) (Pl. 1, fig. 16),
Otocythere callosa Triebel and Klingler, 1959 (Pl. 1, fig. 15),
Cytheropterina cribra ziegleri Wienholz, 1967 (Pl. 1, fig. 18).

This association and the absence of species of the upper stage enable us to identify the whole *Insigne* Zone and the lower part of the *Pseudoradiosa* Zone. We note that in Germany appearance of some taxa, for example, *Praeschuleridea* and *Otocythere callosa* (Knitter and Riegraf, 1984) seem to be older. The difference in time of appearance is very small. The fact seems to be important, and the explanation is perhaps that we have restricted the taxonomic term "*Praeschuleridea*" to evoluted forms.

Association E (Text-fig. 2).

In the two last zones of the Toarcian, the genus *Praeschuleridea* takes predominance in the population of ostracods. One finds a species close to *Praeschuleridea ventriosa* (Plumhoff, 1963) but with a less dense reticulation (Pl. 1, fig. 19). We also note the first appearance of the genus *Aphelocythere* with the species *A. undulata* Triebel and Klingler, 1959, which is succeeded by *A. kuhni* Triebel and Klingler, 1959 into the *Aalense* Zone.

In the Paris Basin, the Aalenian is generally reduced or absent due to erosion. Therefore, it is difficult, if not impossible, to extend this research into the Dogger.

CONCLUSIONS

Firstly, the study of Toarcian ostracods enables us to recognize five main associations. These are more or less contemporaneous with the Ammonites Zones and, therefore, they allow to get some stratigraphic markings. The most important item is the turnover inside the *Tenuicostatum* Zone, and the coexistence of the genus *Ogmoconcha,* heritage of the past, and of the genus *Kinkelinella,* premise of the future.

Since the *Bifrons* Zone, the populations are fundamentally different, legitimately justifying the distinction between the Lower and the Middle Toarcian.

Then three associations allow us to divide the Upper Toarcian:

—the first, at the top of the *Thouarsense* Zone, encloses *Cytheropterina cribra, Fuhrbergiella* cf. *malzi, Trachycythere* sp. and *Pleurocythere cultrata,*

—the second, which includes the *Insigne* Zone and a part of the *Pseudoradiosa* Zone sees the appearance of the genus *Praeschuleridea* s. str.,

—the third begins at the top of the *Pseudoradiosa* Zone and includes the whole *Aalense* Zone.

Only an important palaeogeographical event can explain such a microfaunistic renewal: ostracods populations within the Toarcian find their origin in palaeoenvironmental changes over very large areas.

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Ostracod Zones and Dispersion of Mesozoic Fossils in the Scandinavian North Sea Area

OLE BRUUN CHRISTENSEN
GEOLAB, Forus, Statoil, Norway

ABSTRACT

Faulting activities during the Mesozoic strongly affected the development of basins in the northeastern North Sea. Before the Kimmeridgian, fair ostracod correlation exists between the Danish Sub-basin and the Polish-German basins. During the Volgian and Neocomian, fair correlation exists between the Danish Sub-basin and the English basins. A North Sea–Arctic Seaway during the Jurassic and Lower Cretaceous, probably into lowermost Tertiary, seems to have some controlling effects on deposition and fossil content in the North Sea area. *Mandelstamia* and *Galliaecythereidea,* characteristic genera for the boreal seas, undergo strong differentiation. *Macrodentina* developed in more restricted environments. In shallow areas and in ages with a strong influx of warm surface water, *Cytherelloidea, Bairdia, Protocythere* and related genera occur. Zone index species ought to be selected from among a few genera.

OSTRACOD ZONES AND TIME-CORRELATION

In a special report on the Jurassic from the Geological Society of London (Cope *et al.*, 1980), Torrens and Wright reviewed the stratigraphical work on ostracods in the British Isles. They stated that if there are no better faunas on which to base correlations, ostracods may prove usable. The proposition, of course, is generally true, but they tell us that ostracods as stratigraphical markers may not be useful as ammonites, and this is important. It is also important to define ostracod zones and use these for evaluation of specific stratigraphical events, environments, and time-stratigraphical correlation. Ostracod zones are always established in outcrops or by the use of well-preserved core material from subcrops. Mostly, ostracods have been recognised in apparently thin beds related to the discontinuous sampling technique, necessary in micropalaeontology, or to environmental and diagenetic factors. An ostracod zone is often represented in one or a few samples, related to a slight change of palaeoenvironment for the section. In wells for industrial investigations in subcrops, finds of useful ostracod faunas are relatively uncommon. The ostracod zonation in these subcrops has to be looked upon in relation to the total fossil distribution in the basin. For a common understanding of the limitations and the advances in the use of ostracods, more general zones of index fossils in specific genera ranges may have a future.

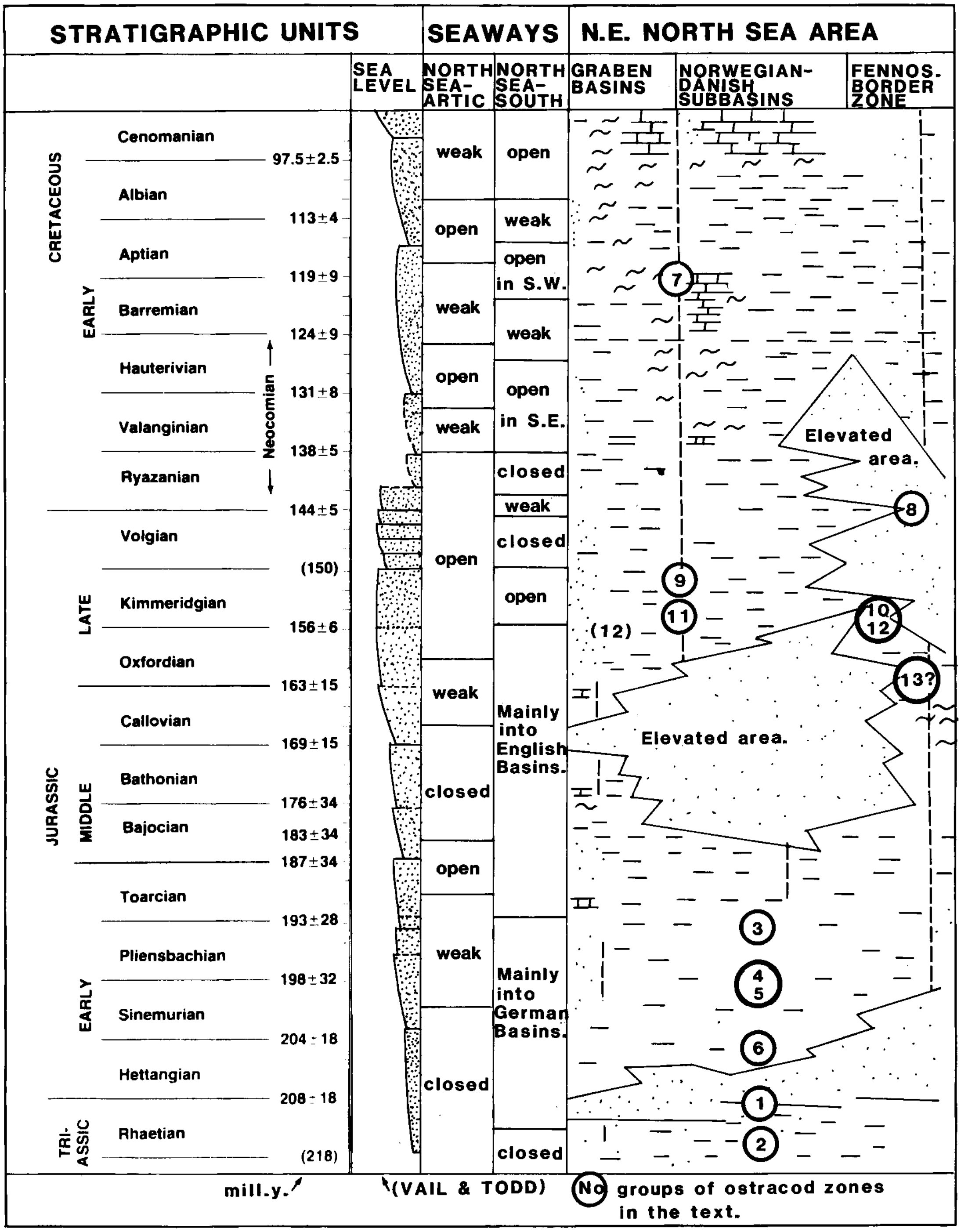
STRUCTURAL EFFECTS

The Scandinavian North Sea area is the northeastern part of the North Sea Basin from the offshore areas of southern Norway, the entire area of Denmark, through southernmost Sweden (Scania) and into the islands of Bornholm in the Baltic Sea. From the late Palaeozoic into the Tertiary, the North Sea areas are characterised by sub-basins of various sizes, relative connections, and with a long-time structural development of complicated faulting events in contrast to most other areas in the Atlantic Ocean Regions. The area was important for development of Mesozoic ostracods (Bate, 1977). Strong compression and tension along the Fennoscandian Sheild affected by the Uralian and the Alpin plate collisions and the initial opening of the North Atlantic Ocean into the Arctic Ocean, seems to have had strong effects on the biological balance of the area. Moderate dislocations with some pull-apart basin effects (Baartmann and Christensen, 1975; Christensen 1975) have not been accepted for Latest Jurassic and Lowermost Cretaceous. Older or younger, minor, but strong structural events with block rotations and dislocations, however, have been described (Hesledal and Hamar, 1983; Pegrum, 1983).

Permian–Triassic rifting of the North Atlantic intensified a long sea-way, present in the North Sea area from the Jurassic and renewed by rifting and faulting in various ages. A connection into the embryonal Artic Ocean is most natural. The older graben structures in the northern North Sea were elevated in the Middle Jurassic and then subsided as part of a North Sea–Arctic Seaway, which crosses and follows the trends of the ancient Caledonides. With the sea-floor spreading sigmoidally developed in the Northern Atlantic during the Late Cretaceous, Tertiary, and Quarternary, the north–south Arctic Seaway does not necessarily terminate in the North Sea area. In the eastern North Sea area, the Ringkøbing-Fyn High, also elevated during Middle Jurassic, has a great local effect on the development of the basins and sub-basins in the Scandinavian North Sea area (Text-fig. 1).

