Odobenus rosmarus.   By Francis H. Fay

Odobenus Brisson, 1762

Odobenus Brisson, 1762:30. Type species *Phoca rosmarus* Linnaeus, 1758.
Trichechus Linnaeus, 1766:49. Not *Trichechus* Linnaeus, 1758, which is the manatee (Ellerman and Morrison-Scott, 1951).
Rosmarus Brünnich, 1772:34. Type species *Phoca rosmarus* Linnaeus, 1758.

CONTEXT AND CONTENT. Order Carnivora, Suborder Caniformia, Superfamily Otarioidea, Family Odobenidae, Subfamily Odobeninae. The genus *Odobenus* has but one species.

Odobenus rosmarus (Linnaeus, 1758)
Walrus

[*Phoca*] *rosmarus* Linnaeus, 1758:38. Type locality arctic zone of Europe, Asia, and America.
Rosmarus arcticus Pallas, 1811:269. Type locality Novaia Zemlia.
Trichechus obesus Illiger, 1815:64. *Nomen nudum.*
[*Trichechus*] *divergens* Illiger, 1815:68. Type locality Chukchi Sea, about 35 mi SW Icy Cape, Alaska.
Trichechus cookii Fremerij, 1831:385. Type locality off Icy Cape, Alaska.
Trichechus orientalis Dybowski, 1922:351. *Nomen nudum.*

CONTEXT AND CONTENT. Context as above. Two subspecies are recognized (Smirnov, 1929):

O. r. rosmarus (Linnaeus, 1758:38), see above (*arcticus* Pallas is a synonym).
O. r. divergens (Illiger, 1815:68), see above (*cookii* Fremerij is a synonym).

DIAGNOSIS. Body rotund, girth nearly equal to length; neck massive; head small, blocky; ear pinnae absent; about 400 short, thick, smooth mystacial vibrissae but no distinct rhinal vibrissae; external nares on dorsal surface of snout (Fig. 1). Upper canines large, elongate, ever-growing tusks in both sexes; other teeth simple, peglike. Tip of tongue rounded to weakly bifid. Foreflippers nearly as wide as long; hindflippers approximately triangular, first and fifth toes much longer than others; cartilaginous extensions of toes less than one-fifth length of hindflippers. Palms and soles hairless and rough; distal half of obverse surfaces of flippers also hairless. Claws on foreflippers and on first and fifth toes of hindflippers rudimentary; claws on other toes well developed. Tail short, enclosed in fold of skin (not free).

Skull approximately rectangular, because of great enlargement of maxillae to accommodate tusks. Tusks situated outside maxillary toothrow; lower canines reduced, aligned with and comparable in form with postcanines. Upper third incisor as large as and in line with first premolar. Lower incisors, first two pairs of upper incisors, fourth upper premolars, and all molars rudimentary or absent. Nasals rectangular; supraorbital processes of frontals absent; alisphenoid canals usually present. Ventral projection of mastoids extremely massive; jugular processes of exoccipitals thin, plate-like, not fused to mastoids; basioccipital broad, pentagonal. Bullae flat, rough, and thick walled; ratio of diameter of tympanic membrane to that of oval window 20:1; auditory ossicles massive. Mandibular symphysis deep, strong, ankylosed early in life; digastric angle of mandible weak, situated ventral to midpoint between last postcanine and base of coronoid.

Usually 14 thoracic, 6 lumbar vertebrae (occasionally 15 and 5, respectively) and 8 bony parts in the sternum. Spinal canal of each vertebra nearly as large in diameter as centrum; transverse processes of lumbars two to three times longer than wide. Scapula roughly triangular; supraspinous fossa only slightly larger than infraspinous. Humerus about as long as ulna; pectoral ridge extending nearly full length of shaft and aligned distally with medial lip of trochlea; deltoid tubercle situated laterally on shaft, rather than on pectoral ridge. Pronator origin distal to midpoint of shaft on radius; deep pit on scapholunar for articulation with magnum. Head of femur distinctly higher than greater trochanter; tibia and fibula usually not fused proximally (Fay, 1981, 1982; King, 1983; Repenning and Tedford, 1977; Scheffer, 1958).

GENERAL CHARACTERS. Standard length of adult males mostly 200 to 350 cm; body mass 800 to 1,700 kg (Belopol'skii, 1939; Brooks, 1954; Chapskii, 1936, 1940; Fay, 1982; Freiman, 1941; Mansfield, 1958). Females about 83% of the length of males and 67% their weight. Adults of *O. r. rosmarus* about 97% of length, 90% of body mass of adult *O. r. divergens*. Females full grown at 10 to 12 years; males at 15 to 16 years, after secondary acceleration of growth (Fay, 1982).

Skin 2 to 4 cm thick over most of body, thicker in males than females, and thicker on neck and shoulders than elsewhere (Fay, 1982). Short brown to tawny hair imparts distinctive chestnut to cinnamon color overall; skin and hair become successively paler with age. Nodular skin on neck and shoulders of adult males sparsely haired, paler than rest of body.

Tusks extend ventrad from corners of mouth. Tusks of males stouter, more elliptical in cross-section than those of females; also straighter and more divergent distally (Fay, 1982). Eyes small, placed laterally, and provide limited binocular vision. Skull dense and blocky, with massive mandible. Condylobasal length of adult Pacific walruses 38 to 43 cm in males, 31 to 36 cm in females; of adult Atlantic walruses, 25 to 38 cm in males and 30 to 34 cm in females (Heptner et al., 1976). Greatest widths across maxillae for males and females average 24 and 16 cm, respectively, in Pacific, 19 and 14 cm in Atlantic walruses (Ognev, 1935). Palate long and highly arched, with large, prominent pterygoid processes. Coronoid processes of mandible distinctively low and rounded.

Adult males have paired, inflatable, pharyngeal pouches extending posterolaterad over the shoulders (Fay, 1960; Sleptsov, 1940). Testes hypodermal, somewhat scrotal; baculum is largest of any mammal, both absolutely and relatively (Fay, 1982; Scheffer and Kenyon, 1963). Seminal vesicles absent (Murie, 1871). Uterus didelphic; each horn opens separately into vagina (Burne, 1909; Cleland, 1900).

