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Animals in aquatic environments: adaptation of mammals to the ocean

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HOW AND WHY THE WHALES HAVE DEVELOPED and why they need such large brains to adapt successfully to the marine environment are questions that have been of great interest for many years.

ORIGIN OF CETACEANS

In his classic review of the origins of the whales Kellogg (20) said: "It is not necessary to assume that any known archaeocete is ancestral to some particular kind of whale, for the archaeocete skull in its general structure seems to be divergent from rather than antecedent to the line of development that led to the telescoped condition of the braincase seen in the skulls of typical cetaceans. On the contrary it is more probable that the archaeocetes are collateral derivatives of the same blood-related stock from which the Mysticeti and the Odontoceti sprang." For the generalized precursor of the three groups Kellogg indicates evidence for a primitive insectivore-creodont stock.

Winge (57) selects as the precursors of modern whales the Hyaenodonts: "The Hyaenodonts, the nearest stock-forms of the cetacea among terrestrial mammals, lived at the beginning of Tertiary times . . . . The whales must have made their appearance somewhere within the territory occupied by the Hyaenodonts, and probably in the old part of the Tertiary: in agreement with this the most primitive cetacean that is yet known, the Hyaenodont-like Protocetus . . . is found . . . in eocene strata . . . . But soon the members of the family must have spread widely. . . . Zeuglodon appears to have found its way during the Eocene to all oceans. . . . The Zeuglodonts died out early in Tertiary."

In Winge's opinion the Balaenidae originated among the more primitive genera of Zeuglodonts and gave rise to the modern Balaena whales. Another group called the Squalodontidae also arose from the Balaenidae which later gave rise to the modern toothed whales; these branched off in Tertiary times during the Miocene. From the Squalodontidae came the Platanistidae which in turn gave rise to the large modern group of Delphinidae. The modern river dolphins, *Inia geoffrensis*, are carry-overs from the primitive Platanistidae (Platanistoidea). The modern Delphinidae include the bottle-nose dolphin *Tursiops truncatus*, the common dolphin *Delphinus delphis*, the pilot whale *Globicephala scammoni*, and the killer whale *Orcinus orca* (*Grampus orca*), as well as members of the family Phocaenidae, the common porpoise *Phocaena phocaena*.