THE NORTH SEA–ARCTIC SEAWAY

The marine connections between various North Sea sub-basins and other shelf areas and oceans are generally important for biostratigraphical evaluations. During the Jurassic, Cretaceous and in the Early Tertiary, the North Sea basins were areas of conversions or interactions between cold, more or less underset slow moving sea currents from the north and relatively warmer sea water from the south, diluted in various degrees by runoff. Besides the large epicontinental sea areas in arctic Alaska, Canada, on the Barents Shelf, and in the Greenland and Norwegian shelf areas, the structurally downwarped areas most probably followed the central trends of the ancient Caledonian range into the North Sea, and not into the Fennoscandian Shield. Hydrographical consistency of the fact that the seaway was rather pronounced and structurally dependant during the Mesozoic, may explain some paradoxes of the Boreal seas evaluated and referred to by Hallam (1969, 1981, 1983), Gordon (1974) and others. The seaway was defined as epicontinental, but not necessarily shallow in all parts. In Text-fig. 1, some Mesozoic reconstructions of marine connections between the arctic areas, the North Sea, and more southern seas are outlined. Influx of polar or boreal water with contemporary marine effects from connections to basins around the North Sea seems to control much of the depositional environment as well. The eustatic sea-level changes and the structural events initiate the more or less pronounced hydrographical effects.



TEXT FIG. 1—Outline of stratigraphic relations between sea level changes (Vail and Todd, 1981), basin developments, and ostracod distribution referred to and numbered in the text.

DISTRIBUTION OF FOSSILS

Generally, the ostracods comprise a minor part of other calcareous fossils recognised in the Scandinavian Mesozoic. They are most well-preserved in the Late Mesozoic deposits and in the southern and eastern areas. Only a few sections with pure ostracod assemblages are found in the Triassic and in Purbeck–Wealden beds. Marine and brackish assemblages dominate. Secondary diagenetic effects on the distribution of calcareous microfossils are seldom greater than the effects of poor life conditions in the northwestern areas. There calcareous ostracods are present, but scarce, compared with other groups of fossils, but very poor compared with the southeastern areas in the Scandinavian North Sea. Solution plays a role in many coarse sediments. In these beds, diagenetic calcite is rather common. Further south and in the eastern areas, probably not so deeply exposed, rich calcareous faunas are relatively common between beds devoid of calcareous fossils. These faunas are mostly very well-preserved, the most important, established through the Scandinavian Upper Jurassic and Lower Cretaceous are noted (refer to numbers in Text-fig. 1).

7. *Mandocythere harrisiana* Zone
    Cythereis luermannae hannoverana Zone
        Cythereis folkestonensis Subzone
    ? *Cythereis l. luermanniae–Neocythere ventrocostata* Zone
        Saxocythere notera senilis Subzone
    Protocythere albae–Dolocythereidea bosquetiana Zone
    Protocythere albae–Dolocytheridea vinculum Zone
        Isocythereis fissicostis Subzone
        Cythereis corrigenda Subzone
    Protocythere nodigera Zone
    ? Unnamed Zone
    Protocythere intermedia Zone
    Protocythere triplicata Zone
    Mandocythere frankei Zone
    Protocythere hannoverana Zone
        Cytherella valanginiana Subzone
        Stravia crossata Subzone
        Paranotacythere globosa Subzone
        Cytheropterina Subzone
    Galliaecytheridea teres Zone

8. *Fabanella boloniensis–Pachycytheridea compacta* Zone
    Cypridea alta formosa Zone
    Cypridea inversa–C. valdensis precursor Zone

9. *Macrodentina reticulata* Zone
    ? *Galliaecytheridea polita* Zone
    Galliaecytheridea spinosa Zone
    ? Unnamed Zone
    Eocytheropteron aquitanum Zone
    ? Unnamed Zone
    Mandelstamia maculata Zone
    Mandelstamia horrida Zone
    ? Unnamed Zone

10. *Mandelstamia inflata* Zone
    Dicrorygma brotzeni Zonule

  Galliaecytheridea formosa Zonule
  Galliaecytheridea oertlii Zonule

11. *Macrodentina steghausi* Zone
    Galliaecytheridea elongata Zone
    Macrodentina proclivis Zone
      Galliaecytheridea mandelst. kilenyi Subzone
    Galliaecytheridea dissimilis Zone

12. *Amphicythere semisulcata–Schuleridea tribeli* Zonule

13. ? *Nophrecythere crusiata oxfordiana* Zone
    ? *Lophocythere interrupta* Zone

TRIASSIC

The Triassic deposits in Scandinavian are mostly devoid of fossils. Red, oxidised continental clastics are most common. An epicontinental sea occupied large areas in central Europe during most of the Triassic. On strong mature landscape plains, a legacy from the Permian Period, marine and lacustrine transgressions may reach large areas in the Scandinavian North Sea, but charophytae recognized in many wells in Denmark and Scania (Sorgenfrei and Buch, 1964; Brotzen, 1950) indicate lacustrine environments in most areas.

Middle Triassic ostracods (*e.g. Triassinella pulcra, Speluncella teres*) are recognised with marine fossils, indicating that the Muschelkalk sea reached the southernmost Danish area (Christensen, 1972). Late Triassic ostracods (*Darwinula* spp., *Christellocythere* sp., *Speluncella vulgaris, S. piriformis*) were collected in outcrops of red to greenish fine clastics in Bornholm and are relatively common in many localities in North Germany and Poland.

An arctic epicontinental sea north of the northern North Sea was hardly connected with the Central European sea through the North Sea grabens, where fine clastics most probably indicate some large lacustrine environments. In the Norian, contemporary with a change to a humid climate, the deposits in the southern areas from the Central Graben into Denmark became rich in fossils. A cyclical development in the sedimentation has been interpretated as due to eustatic sea level changes (Bertelsen, 1978). The initial major transgression, marked by oolitic beds in most areas in Denmark (Christensen, 1972), is probably not marine, but interpreted as lacustrine based on the ostracods, below the *Rhombocythere penarthensis* Zone and beds with *Rhaetavicula contorta,* foraminifera etc.

TRIASSIC OSTRACOD ZONES

The Late Triassic ostracod assemblage is useful for zonation. Closely connected with the general climatic change, a transgression, probably lacustrine, reached most Danish onshore areas. Later, with a sea connection, marine faunas invaded. The zonation in England proposed by Anderson (1964) is mainly based on marine ostracods. A zonation from Northwest Germany by Will (1969) published after his death, it most useful for the Danish area. Anderson seems to have included species from Germany in *Rhombocythere penarthensis.* Using the work of Will, it is easy to evaluate some of those, as well as a number of Anderson's mistaken synonyms for Triassic ostracods in Denmark, illustrated by Christensen (1962). *R. penarthensis* is similar to *Notocythere magna maritina* Will. It occurs in the *N. elegans* Zone of Will with most species of the *R. penarthensis* group and with *N. hechti longa* Will of the *R. ruegeri* group (Plate 1–1), but also above in marine beds. Anderson established his new genus *Rhombocythere* on studies of a small number of English and German species. Will used in his work the genus name *Notocythere* in a wide sense. The genera *Rhombocythere* and *Notocythere* (parts) are closely related to the genus *Emphasia*Ma ndelstam, 1956, but the genera and species *Rhombocythere penarthensis* Anderson and *Notocythere hechti* Will are established, and some genera (*Notocythere*), species, and subspecies need to be re-established. A biostratigraphy close to the intentions of Will and for the Danish formations, revised by Bertelsen (1978) is useful in Denmark:

Late Norian (Rhaet-Keuper)
Member G3 of Gassum Formation with megaspores (*e.g. Trieletes*),
Lepidopteris ottonis Flora.
Member G2 of Gassum Formation with agglutinated foraminifera
(*e.g. Ammodiscus parva*) and marine molluscs (*e.g. Rhaetavicula contorta*) and *R. pernarthensis.*

Early Norian (Steinmergelkeuper)
Beds of Gassum Formation G2 and G1 and Vinding Formations with ostracods.

1. *Rhombocythere penarthensis* Zone (Gassum Formation).
   Rhombocythee pernarthensis Subzone.
   Rhombocythere wicheri-R. *penarthensis* Subzone. (Pl.1 fig.1)
2. *Notocythere media* Zone (Vinding Formation).
   Rhombocythere ruegeri Subzone.
   Notocythere media Subzone (Pl. 1 fig. 2).

The *R. pernarthensis* Subzone is most probably brachyhaline to euhaline. The older Subzones are probably of lacustrine origin. The *Rhombocythere wicheri–R. penarthensis* Subzone has been identified far north of the northern North Sea.

JURASSIC

In a great variety of Jurassic environments, poor ostracod assemblages have been collected from Late and Middle Jurassic in the Viking Graben, more well-preserved assemblages at the margin. In the Central Graben, rich Late Jurassic and scarce Middle Jurassic ostracod assemblages are found. Rather well-preserved Lower Jurassic *Ogmoconcha* and *Kinkelinella* faunas are common in most southern and eastern Scandinavian North Sea areas, but are also present in the Viking Graben. Scarce and poorly preserved Middle Jurassic ostracods are present in some western and southern parts of the Scandinavian North Sea grabens. During the Middle Jurassic most of the Scandinavian areas were uplifted and the Rinkøbing-Fyn High was created as a permanent structure. Volcanic activities in the Central North Sea and in Scania illustrate a trend of faulting activities north of the Ringkøbing-Fyn High. There, fine to coarse clastics often with coal beds but altogether very poor in fossils, are sandwiched between the fine clastics of the marine Early and Late Jurassic.

During the Late Jurassic strong rifting activities continued, with subsidence of most axial parts of the Central and Viking Grabens. Poor benthonic faunas in the deepest part and common occur-

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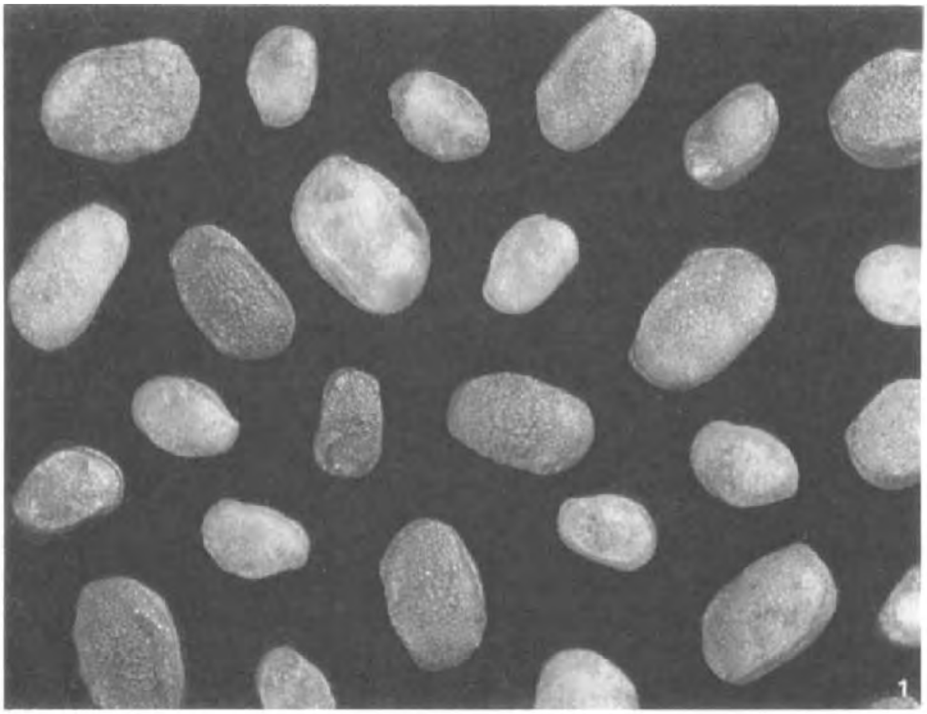
PLATE 1—Some Triassic and Jurassic samples from the Danish Sub-basin. Fig. 1. Assemblage from *Rhombocythere wicheri–R. penarthensis* Subzone with *R. penarthensis, R. elegans, R.* cf. *R. wicheri, R. ruegeri longa, Notocythere media tuberculata* a.o. Fig. 2. Assemblage from *Notocythere media* Subzone with *Limnocythere keuperiana, Notocythere media* Subzone with *Limnocythere keuperiana, Notocythere media prima, Darwinula* spp. a.o. Fig. 3. Monotypic assemblage of *Polydentina*? *quadricostata.*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3

rences in some shallow areas are more an effect of poorly oxygenated seawater than diagenesis. Agglutinated foraminiferal assemblages with a low diversity are common in some intervals. A huge number of more or less pyritized radiolarians in the grabens and along the margins indicate anaerobic to dysaerobic bottom conditions, and a stratified water column with space for a high production of heterotrophic plankton. In the Danish Sub-basin, Late Jurassic radiolarians are uncommon. Calcareous foraminifera occur in certain horizons among the agglutinated foraminifers. They are most common in the shallowest areas, but there also, most intervals are scarce in foraminifera. Ostracods are most common in samples from horizons which also contain mollusc fragments.