FIG. 1. A group of Pacific walruses (*Odobenus rosmarus divergens*) on an ice floe in the Bering Sea. Photograph courtesy of K. J. Frost.
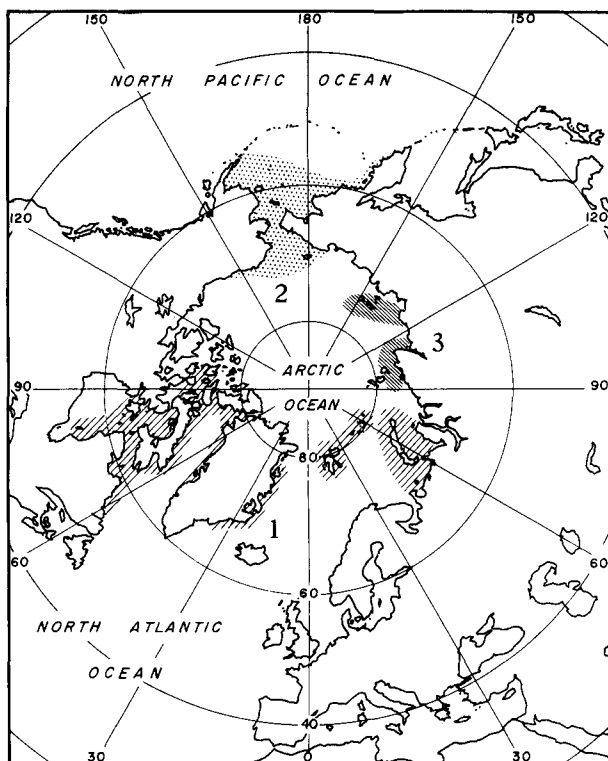
FIG. 2. Present distribution of *Odobenus rosmarus*. Subspecies are: 1, the Atlantic walrus, *O. r. rosmarus*; 2, the Pacific walrus, *O. r. divergens*; 3, the Laptev walrus, whose taxonomic status remains uncertain.

DISTRIBUTION. The species has a discontinuous, arctic distribution (Fig. 2), in which the widest gap is between the eastern Chukchi Sea and the central Canadian Arctic. Records of occurrence in that area are uncommon to rare (Fay, 1982; Harington, 1966; Stirling, 1974). The walruses found on each side of that gap differ more from each other in size and other morphological characters than any other two populations.

The Atlantic walrus, *O. r. rosmarus*, occurs from the eastern Canadian Arctic eastward to the Kara Sea and Franz Josef Land. Within that range, it seems to be divided into two populations. The western population is distributed from Hudson Bay, Foxe Basin, and the channels between Ellesmere, Devon, and Baffin Islands, Canada, eastward to the Thule, Upernavik, Disko, and Godthab areas of western Greenland (Mansfield, 1958, 1966; Vibe, 1950). The eastern population extends from East Greenland to Svalbard, Franz Josef Land, and the Barents and Kara seas. The eastern population may have been continuous in distribution in the past, but it now seems to comprise three of four discontinuous groups, restricted approximately to the areas shown in Fig. 2. The easternmost limit of their range apparently is about 80°E longitude, at the Yenisei estuary (Bychkov, 1975; Chapskii, 1936; Fedoseev, 1976; Øritsland, 1973; Reeves, 1978; Tsalkin, 1937).

The Pacific walrus, *O. r. divergens*, occurs from the Laptev Sea eastward to the Beaufort Sea and southward to the Bering Sea. The population in the Laptev Sea apparently does not range westward much beyond Vilkitskii Strait, between the Taimyr Peninsula and Severnaia Zemlia. In the east, it ranges as far as the New Siberian Islands and the western part of the East Siberian Sea (Chapskii, 1940; G. A. Fedoseev, pers. comm.). The population in the Chukchi Sea ranges from the eastern East Siberian Sea to the western Beaufort Sea and southward in the Bering Sea to Bristol Bay and eastern Kamchatka.

FOSSIL RECORD. The stem of the otarioid stock evidently evolved from an ursine arctoid ancestor at least 22 m.y.b.p. in the North Pacific Ocean (Repenning and Tedford, 1977). The ancestral family Enaliarctidae (Mitchell and Tedford, 1973), known from Miocene marine deposits on the western coast of North America

and in Japan, apparently gave rise first to the family Desmatophocidae at least 17 m.y.b.p., then to the Odobenidae at least 14 m.y.b.p., before becoming the Otariidae about 2 m.y. later (Repenning et al., 1979). The odobenids diversified to their greatest extent in the North Pacific about 8 to 10 m.y.b.p., principally within the subfamily Dusignathinae. The oldest known species of the subfamily Odobeninae, from which lineage the modern walruses arose, is *Aivukus cedrosensis* from Baja Californian deposits, estimated to be about 7 to 9 m.y. old (Repenning and Tedford, 1977; Repenning et al., 1979). Perhaps about 6 to 7 m.y.b.p., animals from that lineage passed via the Central American Seaway into the Atlantic Ocean. Although they later flourished in the North Atlantic, their relatives in the North Pacific evidently became extinct about 2 m.y.b.p. (Repenning et al., 1979).

The presence of those early walruses in the North Atlantic Ocean at least 4 and possibly 5 m.y.b.p. is recorded in Pliocene deposits in North America from Virginia to Florida (Berry and Gregory, 1906; Leidy, 1877; Ray, 1960) and in deposits thought to be of Pleistocene but probably of Pliocene age (C. E. Ray, pers. comm.) in Great Britain, The Netherlands, and Belgium (Beneden, 1877; Diense, 1943–44; DuBus, 1867; Hasse, 1909; Lankester, 1865, 1880; Rutten, 1907). Fossil remains in the North Atlantic of the nominal genera *Alachtherium* DuBus, *Trichecodon* Lankester, and *Prorosmarus* Berry and Gregory now appear to be congeneric with *Ontocetus* Leidy (C. E. Ray, pers. comm.).