TABLE 1. *Brain and Body Weights of Whales (Cetaceans)*

Genus and Species	Common Name	Qty.	Cat. No.	Sex	Brain Wt., g	Body Wt., kg	Body Lgth., m	Remarks and Ref.
Phocaena phocaena (L)	Harbor porpoise	1	70[e]	M	1735[a]	142.43		Crile & Quiring (10)
		1			460[a]	53.80		Warncke's *P. communis*, see von Bonin (56)
Lagenorhynchus albirostris (G)	White-beaked porpoise	1			1126[a]	67.56		Warncke's wt., see von Bonin (56)
Tursiops truncatus (M)	Bottle-nose dolphin	1		F	1100[a]	45.50	1.626	Lilly & Miller (34)
		1		F	1175[b]	66.00	1.981	Lilly (30) and Kruger (23)
		1		F	1330[b]	97.70	2.159	Lilly (30) and Kruger (23)
		1		M	1520[b]	117.30	2.337	Lilly (30) and Kruger (23)
		1		F	1588[b]	140.00	2.400	Lilly (30) and Kruger (23)
		1		F[h]	1685[b]	156.00	2.591	Lilly (30) and Kruger (23)
		1		F	1707[b]	153.60	2.565	Lilly (30) and Kruger (23)
		1			1886[a]	287.00		Warncke's *T. tursio*, see von Bonin (56)
Orcinus orca (L)	Pacific killer whale	1		F	4500[a]	1861.70	5.23	Unpublished data
Globicephala melaena (T)	Pilot whale	1			2458[a]	983.00		Warncke's *G. melas*, see von Bonin (56)
Delphinapterus leucas (P)	White whale	2	1) 32)	F	2354[a]	303.23		Crile & Quiring (10)
		4	7) 19) 23) 34)	M	2349[a]	441.31		Crile & Quiring (10)
Balaenoptera acutorostrata (L)	Little piked whale	1			2490[a]	62,250		Warncke's *B. rostrata*, see von Bonin (56)
Megaptera novaeangliae (B)	Hump-backed whale	1			3531[a]	42,372		Warncke's *M. boöps*, see von Bonin (56)
Balaenoptera physalus (L)	Finback whale	1	Cst.3	F	5970[d]		15.240	Jansen (18, 19)
		1	Cst.1	F	6500[a]		20.726	Jansen (18, 19)
		1	C294	M	6850[d]		16.459	Jansen (18, 19)
		1	C291	M	6920[d]		19.812	Jansen (18, 19)
		1	Cst.2	M	7100[a]		16.459	Jansen (18, 19)
		1	Cst.2	M	7320[c]		16.459	Jansen (18, 19)
		1	C293	M	7150[d]		20.421	Jansen (18, 19)
		1	C292	F	7875[d]		20.421	Jansen (18, 19)
		1			6700[a,f]		18.288	Guldberg's *B. musculus* Company, see Tower (53)
		1			5950[d]			Ries and Langworthy, see Tower (53)
Sibbaldus musculus (L)	Blue or sulfur whale	1			3636[a]	50,904		Warncke's *B. musculus*, see von Bonin (56)
		1	748		6800[a]	58,059		Crile & Quiring (10)
		1			5678[a]			Wilson's *B. sulfurea*, see Tower (53)
Physeter catadon	Sperm whale	16			6400–9200[a,g]	264,000	14.935–16.459	Kojima (22)
		1			7000[a]			Ries and Langworthy, see Tower (53)
		1			7980[a]			Ries and Langworthy, see Tower (53)

[a] Fresh. [b] Fresh, perfused with 10% formalin. [c] After 1 month in 10% formalin. [d] After more than 1 year in 10% formalin. [e] Catalog number used by authors indicated. [f] Without dura. [g] Average, 7800 g. [h] Pregnant.

ADAPTATION

Brain Weights versus Body Length/Body Weight Relationships

In general, the central nervous system of the Archaeoceti as estimated from the cranial capacities are smaller for a given body length than the Miocene and later whales. Among the Archaeoceti the figures for Dorudon given by Kellogg (20) run from 310 cc to 800 cc. The cranial capacity for *Prozeuglodon isis* (60 feet long) is given as greater than 800 cc. Of the modern whales there are no adult forms in the sea with cranial capacities as small as these figures for the Archaeoceti, despite smaller body sizes. Von Bonin (56), Tower (53), Jansen (18, 19), Kojima (22), and Lilly give brain-weight figures for modern whales (table 1). One generalization that apparently can be made from these data is that there is no deep-sea adult cetacean with a brain smaller than about 900 to 1000 g. This finding suggests that to live in the sea, breathing air with a mammalian physiology and a mammalian skin, requires a large brain for a successful adaptation over the millenia. (Presumably this does not apply to the more primitive Platanistidae which inhabit fresh-water rivers and estuaries; these small forms have smaller brain sizes.) Water-breathing forms of comparable body sizes have very much smaller brains, e.g., the brain weight of a 200-kg *Galeocerdo tigrinis*, a tiger shark, is 107.5g (2,10).

At the opposite end of the scale from the smallest of the Cetacea is the largest known brain, that of the sperm whale *Physeter catodon*. Kojima gives 16 brain weights of this species ranging from 6400 to 9200 g (22) in animals whose body lengths range from 40 feet to 60 feet and whose body weights can be up to 60 tons. Because of technical difficulties in handling such large animals, very little is known of their behavior and very few experiments have been done to explain their adaptation to the marine environment. It is known that they dive to at least 620 fathoms in search of giant squid; several of them have been brought up entangled in submarine cables from these depths (15, 27). Relatively little is known of their intelligence, their communication systems, or their physiology at the present time.