JURASSIC OSTRACOD ZONES

An ostracod zonation for the Early Jurassic Fjerritslev Formation was established by Michelsen (1975) for the Danish Sub-basin and for the Central Graben (Michelsen, 1978):

3. *Ogmoconchella adenticulata–Nanacythere simplex* Zone (Late Pliensbachian)
   Grammannella apostolescui–Kinkelinella foveolata Subzone (Early Pliensbachian)
   Progonoidea reticulata Subzone (Early Late Sinemurian)
4. *Ogmoconchella danica* Zone (Late Sinemurian–Early Pliensbachian)
5. *Cristacythere betzi–C. crassireticulata* Zone (Late Sinemurian)
6. *Ogmoconchella aspinata* Zone (Hettangian–Early Sinemurian)

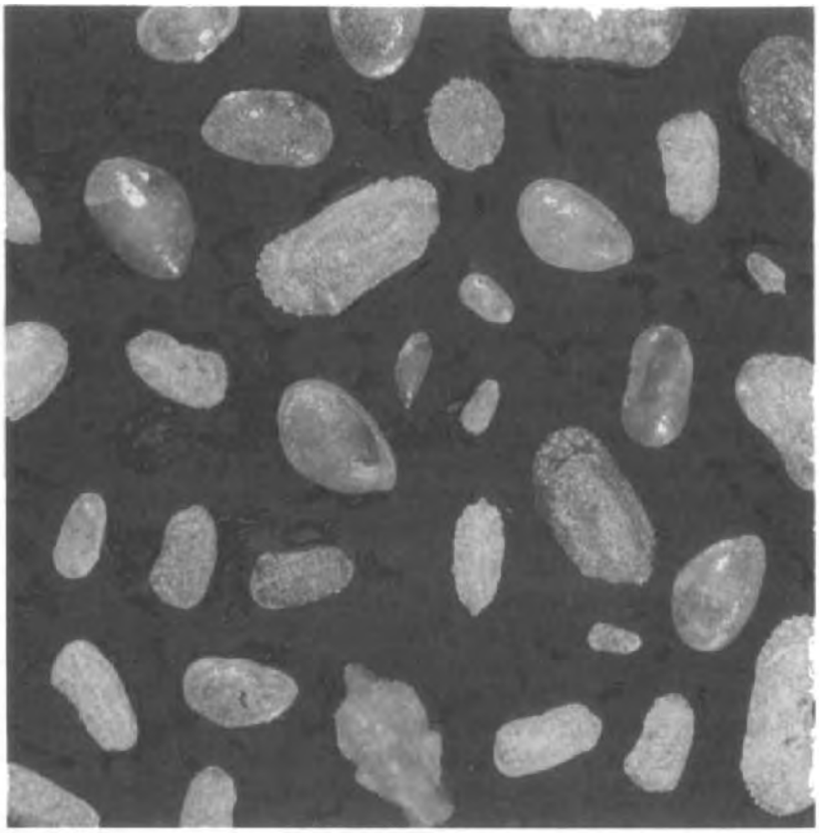
In Scania the *C. betzi–C. crassireticulata* Zone and the *Ogmoconchella danica* Zone are recorded by Sivhed (1980). Ammonites and foraminifera investigated in the Danish wells and in Scania directly support the establishment and general use of these ostracod zones. The affinity between the Danish Sub-basin and the North German Basin is very high for the Lower Jurassic ostracods, except in the Early Sinemurian (Michelsen, 1975).

Marine ostracods (*Camptocythere praecox, Kinkelinella* aff. *adunca, K. oblonga, Pseudomacrocypris subaequabilis*) found along the Fennoscandian Border Zone (Christensen, 1972) from Scania to the Danish Sub-basin indicate Toarcian-Aalenian in the upper part of the Fjerritslev Formation, below the non-marine Haldager Formation, which is difficult to correlate.

From wells in southwestern Scania and in the Hano Bay east of Scania, Norling (1981) indicates marine ostracods from the Bathonian (*Oligocythereis woodwardi, O. fullonica*), from the Callovian (*Lophocythere interrupta interrupta,* Ostracod Nos. 4, 5, 6 Lutze), and from the Callovian-Oxfordian (*Lophyocythere scabra, L. cruciata* spp. *oxfordiana, Paracypris* sp. A Schmidt). These may indicate that during the Middle Jurassic, Scania had a close marine connection with the Polish and North German Basins, east and south of the Ringkøbing-Fyn High. Marine Ostracods from the Middle Jurassic have not been reported from the Danish Sub-basin, but in most parts of the North Sea Grabens ostracods of Bathonian-Callovian age (*Praeschuleridea quadrata, P. batei, P. subtrigonia, Pleurocythere borealis, Lophocythere bradiana, Macrodentina bathonica* and others) can be collected at some horizons. Along the eastern margins of the North Sea–Arctic Seaway, in the northern North Sea, deltaic and coastal deposits successively built up during the Middle Jurassic and closed the Seaway for long intervals after the Toarcian. High deposition rates, and erosion with re-deposition and diagenesis probably resulted in the reduced ostracod assemblage during the Middle Jurassic in Scandinavia.

Oxfordian transgressive events with opening, rifting and successive subsidence of the North

PLATE 2—Examples of boreal ostracod samples from the Danish Sub-basin. Fig. 1. Assemblage from *Galliaecytheridea spinosa* Zone with *G. spinosa* sensu lato, *Mandelstamia* n. sp., *Polydentina rudis, P.* cf. *P. wicheri, Aaleniella* (pro *Pyrocytherura*) *inornata, A. gracilis* a.o. Fig. 2, Assemblage from *Mandocythere frankei* Zone with *M. frankei frankei, Acrocythere hauteriiana, Rehacythereis senckenbergi* a.o.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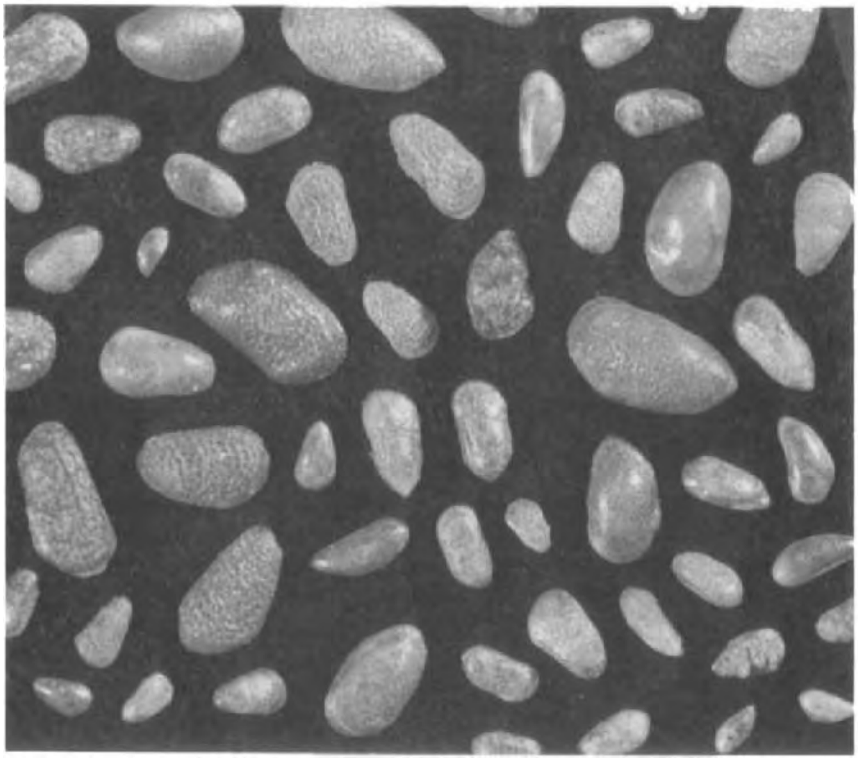
2

Sea–Arctic Seaway renewed the hydrographical conditions in the North Sea basins. Changes to boreal conditions reached the Danish Sub-basin successively from Late Oxfordian to Early Kimmeridgian. At least on one occasion during the Late Oxfordian and Lowermost Kimmeridgian, and contemporary with the deposition of coarser clastics (Flyvbjerg Member), the Danish Sub-basin was part of a Danish-Polish Trough and probably also connected with the North German Basin. A Jurassic ostracod, probably *Polydentina quadricostata* (Pl. 1 fig. 3), known from the Early Kimmeridgian in Central Poland, occurs monotypically (Pl. 2) and is found centrally in the Subbasin and in the western euhaline areas belonging to the *G. dissimilis* Zone, as well. In the Fennoscandian Border Zone an *Amphicythere semisulcata–Schuleridea triebeli* Zonule occurs in Scania and northermost Denmark. It includes a few *Galliaecytheridea dorsetensis.* In the North German basin of Denmark, the zonule is found below the *G. dissimilis* Zone. In the Early Kimmeridgian (*G. dissimilis* and *G. elongata* Zones) an open marine multi-lateral connection was established.