Walruses closely resembling modern *O. rosmarus* are known from numerous Pleistocene specimens found in coastal to offshore localities from southern Quebec and Scandinavia to North Carolina and France (Erdbrink, 1972; Harington, 1977; Kortenbout van der Sluijs, 1983; Ray, 1960, 1975; Ray et al., 1968). Walruses reinvaded the North Pacific region via the Arctic Ocean, possibly during the last (Sangamon) interglacial period. Fossil remains of Pelukian age, some 50,000 to 100,000 years old (Hopkins, 1972), were found on the shores of the Bering and Chukchi seas (Hopkins, 1967; Repenning and Tedford, 1977), and remains probably of mid to late Wisconsin age were found as far south as Tokyo and San Francisco (Harington, 1975; C. A. Repenning, pers. comm.).

FORM. A fine, white, somewhat woolly fetal pelage, 4 to 8 mm long, is shed in utero and ingested by the fetus, 2 to 3 months before birth (Fay, 1982). It is replaced by a natal pelage of smooth, non-medulated hair, 7 to 12 mm long, that reaches its full development soon after birth. The natal pelage is shed and replaced during the first summer, about the same time as the annual molt in adults. The hairs of the adult pelage are somewhat longer (10 to 15 mm) and broader (0.1 to 0.2 mm) than those of the natal coat, but they are otherwise similar in appearance to the hairs on the calf. More than 90% of the hairs in the adult pelage occur singly, about 8% dually, and less than 1% as groups of three per pore. Associated with each hair canal are several sebaceous glands and one apocrine sweat gland. The ducts of those glands tend to enter the hair canals at the same level (Fay, 1982). There are no sweat or sebaceous glands in the hairless parts of the flippers.

The mammae are abdominal and usually four in number, as in the Otariidae, but extra nipples are common. In a sample of 204 specimens from the Bering-Chukchi region that I examined, 173 (85%) had four, 25 (12%) had five, and 6 (3%) had six nipples.

The skin is composed mostly of dermal corium. The epidermis is less than 1 mm thick over most of the body and attains its greatest thickness of about 3 mm on the palms and soles of the flippers and on the incisive area in the front of the mouth. In those areas, its thickness is mostly caused by extreme cornification (Fay, 1982). In the nodules on the neck and shoulders of adult males, the dermis is about 10 mm thicker than elsewhere. The hypodermal layer (blubber) ranges in thickness from about 1 to 15 cm, varying with age, sex, season, reproductive condition, and probably with topographic location on the body.

The dental formula is highly variable. The maximal number of teeth is i 3/3, c 1/1, p 4/3, m 2/2, total 38, but more than half of those teeth are rudimentary and occur with less than 50% frequency (Cobb, 1933; Fay, 1982). The most frequent formula in adults is i 1/0, c 1/1, p 3/3, total 18 (Fig. 3). Each tooth has a single root and simple crown, with a thin cap of enamel abraded off early in life. Each tooth also has a distinctive central core of marbled dentin in which there is a vascular plexus of unknown function. Hypercementosis is characteristic; on the cheekteeth of adult males,

the cement on the root may comprise more than 90% of the volume of the tooth (Fay, 1982).

The musculature is similar to that of other pinnipeds, bearing closer resemblance in some respects to the eared seals (Otariidae), because of their comparable terrestrial locomotion, and in other respects to the hair seals (Phocidae), because of their similar methods of swimming (Howell, 1928; Murie, 1871). The form of the brain also is rather intermediate between phocid and otariid, but it is more primitive than either of those, in that the postsylvian area is more elongate than the presylvian (Fish, 1903). The digestive tract is not remarkably different from that of other pinnipeds and, like the others, differs from terrestrial carnivores principally in the greater length of the small intestine (Eastman and Coalson, 1974). The small intestine of the walrus is 10 to 20 times longer than the nose-tail length and is not clearly separable into duodenum, jejunum, and ileum (Brooks, 1954; Murie, 1871; Owen, 1853). The pyloric caecum varies from absent to well developed.

FUNCTION. Young walruses ordinarily suckle for 2 years, gradually developing their ability to feed on benthic invertebrates. The milk contains less fat and more water than that of other pinnipeds but, like the others, has a high proportion of protein and ash and only trace amounts of sugar, probably glucose (Fay, 1982).

The internal body temperature is about 37°C in adults and tends to be 1 to 2°C higher in the young. The calf at birth apparently requires brooding by the parent for thermoregulation in cold weather (Fay and Ray, 1968). As among hair seals, the primary insulation is blubber, but the short hair probably contributes to maintenance of skin temperature in air by reducing turbulence at the skin surface and retaining radiant heat (Øritsland and Ronald, 1973; Ray and Fay, 1968; Ray and Smith, 1968). Adults appear to be thermoneutral in air at temperatures between about −20 and +15°C (Ray and Fay, 1968).

Young walruses in their first year were estimated to consume the mother's rich milk at the rate of about 7% of their total body mass (TBM) per day. Adults eat relatively much less, probably averaging 3 to 5% of TBM/day (Fay, 1982; Gehnrich, 1984). Adult males tend to fast during the winter breeding season but compensate for that by increasing their intake in the rest of the year. Females may fast for several days at estrus and for a week or more at parturition. During pregnancy and lactation, they increase their average energy intake some 40 to 50% above the maintenance level.

ONTOGENY AND REPRODUCTION. Most females first ovulate at 6 to 7 years (Fay, 1982; Krylov, 1966; Mansfield, 1958); males become fertile at 8 to 10 years but are not physically mature (thus not physically capable of competing successfully for mates) until they are 15 years old or older. Spermiogenesis takes place from November to May, with the peak in December–January for mature males and about 2 months later for adolescents (Fay, 1982). Females appear to ovulate principally in January–February, implantation of the blastocyst is delayed until June–July, and the calves are born 10 to 11 months later, mainly from mid April to mid June. Fecundity is greatest for females 9 to 11 years old; it is lower in youth and in old age because of poor success in conception and gestation. Because pregnancy lasts 15 to 16 months, individual walruses cannot breed every year but at intervals of 2 or more years.