Tursiops truncatus, an Experimental Subject

Currently the type of animal for experimental work with the Cetacea is much smaller than the sperm whale. The numerous Atlantic bottlenose dolphins, *Tursiops truncatus* M., of the coasts and bays of the state of Florida are the best known Cetaceans. This dolphin has been kept in captivity up to 17 years in marine aquaria. Various aspects of their adaptation to the marine environment have been accumulating over the past five decades. The gross anatomy of their brain was described by Langworthy in 1931–2 (24–26). In 1955 a cooperative study by J. Rose, C. W. Woolsey, V. Mountcastle, J. C. Lilly, K. Pribram, L. Malis, L. Kruger, and J. Hind gave some more exact information on the brain weight range in this species as related to given body lengths

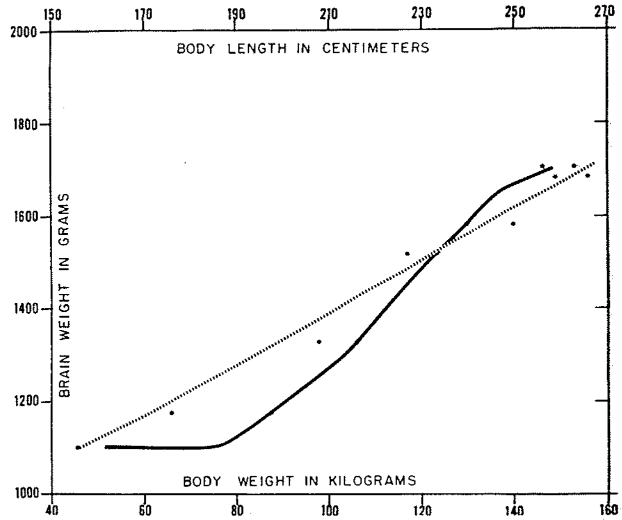

FIG. 1. The brain weight-body weight (*dotted curve*) and the brain weight-body length (*solid line*) relationships in the bottlenose dolphin, *Tursiops truncatus*. The critical value of the mammalian brain weight is approximately 900 to 1000 g. All the brains of this species measured to date are above this threshold.

and body weights (23, 30). Their results are summarized in figure 1.

Recently we acquired a smaller specimen than any of those in the 1955 study, values for which are also given in figure 1. Study of this figure shows that these animals, probably even at birth, have a brain weight of at least 900 to 1000 g and, that during the phase of rapid growth (at least the first 12 years), the brain grows to a weight above that of the average modern man. The brain weight-body length ratio and the brain weight-body weight ratio are fairly close to those of man (1, 8, 9, 55).

The absolute brain weights and the relative ratios of brain weight to other biological variables do not imply per se a high degree of adaptation to the marine environment, nor do they of themselves imply a high degree of intelligence. Quite independent measures of adaptation and of intelligence must be devised for these animals.

Physiological Functions

For the specific problems of the degree of their adaptation to the marine environment, many physiological functions must be investigated and the differences from the land-borne mammals be elucidated. To evaluate the intelligence of a marine-dwelling mammal, appropriate measures must be devised quite separately from biological measures. If by high intelligence we imply a high degree of plasticity and flexibility in the animal's adaptation to its own environment and in its adaptation to novel and strange environments, the two questions can be melded into a general approach to the problems of adaptation of these animals.

In terms of finding supplies essential to the maintenance of mammalian life in water, the problem can be divided into four general areas: the obtaining of oxygen in the gas phase, the procurement of food within the sea, the procurement of supplies of water, and the seeking and obtaining of cooperation from other animals of the same species in the above pursuits.