During the Volgian, the Norwegian-Danish Basin seems to have been exposed to the west as the ostracod assemblage is closely related to the English *Mandelstamia* and *Galliaecytheridea* assemblages. The Polish and German Basins were cut off from the deeper boreal sea. Evaporites indicate a warm, perhaps a more arid climate. In Scania, on the Fennoscandian Border Zone, and in the North German Basin immediately south of the Rinkøbing-Fyn High, an ostracod assemblage of *Macrodentina retirugata* and limnophile genera was found. Fresh to brackish water environments continued during the Portlandian and Berriasian. In Scania and Bornholm, *Cypridea* assemblages are common (Christensen, 1968, 1974). In the Fennoscandian Border Zone, not far from the boreal sea and below the island of Anholt in Kattegat, *Cypridea* assemblages also, seem to be present (Baartmann and Bruun Christensen, 1975).

The author and Tom Kilenyi (1970) developed a proposal for a basic ostracod zonation for the Northwest European Kimmeridgian based on the type section in Dorset in which a great deal of the Danish Middle Volgian (Upper Kimmeridgian) could be included. Wilkinson quite understood our review and gave valuable new information in his recent paper (Wilkinson, 1983), also based on a parallel ammonite zonation. In the Scandinavian Upper Jurassic a great number of *Galliaecytheridea* and *Mandelstamia* species have been collected, but this unfortunately did not include a parallel investigation of other fossil groups. Variation in reticulation and the peripheral outline are important features for determinations in these genera. The species of *Mandelstamia* and *Galliaecytheridea* are most common in open sea deposits in the North Sea (Pl. 2, fig. 1). Species of *Macrodentina* dominate in more restricted environments. Most of the species of these three genera have been observed in the North Sea area. This indicates that they are most indigenous to the boreal sea. *Mandelstamia* and *Galliaecytheridea* (from *G. denticula* Sharapova) are also characteristic genera for the boreal Early Cretaceous in the USSR (Andreev and Mandelstam, 1971), as well.

The species of *Mandelstamia* vary in outline and are in some degree environmentally or regionally dependant. As an example, two smooth species occur in the Danish Sub-basin. One of these is closely related to, perhaps identical with, *Limnocythere*? *inflata* (Steghaus). I have used it as an index for the *Mandelstamia inflata* Zone at the Kimmeridgian–Volgian boundary above the *A. semisulcata–S. trebeli* Zone in the Fennoscandian Border Zone.

The specimens of *Galliaecytheridea* are in many cases difficult to define as species in samples without specimens of both sexes larval individuals. Dorsal views are virtually a necessity for descriptions and illustrations of an acceptable standard.

Species of the thermophilic *Cytherelloidea* have been found reither in the Early nor the Late Jurassic in the Norwegian-Danish Basin. Lack of this genus in the Early Jurassic is also characteristic of the North German Basin, but in England it is relatively common.

CRETACEOUS

A zonation of the Early Cretaceous in the Scandinavian North Sea follows that from England by Neale (1978), Wilkinson and Morton (1983), and from Germany. It is characteristic of the boreal ostracod assemblages, that they are so alike, but with differences, at least in the earliest ages, easy to determine as slight environmental variations mostly related to hydrographical rather than local structural factors.

Effects of an influx of boreal water on the ostracod assemblages are mostly secondary in the Early Cretaceous. Influx of warm surface water quickly stabilized in the Valanginian with a high eustatic sea-level and a relatively thick surface layer of warm seawater in which the various ostracod assemblages developed. I have recognised *Acrocythere hauteriviana* further north in the North Sea–Arctic Seaway than other species. In the Danish area there is no evidence for a specific seaway through the Danish Sub-basin and into a Danish-Polish Trough in the Earliest Cretaceous. Across the submerged central parts of the Ringkøbing-Fyn High, an early connection between the northeast German Basin and the Danish Sub-basin seems to have been established in the Valanginian.

Barremian limestones, rich in *Bairdia, Pontocyprella, Bythocypris* and related genera, from higher levels in some North Sea areas and far north along Norway, is an example of a warm surface influx of seawater in the North Sea during the Early Cretaceous. Hydrographically more stable conditions were established in the Late Cretaceous.

The Late Cretaceous ostracod assemblages in the Scandinavian North Sea Area vary from open sea conditions to mangrove in Scania, and are relatively rich in ostracods, but a few have been studied more intensively. In Denmark the outcrops from the Campanian and Maastrichtian have been studied by Jørgensen from various aspects. He has established (1979) two biozones for ostracods in the homogeneous chalk sequence: *Bythoceratina danica* Zone for the uppermost Maastrichtian, and *Bythoceratina umbonatoides* Zone for the Lower and lowermost part of Upper Maastrichtian.

CONCLUSION

The ostracod assemblages from the Mesozoic in the Scandinavian North Sea area have been studied to varying degrees. The exploration for oil and gas in the area provoked intensive studies of the Jurassic and Lower Cretaceous. During this geological period, strong faulting activities with various basin configurations and many ostracod assemblages were developed in the area, dominated by boreal fauna elements. Differences between the deepest parts of the basins (graben areas) and "more" epicontinental areas (*e.g.* the Norwegian-Danish Basin) seem to be related to hydrographical and structural factors. In many intervals only agglutinated foraminifera are present and recognising or establishing an ostracod zonation is difficult without zonal parallels in other fossil groups for reference to other areas with ostracods in the boreal faunal province. *Galliaecytheridea* and *Mandelstamia* are typical boreal ostracods which migrated along the North Sea–Artic Seaway. This Seaway is considered to have been of great importance in the hydrographical and geological development in the North Sea basins.

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Ostracods from the Mesozoic Coal-Bearing Strata of Northern Shaanxi, China

MAO-YU XU
CCMRI, Ministry of Coal Industry, Xian, P. R. China

ABSTRACT

The Mesozoic coal-bearing strata of Northern Shaanxi contain very abundant non-marine ostracod fossils. These ostracods are characterized by few genera, but a large quantity of individuals and can be divided into four assemblages.

Assemblage I. *Lutkevichinella—Darwinula* assemblage occurs in the Middle Triassic Zhifang Formation. It consists of 14 species belonging to the above two genera. Among them *Lutkevichinella minuta, L. ansulca, L. longovata* and *L.* sp. 1 are very common, *Darwinula* comparatively less and poorly preserved.

Assemblage II. *Tungchuania—Darwinula* assemblage is found in the lower part of the Upper Triassic Tongchuan Formation. There are 9 species assigned to 3 genera in this assemblage. Among them species of *Tungchuania* are dominated by *Tungchuania agrestata, T. aurita* and *T. perelegana. Darwinula* is less common.

Assemblage III. *Darwinula—Tungchuania* assemblage occurs in the upper part of the Upper Triassic Wayaobu Formation. It consists of 14 species of 3 genera, chiefly of *Darwinula.* Among them *Darwinula shensiensis, D. bella, D. liulingchuanensis* and *D. medialis* are very abundant. *Tungchuania aurita* and *T. houae* are also abundant.

Assemblage IV. *Darwinula—Metacypris* assemblage is represented by large-sized species of *Darwinula* and simply ornamented species of *Metacypris* such as *Darwinula magna, D. sarytirmenensis, D.* sp. 5 of the former and *Metacypris shensiensis* and *M. armeniacumiformis* of the latter. This assemblage contains 11 species belonging to 2 genera and occurs in the Middle Jurassic Anding Formation.

INTRODUCTION

The Northern Shaanxi region is the main part of the Ordos Basin. Here very thick Mesozoic non-marine strata are developed which are rich in resources of coal and oil. Ostracod fossils are found in the Middle Triassic, the Upper Triassic and the Middle Jurassic Series (see Table 1).

The Middle Triassic Zhifang Formation underlies the Upper Triassic coal-bearing Yanchang Group and consists of greyish-yellow, greyish-green sandstones and dark-red mudstones. Its thickness varies in different localities from 200 to 1066 m. Ostracods, sporopollen and plant fossils are found in the mudstones.

The Upper Triassic Yanchang Group can be divided into four formations. These are named

TABLE 1—DIVISION OF THE MESOZOIC COAL-BEARING STRATA OF NORTHERN SHAANXI.

Middle Jurassic	Anding Formation ● Zhiluo Formation
Lower Jurassic	Yanan Formation * Fuxian Formation
Upper Triassic	Wayaobu Formation * ● Yongping Formation
(Yanchang Group)	Hujiachun Formation Tongchuan Formation ●
Middle Triassic	Zhifang Formation ●

* Important coal-bearing stratum; ● Containing abundant ostracods

Tongchuan Formation, Hujiachun Formation, Yongping Formation and Wayaobu Formation from bottom to top.

The Tongchuan Formation is equivalent to the T_3y_1 and T_3y_2 members of Zhong Xiao-chun (1964). It consists of greyish-green, thick-bedded to massive, fine-grained arkosic sandstones, dark-grey sandy mudstones and siltstones, with conglomerates and thin coal seems at the bottom, and with black oil shales at the top. It has a thickness from 100 to 580 m and contains ostracods, sporopollen and plant fossils.

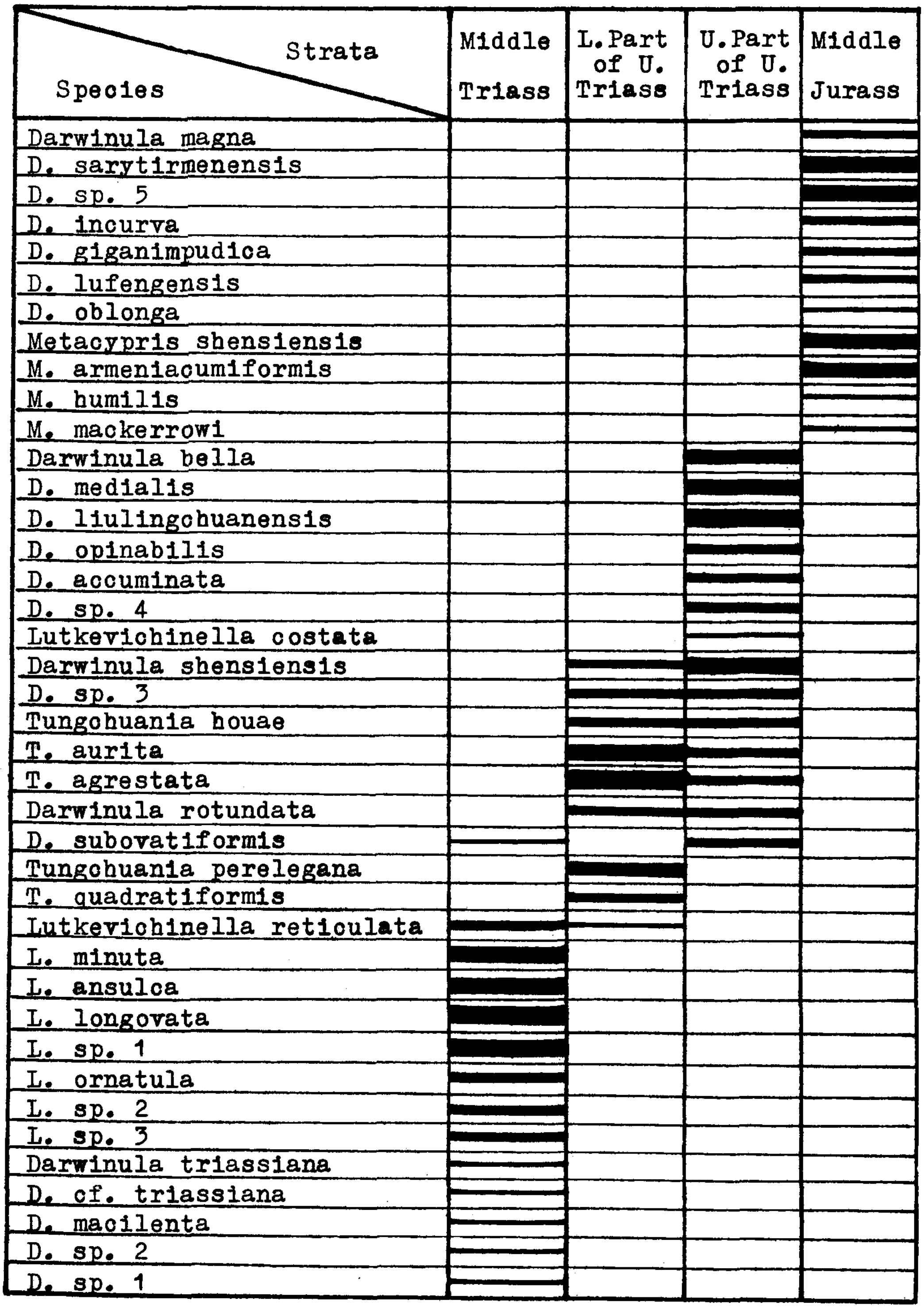
The Hujiachun Formation is the T_3y_3 of Zhong, 1964. It consists of greyish-green, thick-bedded, fine to medium-grained sandstones and dark-grey mudstones with intercalations of black shales and thin coal seams. It is 200 to 550 m thick. It only contains sporopollen and a few ostracod fossils.