The single calf (rarely twins) weighs 60 to 65 kg at birth and is precocial but, for a few weeks, requires parental assistance for thermoregulation and transportation (Brooks, 1954; Fay and Ray, 1968). Its body weight triples in the first year and nearly doubles again by the time of weaning, at 2 years of age.

Walruses are polygynous; the sex ratio of adults in the breeding areas is roughly 1 male:10 females (Fay et al., 1984). Dominant males display visually and acoustically in the water alongside groups of females resting on the ice, presumably to attract them for copulation (Ray and Watkins, 1975).
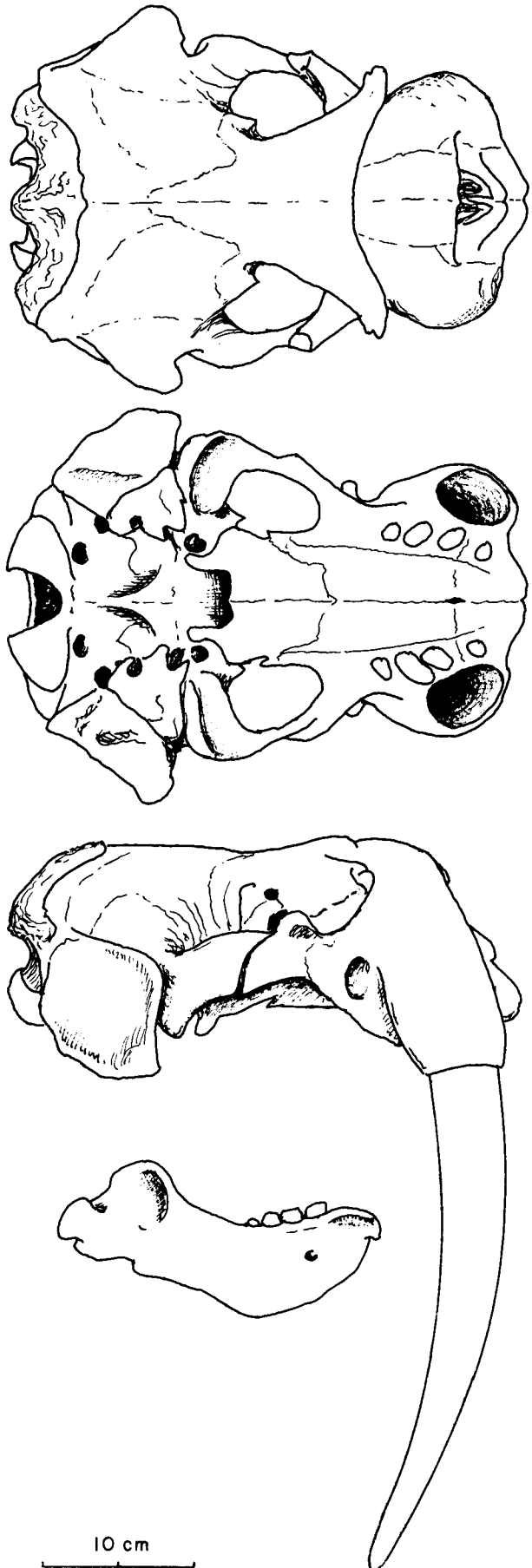
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FIG. 3. Dorsal, ventral, and lateral views of the cranium and lateral view of the right mandible of *Odobenus rosmarus* (USNM 6780, adult female from the North Pacific region). Condylobasal length is 325 mm; mandible length is 230 mm.

10 cm

ECOLOGY. Walruses feed mainly on bivalve mollusks, but they take a wide variety of other benthic invertebrates as well. Occasionally, they supplement that diet with fishes and seals (Brooks, 1954; Chapskii, 1936; Fay, 1982; Krylov, 1971; Loughrey, 1959; Mansfield, 1958; Nikulin, 1941; Tsalkin, 1937; Vibe, 1950). The food organisms range in size from tiny gammarids (Amphipoda) and snails (Gastropoda) weighing less than 0.1 g to bearded seals (*Erignathus barbatus*) weighing more than 200 kg. Of the bivalve and gastropod mollusks, only the fleshy parts are ingested; the shells are rejected. All other organisms, except seals, are swallowed whole. Crabs (Majidae) usually are taken only in the soft-shelled stage; seals somehow are reduced to easily swallowed strips and chunks of skin, blubber, viscera, and skeletal muscle (Lowry and Fay, 1984). Walruses also have been known to feed on dead cetaceans, principally the skin and blubber (Freuchen, 1935; Gray, 1927).

Walruses are primarily dependent on invertebrates of the continental shelf where depths are not greater than 80 to 100 m (Fay, 1982; Vibe, 1950). In winter, walruses generally reside within areas of divergent pack ice, where its constant motion creates an abundance of leads and polynyas (Burns et al., 1981; Fay, 1974, 1982). In summer, males use the beaches of isolated islets and coastal headlands as resting and molting sites, whereas females tend to remain with the pack ice. In summering areas, females and young show a strong tendency to lie selectively on floes with a surface area of about 100 to 200 m² (Wartzok and Ray, 1980). Because females tend to stay with the ice, its absence alone may limit walruses from dispersing farther southward. Their present adaptation primarily to the Arctic may not prevent their advancing into temperate regions, but it seems to act as a deterrent (Fay and Ray, 1968; Ray and Fay, 1968).

Walruses have a reproductive rate that is only about half that of other pinnipeds; therefore, their mortality also is assumed to be much lower (Mansfield, 1958). The 2-year-long period of parental care is believed to insure high survival of young. For calves, the primary causes of mortality appear to be predation by polar bears (*Ursus maritimus*) and killer whales (*Orcinus orca*) and accidental crushing by other walruses. Abandonment of calves also is common but may be counterbalanced to some degree by adoption (Fay, 1982). Adults are known to die from trauma, bacterial infections, and predation by killer whales, but the greatest mortality has been caused by harvest for meat, hides, and ivory by man. Males may have a higher natural mortality than females as a consequence of intense competitive fighting during the breeding season.