RESPIRATION AND INGESTION. The maintenance of an oxygen supply means the development of the blowhole from the primitive nostrils and its gradual shift from the end of the rostrum as in land mammals to a position on the forehead as in present-day whales and dolphins. The anatomy of the Delphinid nose is given in some detail by Lawrence & Schevill (29). This anatomy illustrates in great detail the development over the millenia of a beautifully modified exit to the respiratory tract placed in such a way that the animal merely surfaces the far end of his head in order to obtain air. Studies by the Schevills and in this laboratory show that respiration can take place in a very brief period of time, i.e., 0.3 sec for inspiration and for expiration. Irving *et al.* (17) determined the volumes of the exchange as 5 to 10 liters. Thus the average flow rate is about 50 liters per sec during expiration and during inspiration.

One aspect of respiration control which seems to be a necessary adaptation to the marine environment is the adjustment of respiration time to surfacing time and the inhibition of respiratory acts at all other times. In our experience in 1955 we demonstrated that small doses of anesthetic (10 mg per kg of Nembutal) stopped respiration before any other signs of anesthesia could be elicited (30, 31). Such an unexpected finding has been corroborated in our later unpublished work. The adaptive value of an inhibition of respiration before loss of consciousness may have a high survival value in these animals. In their native habitat a given respiratory event must be related to the stringent circumstances of reaching the surface of the sea at the proper point and relating the respiratory act to all of the other events going on around the animal, including the height of the waves, the position of the animal on a given wave in relation to the strength of the wind, the blowing spray, possible debris, other animals, and the position of potential enemies such as sharks. Such a complex coordination of respiration with all other afferent inputs and with the motor behavior of the animal in reaching the surface implies that the release of the inhibition of the act is controlled at a thalamocortical level.

To support this point of view we implanted electrodes in the thalamus of a dolphin to determine the effects on respiration of electrical stimulation (34). We found that respiration is controlled in the nucleus ellipticus of the thalamus (a special nucleus found only in the cetaceans). Stimulation in this nucleus caused explosive respiratory acts to take place in extremely rapid succession. Thus the Cetacea possess a very well-developed respiratory control center at least as high as the thalamus. Presumably this nucleus also has projections to and from the cerebral cortex; these projections have yet to be demonstrated.

In order to maintain the completely nasal nature of their respiratory pattern, i.e., breathing through the blowhole and not through the mouth, means that whales must somehow cross the respiratory tract through the alimentary tract. The classic literature on cetology maintains that the larynx is inserted in the nasal pharynx and held there by a strong sphincter at all times (44, 57). Recently we have found, as has D. Brown (personal communication), that these animals do not hold the larynx in this position at all times, and that during feeding and swallowing the larynx is freed, laid in the bottom of the pharynx, and the food is passed over it. If one carefully examines the cross-sectional anatomy of these animals, one finds that with the larynx held in the nasal pharynx there is not room between the larynx and the bone of the lower jaw to pass food of the size which these animals normally swallow. If one examines an animal such as those confined in our laboratory during feeding, one can palpate the throat region and find the larynx being pulled downwards and pressed outwards during the swallowing act.

Thus the respiratory pattern must also be related to the swallowing pattern. The two patterns must be carefully differentiated by the animal to prevent swallowing into the respiratory system and blowing of air into the alimentary system. Brown has noted the impaction in a larynx of a rock which came in through the mouth (in a Globicephala) and also some vomitous brown fluids of fish which are swallowed whole (personal communication).

NUTRITION. An interesting modification of this position is that of the mother during lactation. As Eichelberger *et al.* have shown (11), dolphin's milk consists of 103.75 g of protein per liter in *T. truncatus* species (an average of samples from two specimens) and 111.1 g per liter in a *Stenella plagiodon*, and 141 g of fat per liter in *T. truncatus* (an average sample from three animals) and 180 g per liter in one *S. plagiodon*. We have recently found that the baby consumes between 3 and 4 liters of milk per day. Thus the lactating mother must produce, in addition to her own metabolic requirements, the excess fat and protein for the milk. Each gram of fat metabolized to CO_2 and water produces 1.07 ml of water; each gram of metabolized protein could produce 0.4 ml of water. The estimated water requirement for the adult animal is 1.64 liters per day (51). An adult *Tursiops* eats from 5.45 to 6.36 kg of whole fish per day. The food fish is *Poronotus triacanthus* (butterfish) which has a range per body weight (edible portions) of 16.2 to 18.2 per cent protein and 7.6 to 22.2 per cent oil (3). The full ration of the dolphin per day adequately furnishes the necessary supplies without the ingestion of sea or fresh water (51).