The Yongping Formation is the same as the T_3y_4 member of Zhong, 1964. It is 95 to 200 m thick and consists of greyish-white, greyish-green, fine to medium-grained, thick-bedded to massive sandstones with intercalations of greyish-black and sandy mudstones, containing plant, sporopollen and a few ostracod fossils.

The Wayaobu Formation is the uppermost part of the Yanchang Group. It is equal to the T_3y_5 member of Zhong, 1964. It is one of the two most important Mesozoic coal-bearing formations in Northern Shaanxi. It consists of greyish-green, yellowish-green mudstones, sandy mudstones, siltstones and dark-grey, fine-grained sandstones, with intercalations of fresh arkosic sandstones and black carbonaceous mudstones, containing about 30 coal seams. It is 186 to 410 m thick. A large number of ostracod, sporopollen and plant fossils are found in this formation.

The lower part of the Lower Jurassic Fuxian Formation lies unconformably on the Wayaobu Formation. It varies in thickness from 2 to 72 m and in its lithological characteristics in different localities. The bottom of this formation is composed of conglomerates and coarse-grained arkosic sandstones. Above, the lower part of the formation consists of dark-grey mudstones, sandy mudstones, greyish-black carbonaceous mudstones, oil shales and thin coal seams. The upper part of this formation consists of dark-red mudstones and greyish-green sandy mudstones. A lot of Conchostraca are found in the oil shales and sporopollen in the mudstones, but there are no ostracods in this formation.

The upper part of the Lower Jurassic Yanan Formation is another important coal-bearing formation in Northern Shaanxi. The coals can be exploited by opencast working in some localities. This formation has a thickness of 14 to 325 m. Its lower part consists of greyish-white, greyish-yellow, medium to coarse-grained arkosic sandstones intercalated with greyish-black siltstones and mudstones, with conglomerates at the bottom. The upper part of the formation consists of greyish-green, greyish-white sandstones, greyish-black mudstones, siltstones and coal seams. This



Species \ Strata	Middle Triass	L. Part of U. Triass	U. Part of U. Triass	Middle Jurass
Darwinula magna				▬
D. sarytirmenensis				▬
D. sp. 5				▬
D. incurva				▬
D. giganimpudica				▬
D. lufengensis				▬
D. oblonga				▬
Metacypris shensiensis				▬
M. armeniacumiformis				▬
M. humilis				▬
M. mackerrowi				▬
Darwinula bella			▬	
D. medialis			▬	
D. liulingchuanensis			▬	
D. opinabilis			▬	
D. accuminata			▬	
D. sp. 4			▬	
Lutkevichinella costata			▬	
Darwinula shensiensis		▬	▬	
D. sp. 3		▬	▬	
Tungchuania houae		▬	▬	
T. aurita		▬	▬	
T. agrestata		▬	▬	
Darwinula rotundata		▬	▬	
D. subovatiformis	▬		▬	
Tungchuania perelegana		▬		
T. quadratiformis		▬		
Lutkevichinella reticulata	▬	▬		
L. minuta	▬			
L. ansulca	▬			
L. longovata	▬			
L. sp. 1	▬			
L. ornatula	▬			
L. sp. 2	▬			
L. sp. 3	▬			
Darwinula triassiana	▬			
D. cf. triassiana	▬			
D. macilenta	▬			
D. sp. 2	▬			
D. sp. 1	▬			

TEXT-FIG. 1—Stratigraphical distribution of the ostracod species in the Mesozoic coal-bearing strata of Northern Shannxi.

formation contains abundant plant, sporopollen and bivalve fossils. Only two internal moulds of ostracods have been found and these seem to be *Darwinula.*

The lower part of the Middle Jurassic Zhiluo Formation is 80 to 140 m thick. Its lower part consists of grey, massive, arkosic sandstones and its upper part of dark-grey, greyish-green mudstones, and siltstones with intercalated sandstones. Only fragments of ostracod fossils have been found.

The upper part of the Middle Jurassic Anding Formation varies in thickness from 0 to 128 m. The lithological characteristics differ at different places in this region. In the south, its lower part is composed of black mudstones, oil shales and siltstones; its upper part consists of dark-red, yellowish-green mudstones. In the north, this formation consists of dark-red, greyish-green sandstones intercalated with mudstones. A great number of well preserved ostracods and sporopollen occur in this formation.

OSTRACOD ASSEMBLAGES

The ostracods from the Mesozoic coal-bearing strata of Northern Shaanxi are abundant and well preserved. There are 4 genera and 41 species which can be grouped into 4 assemblages (see Text-fig. 1).

Assemblage I, the *Lutkevichinella–Darwinula* assemblage, occurs in the Zhifang Formation. This assemblage is characterized by abundant *Lutkevichinella* which is well preserved. It includes 2 genera and 14 species, namely *Lutkevichinella minuta, L. ansulca, L. longovata, L. ornatula, L. reticulata, L.* sp. 1, *L.* sp. 2, *L.* sp. 3, *Darwinula triassiana, D.* cf. *D. triassiana, D. macilenta, D. subovatiformis, D.* sp. 1 and *D.* sp. 2. Among them *Lutkevichinella minuta, L. ansulca, L.* sp. 1 and *L. longovata* are the most abundant. *Darwinula* is rarer and preserved poorly.

According to the known data, *Lutkevichinella* has been found in the Lower Triassic of the U.S.S.R., the Middle–Upper Triassic of Germany, and the Zhifang Formation and the Yanchang Group of Northern Shaanxi, China. *Darwinula triassiana* is common in the Lower Triassic of the U.S.S.R., *D. subovatiformis* was found not only in the Zhifang Formation, but also in the Tongchuan Formation and the Wayaobu Formation. *D. macilenta* was first discovered in the lower part of the Upper Triassic of South China. In a word, in Assemblage I there are some Early Triassic and some Late Triassic species, but most species and individuals of *Lutkevichinella* are peculiar to the

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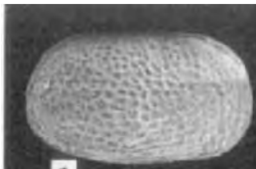
PLATE 1—All specimens illustrated on these plates are deposited in the Institute of Geology and Exploration, CC MRI, Ministry of Coal Industry, China, under the catalog numbers given. All figures are external views and enlarged ×54.

Fig. 1. *Lutkevichinella ansulca* Su *et al.*, 1980, right view, 72016(9)–(1), Fig. 2. *Lutkevichinella minuta* Su *et al.*, 1980, right view, 72015(2)–(2). Fig. 3. *Lutkevichinella* sp. 1, left view, 72016(7)–(12). Occurrence: Middle Triassic Zhifang Formation, Tongchuan, Shaanxi. Fig. 4. *Lutkevichinella costata* (Zhong), 1964, left view, 72093(1). Occurrence: Upper Triassic Wayaobu Formation, Tongchuan, Shaanxi. Fig. 5. *Lutkevichinella longovata* Su *et al.*, 1980, left view, 72016(11)–(3). Fig. 6. *Lutkevichinella ornatula* Su *et al.*, 1980, right view, 72015(3)–(2). Fig. 7. *Lutkevichinella* sp. 3, right view, 72009 (3)–(1). Fig. 8. *Lutkevichinella* sp.2. right view, 72016 (10)–(1). Occurrence: Middle Triassic Zhifang Formation, Tongchuan, Shaanxi. Figs. 9,10. *Metacypris shensiensis* (Zhong), 1964, dorsal and right view, 72242(1)–(1). Figs. 11,12. *Metacypris armeniacumiformis* (Zhong), 1964, right and dorsal view, 72243(1)–(2). Fig. 13. *Metacypris humilis* (Zhong), 1964, right view, 72243 (2)–(1). Occurrence: Middle Jurassic Anding Formation, Zichang, Shaanxi. Fig. 14. *Tungchuania quadratiformis* Su *et al.*, 1980, left view, 72030(1). Fig. 15. *Tungchuania agrestata* Zhong, 1964, right view, 72052(1)–(1). Fig. 16. *Tungchuania perelegana* Zhong, 1964, right view, 72033(2)–(2). Occurrence: Upper Triassic Tongchuan Formation, Tongchuan, Shaanxi. Fig. 17. *Tungchuania houae* Zhong, 1964, right view, 72094(1). Fig. 18. *Tungchuania aurita* Zhong, 1964, left view, 72121(2)–(1). Occurrence: Upper Triassic Wayaobu Formation, Tongchuan, Shaanxi.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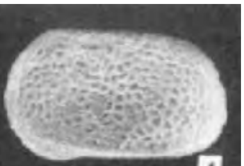
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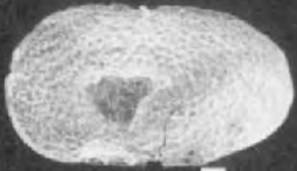
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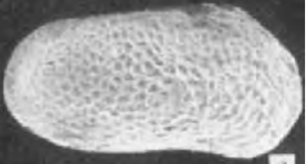
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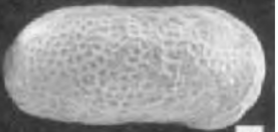
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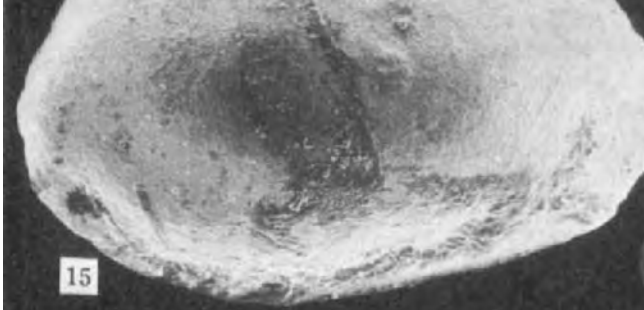
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Zhifang Formation. In addition, the underlying Heshanggou Formation belongs to the Early Triassic in age, so that the Zhifang Formation can be placed in the Middle Triassic.