Adult male Pacific walruses apparently eat little in winter, when they are with females; hence, most food in wintering areas is available to females and young. In summer, most adult males stay in the Bering Sea, whereas females and young migrate northward, into the Chukchi Sea. Their geographical segregation at that time results in partitioning of food resources (Fay, 1982). Such partitioning also may occur in some parts of the North Atlantic (Chapskii, 1936; Tsalkin, 1937). To judge from the feeding regimen of male and female walruses reared in captivity (Gehnrich, 1984), the time of greatest mutual impact of Pacific walruses on their food supplies may be in November and December, during the autumn migration and at a time when advancement of the pack ice permits them to inhabit areas that were little used in other seasons.

The world's population of walruses in 1975 probably exceeded 270,000 animals, about 90% of which were in the Bering and Chukchi seas (Estes and Gol'tsev, 1984; Reeves, 1978). The number in the Laptev Sea probably was not greater than 4,000 to 5,000 (Tavrovskii, 1971), and in the entire North Atlantic region, from eastern Greenland to the Kara Sea, there may have been no more than 1,000 to 2,000 individuals (Bychkov, 1975; Reeves, 1978). The largest population in the North Atlantic region was in the eastern Canadian Arctic and western Greenland, where numbers were estimated to be about 25,000 individuals in the 1960's (Mansfield, 1966) and probably have not changed greatly since then.

The population dynamics of walruses is poorly understood, principally because of a dearth of information on age and sex composition, and survivorship. The composition of only the Bering-Chukchi population has been estimated, based on data from aerial photos and shipboard surveys (Fay, 1982; Fedoseev, 1962; Fedoseev and Gol'tsev, 1969; Krylov, 1968). As of 1972, that population appeared to be composed of about 44% immature animals and 56% breeding adults. The sex ratio of breeding adults was estimated at 1 male:4.6 females.

The Bering-Chukchi and Canadian-West Greenland populations are subjected to significant annual harvests at present, whereas the other populations, because of their depleted state, are given full protection. Harvest rates of 5 to 7% per year are believed to be low enough for sustained yield (Fay, 1982; Fedoseev and Gol'tsev, 1969; Mansfield, 1966).

When captured as calves and given close attention and adequate nutrition, walruses adapt well to captivity (Brown, 1963; Brown and Asper, 1966). One of the primary problems in rearing them has been the diet during suckling, for the calves are unable to digest lactose as a source of energy (Kerry and Messer, 1968). Only within the past 20 years have adequate formulae been developed for ensuring survival and normal growth of captive calves. Walruses in captivity exhibit excessive abrasion of the tusks that leads to bacterial infection of the pulp (Bartsch and Frueh, 1971). The infections are treatable, but the means for preventing the abrasion have not yet been developed. Breeding of walruses in captivity has been accomplished thus far only in one facility, Marineland in Los Angeles, U.S.A., where, by 1983, two adult pairs had produced six calves (Gehnrich, 1984).

BEHAVIOR. Walruses propel themselves through the water principally by means of alternating strokes of the hindflippers, in a manner similar to that of phocid seals (Gordon, 1981; Ray, 1963). Although the forelimbs often are used as paddles at low speeds, they usually are held against the body or used as rudders when swimming at average to high speeds. On land or ice, walruses are quadrupedal, more like otariid than phocid seals. Because of their ponderous bulk, however, they require extensive counterbalancing by head and body movements, to assist their limbs in heaving the bulky torso forward (Gordon, 1981). Occasionally, when emerging to rest on ice or land, the animals use their tusks as additional locomotory appendages, jabbing them into the substrate and pulling the body forward. The usually enter the water head-first.

Some aspects of feeding behavior have been predicted from anatomical characteristics, examination of stomach contents, observation of walruses in captivity and in nature, and inspection of the sea bottom in areas where groups have been seen to dive, presumably to feed (Fay, 1982; Nyholm, 1975; Oliver et al., 1983; Ray, 1973; Tomilin and Kibal'chich, 1975; Vibe, 1950). Together, those sources suggest that the animals move along the bottom, head-first, propelling themselves forward with their hindflippers. They maintain vertical stability by keeping the anterior surface of their snout and tusks in contact with the bottom, and lateral stability by touching their foreflippers on the bottom. They appear to locate most prey tactually with their sensitive mystacial vibrissae; they probably unearth prey mainly by digging with their snout, pig-fashion. Soft-bodied prey are swallowed whole; the fleshy parts of bivalve and gastropod mollusks are removed from their shells, apparently by suction. More than 6,000 individual prey may be taken in a single meal. Feeding dives range in length from 2 to about 10 min, their duration positively correlated with depth.

Gregariousness pervades the social system of walruses. Although the animals occur singly under some circumstances, most are found in groups of two or more (Estes and Gilbert, 1978; Fay, 1982; Fay and Ray, 1968; Miller and Boness, 1983; Wartzok and Ray, 1980). The number of animals per group tends to be largest when they are on shore, smaller on ice, and smallest when they are in the water. The size of the in-water groups varies with their composition and the kind of activity (Miller and Boness, 1983). Swimming groups of males are the smallest. Females are equally gregarious in all seasons; adult males usually occur singly during the breeding season but congregate at other times.

The dominance order in groups on ice or land is primarily a function of body and tusk size and individual aggressiveness (Miller, 1975, 1982). Males strike with tusks more often than females and inflict more damage on each other by doing so. In the breeding season, adult males fight intensively in the water, evidently in competition for display sites near the females (Fay et al., 1984).