NATURAL VERSUS UNNATURAL EXISTENCE. Various other kinds of adaptations of the mammalian body and functions to the marine environment include cardiovascular, skeletal, and soft-tissue adjustments to an existence involving very rapid swimming and neutral buoyancy. One can see this extreme adaptation to such an environment by taking one of these animals out of water. The first requirement is to keep the skin wet, otherwise it sloughs off very rapidly. The skin must not be exposed to the sun or it burns very rapidly. Even if the skin is kept wet and shaded, the animal will probably expire within 6 days, apparently because of cardiovascular overload. Each breath under these conditions is a laborious event; for the first time in its life, the animal must lift a large portion of its own body weight against gravity in order to inflate the lungs. Similarly the intrathoracic pressure rises and impedes venous return to the chest and to the heart. Thus their adaptation to the swimming buoyant environment has eliminated adaptation to the pressures of the gravity-countering forces distributed over smaller areas of the body.

SLEEP. Another adaptation in *T. truncatus* to the buoyant swimming environment is the sleep pattern which has been observed recently in our laboratory. In brief, the sleep pattern consists in waking for every respiration and rising to the surface for each breath, if not already at the surface. An apparently unique feature of their sleep pattern is that they sleep with one eye closed at a time. In a series of ten 24-hour experiments in our laboratory, it was found that closure of both eyes is an extremely rare event. The period of sleep for each eye totals 2 to 3 hours a day. This pattern may assure that the animal is always scanning his environment with at least half of his afferent inputs.

Communication

SONIC AND ULTRASONIC EMISSIONS. Of course vision may be of little use in very murky water, at night without light, or in the depths of the sea. To compensate for this deficiency of vision these animals have developed a sonic-ultrasonic echo ranging and recognition system. This active "sonar" system allows them to scan their environment and recognize objects at fairly sizable distances in spite of the absence of light. The studies of Schevill, Lawrence and Worthington (28, 45–49, 58), Kellogg (21), Norris *et al.* (41, 42), and others have elucidated some of this particular adaptation par excellence of these animals to the sea. Some of the anatomical factors which may be involved in this system are presented by Lawrence & Schevill (29), Fraser & Purves in their monograph on cetacean ears and hearing (14), and Reysenbach de Haan (43).

This sonar ability may allow each animal to detect the presence of friend or foe or food under any and all conditions. However, these animals apparently have additional means of receiving information from others of their own species by vocalizations and thus cooperating in food hunting, in their rescue operations, and in their attack and defense against sharks. Several observations by Caldwell *et al.* (4–7, 50), Moore (39, 40), and Hubbs (16) in the wild demonstrate this cooperative action. Other observations in oceanaria by Townsend (54), McBride and Hebb (36–38), and Essapian and Tavolga (12, 13, 52) further elucidate these points.

In our experience we discovered a particular whistle which they emit when they are in distress and which elicits the full cooperation of any animals within earshot (30–32). This whistle rises in frequency and then falls in frequency in a particular attention-getting and demanding fashion. We have also found that the first part of the distress whistle, i.e., the part which rises in frequency, is used alone as an attention call when one animal is trying to attract the attention of others in the neighborhood. Lilly & Miller (33) describe vocal exchanges between pairs of dolphins which bear a formal resemblance to human conversation in that each animal transmits only during the silences of the other animal and that vocal exchanges in the proper sense of that term take place. Such exchanges are found for clicks and for whistles. These findings have given rise to a postulated dolphin language called "Delphinese."