Assemblage II, the *Tungchuania–Darwinula* assemblage, occurs in the Tongchuan Formation. This assemblage is characterized by a moderate number of both taxa and individuals. It is dominated by *Tungchuania* and the ostracods include *Tungchuania agrestata, T. aurita, T. perelegana, T. houae, T. quadratiformis, Darwinula rotundata, D. shensiensis, D.* sp. 3 and *Lutkevichinella reticulata.* The first three species of *Tungchuania* are comparatively abundant, *Darwinula rotundata* and *D.* sp. 3 take second place whilst *Lutkevichinella reticulata* is rare.

Tungchuania, established by Zhong Xiao–Chun in 1964, is a peculiar Upper Triassic genus of the Ordos Basin. Except for a few internal moulds of *Tungchuania* which were found in the Lower Jurassic Xinqiao Formation of Fujian, the genus *Tungchuania* always occurs in the Yanchang Group of the Ordos Basin, especially in the Wayaobu Formation and the Tongchuan Formation. *Darwinula rotundata, D. shensiensis* and *D.* sp. 3 are found in both the Tongchuan Formation and the Wayaobu Formation, even more abundantly in the latter. *Lutkevichinella reticulata* is a continuation from the Zhifang Formation and shows a decline in abundance. From the above, most of the ostracod species of the Tongchuan Formation in this region are closely related to the Wayaobu Formation. Thus the Tongchuan Formation should be regarded as Late Triassic in age, like the Wayaobu Formation. Because the Tongchuan Formation is at the bottom of the Yanchang Group and the Wayaobu Formation at the top, we can assign to the former an early Late Triassic age and to the latter a late Late Triassic age.

Assemblage III, the *Darwinula–Tungchuania* assemblage occurs in the Wayaobu Formation. It is composed of 3 genera and 14 species, namely *Darwinula shensiensis, D. liulingchuanensis, D. opinabilis, D. medialis, D. bella, D. accuminata, D. rotundata, D. subovatiformis, D.* sp. 3, *D.* sp. 4, *Tungchuania agrestata, T. aurita, T. houae* and *Lutkevichinella costata.* This assemblage is characterized by a great number of small sized *Darwinula* associated with *Tungchuania.* Among the above species, *Darwinula shensiensis, D. liulingchuanensis, D. medialis* and *D. bella* predominate. *Tungchuania aurita* and *T. houae* are second in abundance whilst *Lutkevichinella costata* is well preserved but rare.

The ostracod assemblage from the Wayaobu Formation, composed of small sized *Darwinula* and *Tungchuania,* differs entirely from the Jurassic assemblage of the Anding Formation which is represented by large-sized *Darwinula* and *Metacypris.* The Wayaobu Formation has such typical species as *Darwinula shensiensis, D. bella, D. liulingchuanensis, D. medialis, D. opinabilis, Tungchuania aurita, T. houae, T. agrestata* etc. *Darwinula liulingchuanensis* and *D. bella* were also found in the Upper Triassic of South China and Southwestern China. *D. rotundata, D. subovatiformis* and *D.* sp. 3 also occur in the Zhifang Formation or the Tongchuan Formation. *D. accuminata* was first found in the lower Triassic of the U.S.S.R. and later found in the Zhifang Formation of this region (see Su *et al.,* 1980). None of the species of *Darwinula* from the Wayaobu Formation have

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PLATE 2—Fig. 1. *Darwinula triassiana* Belousova, 1960, right view, 72002(2)–(1). Fig. 2. *Darwinula macilenta* Fang and Xu, 1978, right view, 72016(2)–(1). Fig. 3. *Darwinula* sp. 1, left view, 72011(1)–(1). Occurrence: Middle Triassic Zhifang Formation, Tongchuan, Shaanxi. Fig. 4. *Darwinula subovatiformis* Su *et al.,* 1980, left view, 72126(3). Fig. 5. *Darwinula rotundata* Lubimova, 1955, left view, 72128(3). Fig. 6. *Darwinula* sp. 3, right view, 72099(3). Fig. 7. *Darwinula shensiensis* Zhong, 1964, right view, 72093(3)–(1). Fig. 8. *Darwinula liulingchuanensis* Zhong, 1964, right view, 72107(1). Fig. 9. *Darwinula bella* Zhong, 1964, right view, 72106(2)–(1). Fig. 10. *Darwinula* sp. 4, left view, 72128(5). Fig. 11. *Darwinula medialis* Zhong, 1964, right view, 72126(2)–(1). Fig. 12. *Darwinula accuminata* Belousova, 1961, left view, 72094(2). Occurrence: Upper Triassic Wayaobu Formation, Tongchuan, Shaanxi. Fig. 13. *Darwinula* sp. 5. right view, 72257(3)–(3). Fig. 14. *Darwinula incurva* Bate, 1967, right view 72248(2)–(1). Fig. 15. *Darwinula giganimpudica* Wang and Ye, 1977, right view, 72259(1'). Fig. 16. *Darwinula sarytirmenensis* Sharapova, 1947, right view, 72248(3)–(2). Fig. 17. *Darwinula magna* Jiang, 1963, right view, 72245 (1)–(1). Fig. 18. *Darwinula lufengensis* Wang and Ye, 1977, right view, 72257(4)–(5). Occurrence: Middle Jurassic Anding Formation, Zichang, Shaanxi.


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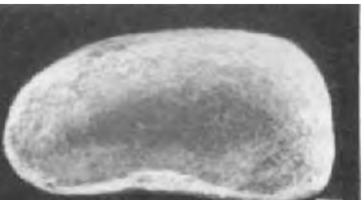
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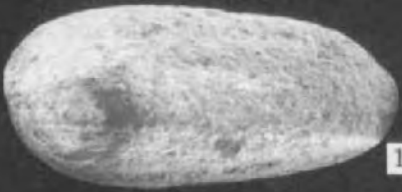
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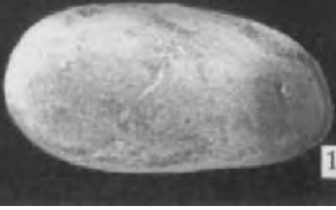
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been found so far in the overlying Jurassic strata or associated with known Jurassic ostracods. Species of *Tungchuania* from the Wayaobu Formation are also found in the Tongchuan Formation. It can be said that Assemblage III from the Wayaobu Formation shows a Late Triassic aspect and is similar to Assemblage II from the Tongchuan Formation. The two assemblages have the same genera and quite a number of common species such as *Tungchuania agrestata, T. aurita, T. houae, Darwinula shensiensis, D. rotundata* and *D.* sp. 3. The difference between them is that Assemblage III contains more species and many more individuals than Assemblage II. In addition, *Darwinula* predominates in the Wayaobu Formation while *Tungchuania* is more representative in the Tongchuan Formation. Thus the Wayaobu Formation can be regarded as late Late Triassic in age and the Tongchuan Formation as early Late Triassic.

The ostracods from the Hujiachun Formation and the Yongping Formation are the same as those from the Wayaobu Formation. *Tungchuania aurita, T. houae* and *Darwinula shensiensis* are also found in these two formations but are very few in number. The Hujiachun Formation and the Yongping Formation, which lie between the Tongchuan Formation and the Wayaobu Formation, should certainly be assigned to a middle Late Triassic age.

Assemblage IV, the *Darwinula–Metacypris* assemblage is represented by large-sized *Darwinula* and simply ornamented *Metacypris* and occurs in the Anding Formation. Only two genera, but very numerous individuals, appear in this assemblage which includes *Darwinula magna, D. incurva, D. sarytirmenensis, D. giganimpudica, D. lufengensis, D. oblonga, D.* sp. 5, *Metacypris armeniacumiformis, M. shensiensis, M. humilis* and *M. mackerrowi.* Among them, *Darwinula sarytirmenensis, D.* sp. 5, *Metacypris shensiensis* and *M. armeniacumiformis* are most abundant. *Darwinula oblonga, Metacypris mackerrowi* and *M. humilis* are rare. Other species occur in moderate quantity. Almost all the specimens are well preserved.

This assemblage, composed of large-sized *Darwinula* and *Metacypris,* is commonly seen in the Middle Jurassic of Europe and China. *Darwinula magna* is a typical Middle Jurassic species in China with a wide distribution in Xinjiang, Yunnan, Sichuan, Henan, Shaanxi, Qinhai and Gansu. *D. sarytirmenensis,* first found in the Middle Jurassic of the U.S.S.R., was also found in the Middle Jurassic in the above places in China associated with *D. magna.* and *D. incurva,* an English Middle Jurassic species also occurs in the Middle Jurassic of Yunnan, China. *D. giganimpudica* and *D. lufengensis* are the important members of the Lower Jurassic or Middle Jurassic ostracods in Hunan, Guangxi and Yunnan. *Metacypris shensiensis, M. armeniacumiformis* and *M. humilis,* named by Zhong in 1964, are the endemic species of the Anding Formation of this region. *M. mackerrowi,* first found in the Middle Jurassic of England, has also been found in China in the Middle Jurassic of Henan, Sichuan, Qinhai and Gansu. From the above, it is clear that most of the ostracod fossils of the Anding Formation are common in the Middle Jurassic of Europe and China. Accordingly, the age of the Anding Formation can be regarded as Middle Jurassic. As the important species *Darwinula magna, D. sarytirmenensis* and *D. incurva* are discovered more commonly in the upper part of the Middle Jurassic in the above mentioned places in China, and the underlying Zhiluo Formation is also assigned to the Middle Jurassic, the Anding Formation can be assigned to the late Middle Jurassic.

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Records of Late Carboniferous Ostracods from Jingyuan, Gansu, Northwestern China

CONG-GUANG SHI AND ZU-WANG LI
Nanjing Institute of Geology and Palaeontology, Academia Sinica, and Coal Geological Prospecting Company, Gansu, P. R. China

ABSTRACT

The Strata in the Ciyao area of Jingyuan, Gansu, northwestern China, may be divided from top to bottom into the Qinheishan Formation, the Chouniugou Formation, the Yushuliang Formation, the Jingyuan Formation, the Yanghugou Formation and the Taiyuan Formation. These are all well preserved and there are no conspicuous sedimentary gaps between them. The fossil ostracods described in this paper were obtained from the Jingyuan, the Yanghugou and the Taiyuan Formations. They contain seven genera, one subgenus and nine species, including one new subgenus and six new species.