Because the breeding season is in mid-winter, when the herds are accessible only via icebreaking ships, reproductive behavior has not been studied thoroughly. Observations in late February and March, at the end of the breeding season, suggest that each herd of 20 to 50 females and young is followed by one or more bulls. Some of those bulls display in the water, alongside floes where females lie; other bulls remain nearby but do not display. The males' display sites alongside floes are 7 to 10 m apart, and each bull performs a stereotyped visual and acoustical display that appears

to function as advertisement to females and as warning to other males (Fay et al., 1984). Each of those displays lasts 2 to 3 min and includes a distinctive sequence of underwater pulses and bell-like sounds, followed at the surface by a series of single pulses and a short whistle (Ray and Watkins, 1975). Some females appear to be attracted to the bulls by those displays; others apparently are chased by the bulls and pulled into the water, where copulation presumably ensues.

Parturient females often isolate themselves from other walruses. Soon after giving birth, they may join a "nursery herd" of other females with new calves (Burns, 1965). Females and their calves are almost inseparable; bonds appear to be maintained mostly by females in the first days after birth, but calves assume increasing responsibility for their maintenance thereafter (Gehnrich, 1984). Females continue to lead, feed, and defend their calves for about 2 years.

GENETICS. The karyotype of the Pacific walrus (2n = 32) includes six pairs of metacentric and nine pairs of submetacentric chromosomes and the sex autosomes (Arnason, 1974; Fay et al., 1967). The karyotype is easily distinguished from that of all other pinnipeds by its large pair of submetacentric satellited chromosomes. G-banding studies by Arnason (1977) indicate that the chromosomes of the walrus are basically homologous with those of the otariid karyotype, though somewhat modified in arrangement.

REMARKS. I follow Repenning and Tedford (1977) in assigning the genus *Odobenus* to the superfamily Otarioidea, family Odobenidae, rather than to the superfamily Canoidea and family Otariidae, as proposed by Mitchell (1968) and Mitchell and Tedford (1973). The systematics and taxonomy of fossil and living otarioids has been in a state of rapid flux in recent years, because of a number of finds of new and significant fossils, which have required major revision of the concepts of evolution and zoogeography of the group (Repenning, 1976; Repenning et al., 1979).

The walruses of the Laptev Sea have been regarded as a subpopulation of *O. r. rosmarus* by some investigators (e.g., Bobrinskii et al., 1944; Hall, 1981) and as a subpopulation of *O. r. divergens* by others (e.g., King, 1983; Scheffer, 1958), as I have considered them here. Some Soviet investigators regard the Laptev walruses as a third subspecies, *O. r. laptevi* (e.g., Chapskii, 1940; Heptner et al., 1976). The taxonomic status of that population remains uncertain, because of the small number of specimens available for comparison. I examined those specimens and believe that the Laptev walruses, though very small, are most similar in form to *O. r. divergens*.

Whether walruses in the Pleistocene epoch re-entered the North Pacific region via the Canadian or the Soviet Arctic is unknown. Re-entry via the Soviet Arctic is implied by the more transitional morphology of the Laptev walruses between the Atlantic and Pacific forms, versus the wide morphological difference between the Chukchi and eastern Canadian forms (Heptner et al., 1976; Fay, 1981, 1982).

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LITERATURE CITED

ARNASON, U. 1974. Comparative chromosome studies in Pinnipedia. Hereditas, 76:179–226.

———. 1977. The relationship between the four principle pinniped karyotypes. Hereditas, 87:227–242.

BARTSCH, R. C., AND R. J. FRUEH. 1971. Alveolitis and pulpitis of a canine tooth in a walrus. J. Amer. Vet. Med. Assoc., 159:575–577.

BELOPOL'SKII, L. O. 1939. On the migrations and ecology of reproduction of the Pacific walrus (*Odobaenus rosmarus divergens* Illiger). Zool. Zhurnal, 18:762–774.

BENEDEN, P. J. VAN. 1877. Descriptions des ossements fossiles des environs d'Anvers. Pt. 1, Pinnipedes ou Amphitheriens. Ann. Musee Royal His. Nat. Belgique, 1:1–88.

BERRY, E. W., AND W. K. GREGORY. 1906. *Prorosmarus alleni,* a new genus and species of walrus from the upper Miocene of Yorktown, Virginia. Amer. J. Sci., Ser. 4, 21:444–450.

BOBRINSKII, N. A., B. A. KUZNETSOV, AND A. P. KUZIAKIN. 1944. Guide to the mammals of the USSR. Sovietskaia Nauka, Moscow, 439 pp.

BRISSON, M. J. 1762. Regnum animale in classes IX, second ed. Lugduni Batavorum, 296 pp.

BROOKS, J. W. 1954. A contribution to the life history and ecology of the Pacific walrus. Unpubl. M.S. thesis, Univ. Alaska, Fairbanks, 103 pp.

BROWN, D. H. 1963. The health problems of walrus calves and remarks on their general progress in captivity. Internatl. Zoo Yearb., 4:13–23.

BROWN, D. H., AND E. D. ASPER. 1966. Further observations on the Pacific walrus, *Odobenus rosmarus divergens,* in captivity. Internatl. Zoo Yearb., 6:78–82.

BRÜNNICH, M.T. 1772. Zoologiae fundamenta praelectionibus academicis accomodata. Grunde i dyrelaeren. Leipsig, 254 pp.

BURNE, R. H. 1909. Notes on the viscera of a walrus (*Odobaenus rosmarus*). Proc. Zool. Soc. London, 1909:732–738.

BURNS, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dept. Fish and Game, Juneau, 48 pp.

BURNS, J. J., L. H. SHAPIRO, AND F. H. FAY. 1981. Ice as marine mammal habitat in the Bering Sea. Pp. 781–797, *in* The eastern Bering Sea shelf: oceanography and resources (D. W. Hood and J. A. Calder, eds.). Univ. Washington Press, Seattle, 2:629–1339.

BYCHKOV, V. A. 1975. Marine mammals. Pp. 27–38, *in* Rare mammals, birds, and their protection in the USSR (L. V. Zhirnov, A. A. Vinokurov, and V. A. Bychkov, eds.). Ministry of Agriculture, Moscow, 82 pp.