LANGUAGE CONCEPTS. The existence of such a language, if proved, will give these animals a means of cooperative adaptation to the marine environment par excellence which could not be obtained by individuals isolated from one another. If this postulated language is more complex than that of birds, fishes, reptiles, and the smaller brained mammals from the chimpanzee down, the degree of adaptation will correspond to the degree of the complexity and levels of abstraction which can be transmitted from one animal to the other. The fantastically great gain in adaptive abilities of those who have such a language is most easily demonstrated by another species, *Homo sapiens*. As soon as man acquired a language, he adapted so rapidly and so well to his environment that he was able to eliminate practically all competing species.

The large brains of cetaceans have raised many additional intriguing questions. One may well ask if such a large brain may not be capable of not only a natural language but of possibly even adaptively learning a human language. Experiments in the Communication Research Institute along these lines have revealed the following findings (35).

1. These animals are capable of phonation of proper dolphin noises in air as well as under water.
2. If in contact close enough and long enough with persons who are speaking, these animals gradually modify the noises they emit and gradually acquire new noises which begin to resemble the noises of human speech.
3. Slowly but surely some of these emissions begin to correspond to distinct human sounds; recognizable words are separated out.
4. Modifications and variations of these words are produced in great profusion.

Such flexibility and plasticity of the use of the phonation apparatus of these animals demonstrates an adaptive capability heretofore completely unsuspected. In a sense these animals who are producing humanoid sounds have adapted to a totally new set of circumstances, i.e., close contact with man, in such a way as to excite interest on our part and to prompt further care of the animals. In a sense, then, the animals are taking full advantage of this artificial environment for their own survival and well-being in a fashion similar to most of the successful individuals of the species *Homo sapiens*.

REFERENCES

1. ARIËNS KAPPERS, C. U., G. C. HUBER, AND E. C. CROSBY. *The Comparative Anatomy of the Nervous System of Vertebrates Including Man*. New York: Hafner, 1960, vols. I–III.
2. BIGELOW, H. B., AND W. C. SCHROEDER. Sharks. In: *Fishes of the Western Atlantic*, edited by A. E. Parr. New Haven: Yale Univ. Press, 1948, pt. I.
3. BUTLER, C. Nutritional value of fish in reference to atherosclerosis and current dietary research. *Com. Fisheries Rev.* 20(7): 7–16, 1958.
4. CALDWELL, D. K. Evidence of home range of an Atlantic bottlenose dolphin. *J. Mammalogy* 36: 304–305, 1955.
5. CALDWELL, D. K. Notes on the spotted dolphin, *Stenella plagiodon*, and the first record of the common dolphin, *Delphinus delphis*, in the Gulf of Mexico. *J. Mammalogy* 36: 467–470, 1955.
6. CALDWELL, D. K. Observations of an unidentified dolphin of the family Delphinidae in Jamaican waters. *Caribbean J. Sci.* 1: 4, 1961.
7. CALDWELL, D. K., AND H. M. FIELDS. Surf-riding by the Atlantic bottle-nosed dolphins. *J. Mammalogy* 40: 454–455, 1959.
8. CONEL, J. L. *The Postnatal Development of the Human Cortex*. Vol. I–VI. *The Cortex of the New Born*. Cambridge: Harvard Univ. Press, 1939.
9. COPPOLETTA, J. M., AND S. B. WOLBACH. Boston Children's Hospital data, 1,198 records. *Am. J. Pathol.* 9: 55–70, 1933.
10. CRILE, G., AND D. P. QUIRING. A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio J. Sci.* 40: 219–256, 1940.
11. EICHELBERGER, L., E. S. FETCHER, JR., E. M. K. GEILING, AND B. J. VOS, JR. The composition of dolphin milk. *J. Biol. Chem.* 134: 171–176, 1940.
12. ESSAPIAN, F. S. The birth and growth of a porpoise. *Nat. Hist.* 62: 392–396, 1953.
13. ESSAPIAN, F. S. Speed-induced skin folds in the bottle-nosed porpoise, *Tursiops truncatus*. *Brev. Museum Comp. Zool. Harvard* 43: 1–4, 1955.
14. FRASER, F. C., AND P. E. PURVES. Hearing in cetaceans. Evolution of the accessory air sacs and the structure and function of the outer and middle ear in recent cetaceans. *Bull. Brit. Museum Zool.* 7: 1–140, 1960.