This contribution starts with a brief description of the strata and their fossil ostracod content which is listed below, starting with the highest beds.

Overlying Strata:
Lower Permian.
Dahuanggou Formation—purple, grey-green sandstones, its base consisting of conglomerates.
........Parallel unconformity........
Upper Carboniferous
Taiyuan Formation—grey, grey-black limestone, with intercalated black shales and with siliceous rocks in the upper part, 41 m thick. The basal part yields *Cryptobairdia hongtuwaensis* n. sp., *Pseudobythocypris pediformis* (Knight), *Roundyella simplicissima* (Knight), *Waylandella informa* n. sp. and *Waylandella* sp.
————Conformity————
Yanghugou Formation
Upper section: The upper part consists of alternating black sandy shales, grey-black limestones and marls, with intercalated coal seams. The lower part comprises yellowish-brown siltstones, sandy shales, and fine-grained sandstones containing thin-bedded coal seams. The total thickness is 48 m and the beds yield *Cribroconcha jingyuanensis* n. sp., *Knoxina* (*Paraknoxina*) *ovata* subgen. et n. sp., and *Knoxiella normalis* n. sp.
Lower section: The top part consists of black marls and limestones. The middle and upper parts are black shales and grey-black sandy shales with intercalated medium-grained sandstones, thin-bedded limestones and coal seams. The lower part consists of greyish-white, coarse-grained sandstone. The total thickness is 35 m.

———————Conformity———————

Jingyuan Formation

Upper section: Grey-black and black sandy shales, with intercalated grey-black limestones, shales and coal seams, 73 m thick, yielding *Roundyella simplicissima* (Knight) and *Waylandella* sp.

Lower section: Grey-black and black shales, grey-white medium-and fine-grained sandstones, 29 m thick.

———————Conformity———————

Bottom

Underlying Strata:

Lower Carboniferous

Yushuliang Formation—grey-white sandstones, grey-black and black-grey shales, sandy shales, with intercalated black limestones, thin coal seams and thin-bedded gypsum.

The ostracods contained in the above-mentioned strata are mostly new species, the majority of which are close to those from the Carboniferous of the U.S.A. and Canada. *Cribroconcha jingyuanensis* sp. nov. is similar to *C. triqueta* Green from the lower Mississippian of Alberta, Canada; *Knoxina* (*Paraknoxina*) *gansuensis* n. sp. is very close in lateral outline to *K.* (*K.*) *texana* from the Upper Pennsylvanian of Texas, U.S.A., the character of abrupt convergence in the posterior quarter being reminiscent of *K.* (*K.*) *inflata* Croneis and Gale from the Upper Mississippian of Illinois; *Cryptobairdia hongtuwaensis* n. sp. approaches *C. folgeri* (Kellett) from the Upper Pennsylvanian of Oklahoma, U.S.A. In the present fauna two known species, *Roundyella simplicissima* (Knight) from the Jingyuan and Taiyuan Formations and *Pseudobythocypris pediformis* (Knight) from the Taiyuan Formation are of particular age significance. The former was first found in the Pennsylvanian of Missouri, U.S.A. Since then, most have been reported by subsequent researchers from the Upper Carboniferous of the U.S.A. and Spain. None have so far been reported from the lower Carboniferous. *P. pediformis* is a Pennsylvanian species from Kansas and Missouri, U.S.A. and the Upper Carboniferous of Spain. Judging from the above data, strata containing these ostracods should be assigned to the Upper Carboniferous and may be more or less compared with the Pennsylvanian of North America.

DESCRIPTION

Order PALAEOCOPIDA Henningsmoen, 1953
Suborder BEYRICHICOPINA Scott, 1961
Superfamily KIRKBYACEA Ulrich and Bassler, 1906
Family SCROBICULIDAE Posner, 1951
Genus ROUNDYELLA Bradfield, 1935

ROUNDYELLA SIMPLICISSIMA (Knight, 1928)
(Pl. 2, Figs. 10, 11)

Amphissites simplicissima KNIGHT, 1928, p. 266, pl. 32, figs. 11a-d, pl. 34, fig. 6.
Roundyella simplicissima, BRADFIELD, 1935, p. 66; COOPER, 1946, p. 108, pl. 17, figs. 29–36; SOHN, 1961,

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PLATE 1—Figs. 1, 2. *Cryptobairdia hongtuwaensis* n. sp. 1a, b, right and dorsal views of carapace. Holotype, Cat. No. Jc20411, ×63; 2a, b, right and dorsal views of carapace. Paratype, Cat. No. Jc20412, ×63. Figs. 3, 4. *Knoxiella normalis* n. sp. 3a, b, left and dorsal views of carapace (right valve damaged anteriorly). Holotype, Cat. No. Jc20311, ×63; 4a, b, left and dorsal views of carapace (right valve damaged posteriorly). Paratype, Cat. No. Jc20312, ×63.

1a

1b

2a

2b

3a

3b

4a

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pp. 150, 151; SANCHEZ DE POSADA, 1977, p. 417, pl. 3, figs. 4, 5; BECKER and MAIN, 1982, p. 326, pl. 2, fig. 2; pl. 3, figs. 3, 4.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Plesiotype	Jc20111	550	340	—
Plesiotype	Jc20112	680	430	—

Horizon.—The upper section of the Jingyuan Formation and the basal part of the Taiyuan Formation.

Superfamily KLOEDENELLACEAE Ulrich and Bassler, 1908
Family BEYRICHIOPSIDAE Henningsmoen, 1953
Genus KNOXINA Coryell and Rogatz, 1932

Discussion.—When establishing the genus *Knoxina,* Coryell and Rogatz (1932: 283) pointed out that in addition to the characters of shell outline and surface ornamentation, another character is "left valve overlapping the entire margins of the right except dorsal margin." At the same time as Coryell and Rogatz described the four species with the left valve larger than the right, they assigned *Jonesina texana* to *Knoxina texana.* Since then, some researchers have also established new species based on the relative size of the two valves. The species founded by Upson (1933), Croneis and Gale (1939) were also based on the left valve being larger than the right. When establishing *Knoxina rogatzi,* Croneis and Gukte (1939) pointed out that the two valves of their new species were equal or subequal in size, but did not indicate which valve was the larger. It was Green (1963) who established two new species in which the right valve was the larger.

The writers observe that the shell outline (shape) and ornamentation as well as other characters of the ostracods obtained from Jingyuan (including the lower Carboniferous forms) have the essential characters of the genus *Knoxina,* but their right valves are all larger than their left. Except for *Knoxina rogatzi* which has equal-sized valves, all other species of *Knoxina* have the left valve larger than the right or *vice versa.* The different overlaps of the two valves are of importance in the classification of genera. Thus, the writers suggest that based on the difference in size of the two valves, *Knoxina* may be subdivided into two subgenera, namely, *Knoxina* (*Knoxina*) and *Knoxina* (*Paraknoxina*) n. subgen.

Subgenus KNOXINA Coryell and Rogatz, 1932

Type species.—*Knoxina* (*Knoxina*) *lecta* Coryell and Rogatz, 1932

Diagnosis.—Carapace subquadrate to truncately ovate in lateral view; dorsal margin straight; trilobate; with a parallel ventral marginal ridge. Left valve larger, overlapping the right all

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PLATE 2—Figs. 1 2. *Waylandella* sp. 1, lateral view of technomorphic right valve inside-mould. Described specimen, Cat. No. Jc20621, × 63; 2, lateral view of technomorphic right valve inside-mould. Described specimen, Cat, No. Jc20622, ×63; Figs. 3a, b. *Cribroconcha jingyuanensis* n. sp. right and dorsal views of carapace (right valve damaged posteriorly). Holotype, Cat. No. Jc20511, ×63. Figs. 4, 5. *Waylandella informa* n. sp. 4a–c, right, dorsal and left views of carapace. Holotype, Cat. No. Jc 20611, ×63; 5, right view of carapace. Paratype, Cat. No Jc 20612, ×63. Figs. 6, 7. *Pseudobythocypris pediformis* (Knight). 6a, b, right and dorsal views of carapace. Plesiotype, Cat. No. Jc20711, ×63; 7, right view of carapace. Plesiotype, Cat. No. Jc 20712, ×63. Figs. 8a, b. *Knoxina* (*Paraknoxina*) *gansuensis* subgen. n. sp. left and dorsal views of carapace. Holotype, Cat. No. Jc20211, ×63. Figs. 9a, b. *Knoxina* (*Paraknoxina*) *subovata* subgen. n. sp. left and dorsal views of carapace. Holotype, Cat. No. Jc20221, ×63.·Figs. 10, 11. *Roundyella simplicissima* (Knight). 10, lateral view of technomorphic left? valve inside-mould. Plesiotype, Cat. No. Jc20111, ×63; 11, lateral view of technomorphic left? valve. Plesiotype, Cat. No. Jc20112, ×63.

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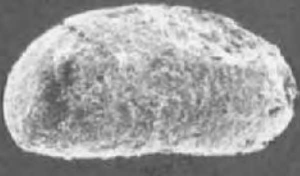

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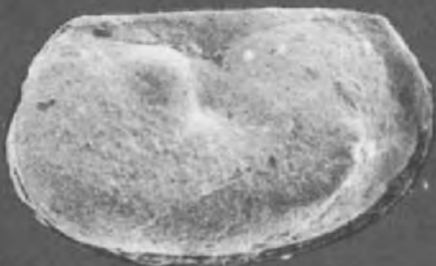

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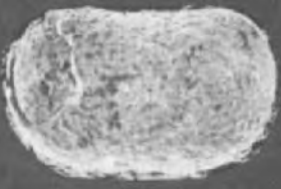

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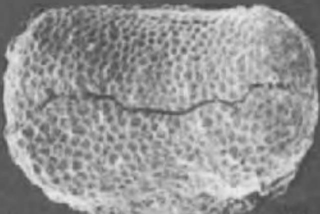

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around the free margin, most strongly at the ventral margin. Surface ornamented with fine tubercles or reticulations. Elliptical or cuneiform in dorsal view.

This subgenus *Knoxina* (*Knoxina*) includes the following species: *Knoxina* (*Knoxina*) *elliptica* Coryell and Rogatz, 1932, *Knoxina* (*Knoxina*) *incurvata* Coryell and Rogatz, 1932, *Knoxina* (*Knoxina*) *inflata* Croneis and Gale, 1932, *Knoxina* (*Knoxina*) *nebraskensis* Upson, 1939, *Knoxina* (*Knoxina*) *texana* (Harlton, 1929).

Subgenus PARAKNOXINA n. subgen.

Type species.—*Knoxina* (*Paraknoxina*) *gansuensis* n. subgen., n. sp.