CHAPSKII, K. K. 1936. The walrus of the Kara Sea. Trudy Vsesoiuz. Arkt. Inst., 67:1–124.

———. 1940. Distribution of the walrus in the Laptev and East Siberian seas. Problemy Severa, 1940(6):80–94.

CLELAND, J. 1900. Duplicity of cervix uteri in *Trichechus* and *Otaria.* J. Anat. Physiol., n.s., 14:159–163.

COBB, W. M. 1933. The dentition of the walrus, *Odobenus obesus.* Proc. Zool. Soc. London, 1933:645–668.

DIENSE, A. B. VAN. 1943–44. Over Resten van fossiele en recente Pinnipedia, aangetroffen in Zeeland en elders Nederland. De Levende Natuur, 48:84–87, 97–101, 119–125, 133–136. (not seen; cited from Ray, 1960)

DYBOWSKI, B. 1922. Spis. System Gatunkow Rus. Arch. Tow. Naukow we Lwowie, Vol. 1. (not seen; cited from Ognev, 1935)

DUBUS, B. 1867. Sur quelques mammiferes du Crag d'Anvers. Acad. Sci. Belgique Bull., Ser. 2, 24:562–577.

EASTMAN, J. T., AND R. E. COALSON. 1974. The digestive system of the Weddell seal, *Leptonychotes weddelli*—a review. Pp. 253–320, *in* Functional anatomy of marine mammals (R. J. Harrison, ed.). Academic Press, London, 2:1–366.

ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1951. Checklist of Palaearctic and Indian mammals 1758 to 1946. British Mus. (Nat. Hist.), London, 810 pp.

ERDBRINK, D. P. 1972. Two late Pleistocene pinnipede remains in a private collection. Lutra, 14:24–32.

ESTES, J. A., AND J. R. GILBERT. 1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). J. Fish. Res. Board Canada, 35:1130–1140.

ESTES, J. A., AND V. N. GOL'TSEV. 1984. Abundance and distribution of the Pacific walrus (*Odobenus rosmarus divergens*): results of the first Soviet-American joint aerial survey, autumn 1975. Pp. 67–76, *in* Soviet-American cooperative research on marine mammals. Pinnipeds (F. H. Fay and G. A. Fedoseev, eds.). NOAA Tech. Rept. NMFS, 12:1–104.

FAY, F. H. 1960. Structure and function of the pharyngeal pouches of the walrus (*Odobenus rosmarus* L.). Mammalia, 24:361–371.

———. 1974. The role of ice in the ecology of marine mammals of the Bering Sea. Pp. 383–399, *in* Oceanography of the Bering Sea (D. W. Hood and E. J. Kelley, eds.). Occas. Publ., Inst. Marine Sci., Univ. Alaska, Fairbanks, 2:1–623.

———. 1981. Walrus, *Odobenus rosmarus* (Linnaeus, 1758). Pp. 1–23, *in* Handbook of marine mammals, the walrus, sea

lions, fur seals and sea otter (S. H. Ridgway and R. J. Harrison, eds.). Academic Press, New York, 1:1–235.

———. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N. Amer. Fauna, 74:1–279.

FAY, F. H., AND [G.] C. RAY. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. Zoologica, 53:1–18.

FAY, F. H., V. R. RAUSCH, AND E. T. FELTZ. 1967. Cytogenetic comparison of some pinnipeds (Mammalia:Eutheria). Canadian J. Zool., 45:773–778.

FAY, F. H., G. C. RAY, AND A. A. KIBAL'CHICH. 1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. Pp. 81–88, *in* Soviet-American cooperative research on marine mammals. Pinnipeds (F. H. Fay and G. A. Fedoseev, eds.). NOAA Tech. Rept. NMFS, 12:1–104.

FEDOSEEV, G. A. 1962. On the status of the stocks and the distribution of the Pacific walrus. Zool. Zhurnal, 41:1083–1089.

———. 1976. Giants of the polar seas. Priroda, 1976 (8): 76–83.

FEDOSEEV, G. A., AND V. N. GOL'TSEV. 1969. Age-sex structure and reproductive capacity of the Pacific walrus population. Zool. Zhurnal, 48:407–413.

FISH, P. A. 1903. The cerebral fissures of the Atlantic walrus. Proc. U.S. Natl. Mus., 26:675–688.

FREIMAN, S. IU. 1941. Materials on the biology of the Chukchi walrus. Izv. TINRO, 20:3–20.

FREMERIJ, N. C. DE. 1831. Bijdragen tot der natuurlijke Gescheidenis van den *Walrus* (*Trichechus rosmarus* Linn.), en de Kennis der Verscheidenheden, welke onder deze Dierenvoorkomen. Bijdragen tot de Natuurkundige Wetenschappen, 6: 360–392.

FREUCHEN, P. 1935. Mammals, Part II. Field notes and personal observations. Rept. Fifth Thule Exped., 2(2–4):68–278.

GEHNRICH, P. H. 1984. Nutritional and behavioral aspects of reproduction in walruses. Unpubl. M.S. thesis, Univ. Alaska, Fairbanks, 147 pp.

GORDON, K. R. 1981. Locomotor behaviour of the walrus (*Odobenus*). J. Zool., 195:349–367.

GRAY, R. W. 1927. The walrus. Nature, 119:923.

HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 2:601–1175 + 90.

HARINGTON, C. R. 1966. Extralimital occurrences of walruses in the Canadian Arctic. J. Mamm., 47:506–513.

———. 1975. A postglacial walrus (*Odobenus rosmarus*) from Bathurst Island, Northwest Territories. Canadian Field-Nat., 89:249–261.

———. 1977. Marine mammals in the Champlain Sea and the Great Lakes. Ann. New York Acad. Sci., 288:508–537.

HASSE, G. 1909. Les morses du Pliocene poederlien a Anvers. Bull. Soc. Belge Geol., Paleontol., Hydrol., Mem., 23:293–322.