15. HEEZEN, B. C. Whales entangled in deep sea cables. *Deep-Sea Res.* 4: 105–115, 1957.
16. HUBBS, C. L. Dolphins protecting dead young. *J. Mammalogy* 34: 498, 1953.
17. IRVING, L., P. F. SCHOLANDER, AND S. W. GRINNELL. The respiration of the porpoise, *Tursiops truncatus*. *J. Comp. Physiol.* 17: 145–168, 1941.
18. JANSEN, J. On the whale brain with special reference to the weight of the brain of the fin whale (*Balaenoptera physalus*). *Norweg. Whaling Gazette* 9: 480–486, 1952.
19. JANSEN, J. Studies on the cetacean brain. The gross anatomy of the rhombencephalon of the fin whale (*Balaenoptera physalus* (L)). *Hvalradets Skrifter Norske Videnskaps-Akad. Oslo* 37: 1–35, 1953.
20. KELLOGG, R. *A Review of the Archaeoceti*. Washington, D.C.: Carnegie Inst. Washington, 1936.
21. KELLOGG, W. N. *Porpoises and Sonar*. Chicago: Univ. Chicago Press, 1961.
22. KOJIMA, T. On the brain of the sperm whale (*Physeter catodon*, L). *Sci. Rept. Whales Res. Inst., Tokyo* 6: 49–72, 1951.
23. KRUGER, L. The thalamus of the dolphin (*Tursiops truncatus*) and comparison with other mammals. *J. Comp. Neurol.* 111: 133–194, 1959.
24. LANGWORTHY, O. R. Central nervous system of the porpoise *Tursiops truncatus*. *J. Mammalogy* 12: 381–389, 1931.
25. LANGWORTHY, O. R. Factors determining the differentiation of the cerebral cortex in sea-living mammals (the Cetacea). A study of the brain of the porpoise, *Tursiops truncatus*. *Brain* 54: 225–236, 1931.
26. LANGWORTHY, O. R. A description of the central nervous system of the porpoise (*Tursiops truncatus*). *J. Comp. Neurol.* 54: 437–499, 1932.
27. LAURIE, A. H. Some aspects of the central nervous system of the porpoise (*Tursiops truncatus*). *J. Comp. Neurol.* 54: 437–500, 1932.
28. LAWRENCE, B., AND W. E. SCHEVILL. *Tursiops*, an experimental subject. *J. Mammalogy* 35: 225–232, 1954.
29. LAWRENCE, B., AND W. E. SCHEVILL. The functional anatomy of the Delphinid nose. *Bull. Museum Comp. Zool. Harvard Coll.* 114: 103–151, 1957.
30. LILLY, J. C. Some considerations regarding the basic mechanisms of positive and negative types of motivations. *Am. J. Psychiat.* 115: 498–504, 1958.
31. LILLY, J. C. *Man and Dolphin*. Garden City, N.Y.: Doubleday, 1961.
32. LILLY, J. C., AND A. M. MILLER. Sounds emitted by the bottlenose dolphin. *Science* 133: 1689–1693, 1961.
33. LILLY, J. C., AND A. M. MILLER. Vocal exchanges between dolphins. *Science* 134: 1873–1876, 1961.
34. LILLY, J. C., AND A. M. MILLER. Operant conditioning of the bottlenose dolphin with electrical stimulation of the brain. *J. Comp. Physiol. Psychol.* 55: 73–79, 1962.
35. LILLY, J. C. Vocal behavior of the bottlenose dolphin. *Proc. Am. Phil. Soc.* 106: 520–529, 1962.
36. MCBRIDE, A. F. Meet Mister Porpoise. *Nat. Hist.* 45: 16–29, 1940.
37. MCBRIDE, A. F., AND D. O. HEBB. Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. *J. Comp. Physiol. Psychol.* 41: 111–123, 1948.