Diagnosis.—Except that the right valve is larger than the left, characters are the same as for *Knoxina* (*Knoxina*).

This new subgenus, *Knoxina* (*Paraknoxina*), is here proposed to include the following species: *Knoxina* (*Paraknoxina*) *costata* Green, 1963, *Knoxina* (*Paraknoxina*) *marginata* Green, 1963, *Knoxina* (*Paraknoxina*) *gansuensis* n. sp. and *Knoxina* (*Paraknoxina*) *subovata* n. sp.

KNOXINA (PARAKNOXINA) GANSUENSIS n. subgen., n. sp.

(Pl. 2, figs. 8a, b)

Description.—Carapace truncately ovate in lateral view; dorsal margin straight and long; anterior end higher than the posterior; the upper parts of both ends united with dorsal margin form equally obtuse angles; ventral margin evenly convex. Greatest height near the centre. Greatest length near the mid-line. S_1 short and shallow; S_2 deep, wide and connected with a pit at its lower end. L_1 rounded, parallel to ventral margin from the midventral, developing into a wing-like ridge in a posterior direction to the mid-posterior part. Surface granulated. Cuneiform in dorsal view, strongly compressed in the posterior quarter of the length which gives a concave outline to each valve, delimitting the posterior caudal process. The middle and the anterior quarter concave. Right valve larger, overlapping the left all around the free margin.

Measurement.—(μm)

Type	Cat. No.	L.	H.	W.
Holotype	Jc20211	920	530	400

Discussion.—This new species and the lower Mississippian *Knoxina* (*Paraknoxina*) *costata* Green (1963: 106, Pl. 4, figs. 21, 22) from the northwestern terrace of Banff in Alberta of Canada as well as *Knoxina* (*Paraknoxina*) *marginata* Green (1963: 107, Pl. 5, figs. 1–6) all have the same type of overlap in that the right valve is larger than the left. *K. gansuensis* differs from the other two species, however, in its cuneiform dorsal view and the sharp compression in the posterior quarter of its length. The new species is similar in lateral view to the Upper Pennsylvanian *Knoxina* (*Knoxina*) *texana* Coryell and Rogatz (Harlton, 1929: 146, Pl. 1, fig. 14) from Texas and in its sharp posterior compression the new species is reminiscent of the Upper Mississippian *Knoxina* (*Knoxina*) *inflata* Croneis and Gale (1939: 266, Pl.6, figs. 17, 18) of Illinois. The chief difference lies in the larger right valve of the new species and the larger left valve of the other two.

Horizon.—The upper section of the Yanghugou Formation.

KNOXINA (PARAKNOXINA) SUBOVATA n. subgen. and sp.

(Pl. 2, figs. 9a, b)

Description.—Carapace small in size, truncately oblique-ovate in lateral view; dorsal margin straight and long; postéro-dorsal angle larger than the anterodorsal one. Anterior end apparently higher than the posterior, broadly rounded, meeting the ventral margin roundly. The upper part of the posterior end truncated, the lower meeting the ventral margin evenly. Free margin rounded in outline, inclined forward. Greatest height at the anterior one-third and greatest length near the mid-line. S_1 short and shallow, S_2 deep and wide, the lower part united with a pit. L_1 rounded, from the mid-ventral part parallel to the ventral margin and developing posteriorly into a wing-like ridge. Surface reticulated. Elongate ovate in dorsal view, the posterior one-third converging posteriorly. Anterior end bluntly rounded; posterior end pointedly rounded. Curved inwards in the middle and the anterior quarter of the length. Right valve larger, overlapping the left all around the free margin.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Holotype	Jc20221	600	370	290

Discussion.—This new species is distinguished from *Knoxina* (*Paraknoxina*) *gansuensis* n. sp. in its dorsal and lateral outlines.

Horizon.—The upper section of the Yanghugou Formation.

Family GEISINIDAE Sohn, 1961
Genus KNOXIELLA Egorov, 1950
KNOXIELLA NORMALIS n. sp.
(Pl. 1, figs. 3a–4b)

Description.—Carapace truncately elliptical in lateral view; dorsal margin straight and long; anterior and posterior dorsal angles subequal. Anterior end higher than the posterior, broadly rounded and slightly inclined downward. Posterior end narrowly rounded and inclined upward. The middle part of the ventral margin nearly straight, broadly rounded at the anterior and inclined upwards in its posterior part. Greatest height in the middle and greatest length near the midline.

Nearly straw sandal-shaped in dorsal view, concave in the middle part. Hinge groove slender. Anterior and posterior ends of the right valve overreaching the left valve. Greatest thickness in the posterior one-third. S_1 short and shallow, sometimes inconspicuous. S_2 deep and long, with a faintly visible rounded node in the front. Surface reticulated. Right valve larger, overreaching and overlapping all a round the free margin of the left.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Holotype	Jc20311	1060	600	440
Paratype	Jc20312	1100	650	430

Discussion.—*K. normalis* is distinguished from *Knoxiella ischimensis* Polenova (1953: 49, Pl. 4, figs. 5, 6) from the Upper Devonian of the U.S.S.R. in that the right valve of the latter overreaches the left valve dorsally. Roundly oblong in lateral view with a smooth surface.

Horizon.—The upper section of the Yanghugou Formation.

Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily BAIRDIACEA, Sars, 1887
Family BAIRDIIDAE Sars, 1887
Genus CRYPTOBAIRDIA Sohn, 1960
CRYPTOBAIRDIA HONGTUWAENSIS n. sp.
(Pl. 1, figs. 1a–2b)

Description.—Carapace nearly rhomboidal in lateral view; dorsal margin arched; anterodorsal margin straight, with the lower part inwardly concave. Anterior end rounded. Posterior beak conspicuous, and lying a little below the midline. The middle part of the ventral margin slightly concave, anterior and posterior parts inclined upward. Greatest thickness in the anterior one-third. Fusiform in dorsal view, thickest in the middle. Left valve larger, almost completely overlapping the free margin and the hinge area more or less overreaching the right valve. The overlapping areas on the antero- and postero-dorsal margins and the ventral margin are relatively wide. Surface granulated or pitted.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Holotype	Jc20411	1160	600	500
Paratype	Jc20412	1170	630	480

Discussion.—This new species is similar to the Upper Mississippian *Cryptobairdia folgeri* (Kellett, 1934: 136, Pl. 18, figs. 1, 4: 19, figs. 1, 4, 6) from Oklahoma, but differs from the latter in its sloping anterodorsal margin and in its smooth surface.

Horizon.—The basal part of the Taiyuan Formation.

Suborder METACOPINA Sylvester-Bradley, 1961
Superfamily HEALDIACEA Harlton, 1933
Family HEALDIIDAE Harlton, 1933
Genus CRIBROCONCHA Cooper, 1941
CRIBROCONCHA JINGYUANENSIS n. sp.
(Pl. 2, figs. 3a, b)

Description.—Carapace obliquely elliptical in lateral view; dorsal margin bluntly angulate and curved outward. Posterior end higher than the anterior, broadly rounded. Anterior end inclined downward and rounded. Ventral margin nearly straight. Greatest height in the middle. Greatest length near the midline. Nearly cuneiform in dorsal view. Greatest thickness at the ridges. A groove-shaped ridge opens forward in the posterior part of the carapace, its upper part overreaches the margin and its posterior part forms a sloping ridge. Inside the groove-shaped ridge are longitudinal reticulations. Left valve larger, overlapping the right all around the free margin.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Holotype	Jc20511	700	400	330

Discussion.—In dorsal view *C. jingyuanensis* resembles the lower Mississippian *Cribroconcha triquelia* Green (1963: 161, Pl. 13, figs. 17–20) from northern Jasper, Canada, but the latter differs in that its dorsal margin is strongly arched in lateral view and the anterior end is lower than the posterior, the surface is covered by coarse, sparse reticulation and the arched posterior ridge does not over-reach the dorsal margin.

Horizon.—The upper section of the Yanghugou Formation.

Genus WAYLANDELLA Coryell and Billings, 1972
WAYLANDELLA INFORMA n. sp.
(Pl. 2, figs. 4a–5)

Description.—Carapace nearly elliptical in lateral view; dorsal margin evenly convex. Posterior end rounded, higher than the anterior. Anterior end rounded and inclined downward. The middle part of the ventral margin slightly concave. Greatest height in the middle. Greatest length near the middle. Posteroventral corner of right valve with a tubercle; posteroventral corner of left valve with only a slight swelling. Left valve larger, overlapping the right all around the free margin. Surface smooth.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Holotype	Jc20611	560	320	250
Paratype	Jc20612	560	320	300

Discussion.—*Waylandella informa* n. sp. differs from the other species of *Waylandella* in being slightly swollen at the posteroventral corner of left valve and in having a tubercle at the posteroventral corner in the right valve.

Horizon.—The basal part of the Taiyuan Formation.

WAYLANDELLA sp.
(Pl. 2, figs. 1–2)

Description.—Reniform in lateral view; dorsal margin evenly convex. Posterior end higher than the anterior, obliquely rounded. Greatest height in the middle or behind the middle. Greatest length near the midline. There is a spine on the posterodorsal part of the valve and an inconspicuous tubercle near the posteroventral angle.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Described specimen	Jc20621	620	330	—
Described specimen	Jc20622	620	330	—

Discussion.—The specimens described herein are close in lateral view to *Waylandella dartyensis* (Benson and Collinson, 1958: 9, Pl. 1, figs. 4–6) from Missouri, U.S.A. *W. dartyensis,* however, is distinguished by its prominent posteroventral spines and its lack of a posteroventral tubercle. As the present specimens are only inner moulds, they are not given a specific name.

Horizon.—The upper section of the Jingyuan Formation.

Family BAIRDIOCYPRIDIDAE Shaver, 1961
Genus PSEUDOBYTHOCYPRIS Shaver, 1958
PSEUDOBYTHOCYPRIS PEDIFORMIS (Knight, 1928)
(Pl. 2, figs. 6a–7)

Bythocypris pediformis KNIGHT, 1928, p. 326, 328, Pl. 44, fig. 3.

Pseudobythocypris pediformis, SHAVER, 1958, p. 122–124; SANCHEZ DE POSADA, 1977, p. 423, Pl. 5, figs. 5–9.

Discussion.—Except that a few are smaller, wider and have a blunt posteroventral angle, the present specimens have the same chief characters as those of *Bythocypris pediformis* described by Knight (1928) from the Pennsylvanian of Missouri, U.S.A. Their adductor muscle scars are faintly visible and consist of many minute scars forming a round scar group.

Measurements.—(μm)

Type	Cat. No.	L.	H.	W.
Plesiotype	Jc20711	550	300	220
Plesiotype	Jc20712	510	270	210

Horizon.—The basal part of the Taiyuan Formation.

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Indexes

Genera and Species Index

(including names of new suprageneric taxa)

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General and Author Index

References to papers which appear in this volume are shown in bold face.