38. MCBRIDE, A. F., AND H. KRITZLER. Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *J. Mammalogy* 32: 251–266, 1951.
39. MOORE, J. C. Distribution of marine mammals to Florida waters. *Am. Midland Naturalist* 49: 117–158, 1953.
40. MOORE, J. C. Bottle-nosed dolphins support remains of young. *J. Mammalogy* 36: 466–467, 1955.
41. NORRIS, K. S., J. H. PRESCOTT, P. V. ASA-DORIAN, AND P. PERKINS. An experimental demonstration of echo-location behavior in the porpoise, *Tursiops truncatus* (Montagu). *Biol. Bull.* 120: 163–176, 1961.
42. NORRIS, K. S., AND J. H. PRESCOTT. Observations on Pacific cetaceans in California and Mexican waters. *Univ. California, Berkeley, Publ. Zool.* 63: 291–402, 1961.
43. REYSENBACH DE HAAN, F. W. Hearing in whales. *Acta Oto-Laryngol. Suppl.* 134: 1–114, 1961.
44. SCHEVILL, W. E. Cetacea. In: *The Encyclopedia of the Biological Sciences*, edited by P. Gray. New York: Reinhold, 1961, pp. 205–209.
45. SCHEVILL, W. E., AND B. LAWRENCE. Underwater listening to the white porpoise (*Delphinapterus leucas*). *Science* 109: 143–144, 1949.
46. SCHEVILL, W. E., AND B. LAWRENCE. Auditory response of a bottlenose porpoise, *Tursiops truncatus*, to frequencies above 100 kc. *J. Exptl. Zool.* 124: 147–165, 1953.
47. SCHEVILL, W. E., AND B. LAWRENCE. High-frequency auditory response of a bottlenose porpoise, *Tursiops truncatus* (Montagu). *J. Acoust. Soc. Am.* 25: 1016–1017, 1953.
48. SCHEVILL, W. E., AND B. LAWRENCE. Food-finding by a captive porpoise (*Tursiops truncatus*). *Brev. Museum Comp. Zool. Harvard* 53: 1–15, 1956.
49. SCHEVILL, W. E., AND A. F. MCBRIDE. Evidence for echolocation by cetaceans. *Deep-Sea Res.* 3: 153–154, 1956.
50. SIEBENALER, J. B., AND D. K. CALDWELL. Cooperation among adult dolphins. *J. Mammalogy* 37: 126–128, 1956.
51. SMITH, H. W. *From Fish to Philosopher*. Garden City, N.Y.: Doubleday, 1961.
52. TAVOLGA, M. C., AND F. S. ESSAPIAN. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): mating, pregnancy, parturition and mother-infant behavior. *Zoologica* 42: 11–31, 1957.
53. TOWER, D. B. Structural and functional organization of mammalian cerebral cortex: the relation of neurone density with brain size. *J. Comp. Neurol.* 101: 19–52, 1954.
54. TOWNSEND, C. H. The porpoise in captivity. *Zoologica* 1: 289–299, 1914.
55. VIERORDT, H. Das Massenwachsthum der Körperorgane des Menschen. *Arch. Anat. Physiol. Anat.* 1890, vol. s62.
56. VON BONIN, G. Brain-weight and body-weight of mammals. *J. Gen. Psychol.* 16: 379–389, 1937.
57. WINGE, H. A review of the interrelationships of the Cetacea, translated by G. S. Miller, Jr. *Smithsonian Inst. Misc. Collections* 72: 1–19, 1921.
58. WORTHINGTON, L. V., AND W. E. SCHEVILL. Underwater sounds heard from sperm whales. *Nature* 180: 291, 1957.