HEPTNER, V. G., K. K. CHAPSKII, V. A. ARSEN'EV, AND V. E. SOKOLOV (EDS.). 1976. Pinnipeds and toothed whales. Mammals of the Soviet Union. Vyshaya Shkola, Moscow, 2(3):1–718.

HOPKINS, D. M. 1967. Quaternary marine transgressions in Alaska. Pp. 47–90, *in* The Bering land bridge (D. M. Hopkins, ed.). Stanford Univ. Press, Stanford, California, 495 pp.

———. 1972. The paleogeography and climatic history of Beringia during late Cenozoic time. Inter-Nord, 12:121–150.

HOWELL, A. B. 1928. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). Proc. U.S. Natl. Mus., 73(15):1–142.

ILLIGER, J. C. 1815. Ueberblick der Säugethiere nach ihrer Vertheilung über die Welttheile. Abh. Phys. Klasse der Königlich-Pruess. Acad. Wiss. Berlin, 1804–1811:39–159.

KERRY, K. R., AND M. MESSER. 1968. Intestinal glycosidases of three species of seals. Comp. Biochem. Physiol., 25:437–446.

KING, J. E. 1983. Seals of the world. Second ed. British Mus. (Nat. Hist.), London, 240 pp.

KORTENBOUT VAN DER SLUIJS, G. 1983. De resten van zoogdieren uit de Noordzee. Grondboor en Hamer, 1983:4–8.

KRYLOV, V. I. 1966. Sexual maturation of Pacific walrus females. Zool. Zhurnal, 45:919–927.

———. 1968. Present status of stocks of the Pacific walrus and prospects of their rational exploitation. Pp. 189–204, *in* Pinnipeds of the northern part of the Pacific Ocean (V. A. Arsen'ev and K. I. Panin, eds.). Pischevaya Promyshlennost', Moscow, 284 pp.

———. 1971. On the food of the Pacific walrus (*Odobenus rosmarus divergens* Ill.). Trudy AtlantNIRO, 39:110–116.

LANKESTER, E. R. 1865. On the sources of the mammalian fossils of the Red Crag, and on the discovery of a new mammal in that deposit, allied to the walrus. Quart. J. Geol. Soc. London, 21:221–232.

———. 1880. On the tusks of the fossil walrus, found in the Red Crag of Suffolk. Trans. Linnean Soc. London, Ser. 2 Zool., 2:213–221.

LEIDY, J. 1877. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. J. Acad. Nat. Sci. Philadelphia, Ser. 2, 8:209–261.

LINNAEUS, C. 1758. Systema naturae. Regnum Animale, Tenth ed. 1. Laurentii Salvii, Stockholm, 1:1–824.

———. 1766. Systema naturae, Twelfth ed. Laurentii Salvii, Stockholm, 1:1–532. (not seen; cited from Ellerman and Morrison-Scott, 1951)

LOUGHREY, A. G. 1959. Preliminary investigation of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus). Canadian Wildl. Serv., Wildl. Mgmt. Bull., Ser. 1, 14:1–123.

LOWRY, L. F., AND F. H. FAY. 1984. Seal eating by walruses in the Bering and Chukchi seas. Polar Biol., 3:1–8.

MANSFIELD, A. W. 1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus) in the eastern Canadian Arctic. Fish. Res. Board Canada, Manuscript Rept. Ser. (Biol.), 653:1–146.

———. 1966. The walrus in Canada's Arctic. Canadian Geogr. J., 72:88–95.

MILLER, E. H. 1975. Walrus ethology. I. The social role of tusks and applications of multidimensional scaling. Canadian J. Zool., 53:590–613.

———. 1982. Herd organisation and female threat behaviour in Atlantic walruses, *Odobenus rosmarus rosmarus* (L.). Mammalia, 46:29–34.

MILLER, E. H., AND D. J. BONESS. 1983. Summer behavior of Atlantic walruses *Odobenus rosmarus rosmarus* (L.) at Coats Island, N.W.T. (Canada). Z. Saugetierk., 48:298–313.

MITCHELL, E. 1968. The Mio-Pliocene pinniped *Imagotaria*. J. Fish. Res. Board Canada, 25:1843–1900.

MITCHELL, E., AND R. H. TEDFORD. 1973. The Enaliarctinae, a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bull. Amer. Mus. Nat. Hist., 151: 201–284.

MURIE, J. 1871. Researches upon the anatomy of the Pinnipedia. Part I. On the walrus (*Trichechus rosmarus*, Linn.). Trans. Zool. Soc. London, 7:411–464.

NIKULIN, P. G. 1941. The Chukchi walrus. Izv. TINRO, 20:21–59.

NYHOLM, E. S. 1975. Observations on the walrus (*Odobenus rosmarus* L.) in Spitzbergen in 1971–1972. Ann. Zool. Fennici, 12:193–196.

OGNEV, S. I. 1935. Mammals of the USSR and adjacent countries. Carnivora (Fissipedia and Pinnipedia). Akad. Nauk SSSR, Moscow, 3:1–641.

OLIVER, J. S., P. N. SLATTERY, E. F. O'CONNOR, AND L. F. LOWRY. 1983. Walrus, *Odobenus rosmarus*, feeding in the Bering Sea: a benthic perspective. Fish. Bull., 81:501–512.

ØRITSLAND, N. A., AND K. RONALD. 1973. Effects of solar radiation and windchill on skin temperature of the harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). Comp. Biochem. Physiol., 44A:519–525.

ØRITSLAND, T. 1973. Walrus in the Svalbard area. Pp. 59–68, *in* Seals: proceedings of a working meeting of seal specialists. Internatl. Union Cons. Nature Nat. Res., Morges, Switzerland, Suppl. Paper, 39:1–176.

OWEN, R. 1853. On the anatomy of the walrus. Proc. Zool. Soc. London, 1853:103–106.

PALLAS, P. S. 1811. Zoographia Rosso-Asiatica. Imper. Acad. Sci., Petersburg, 1:1–568.

RAY, C. E. 1960. *Trichecodon huxleyi* (Mammalia: Odobenidae). Bull. Mus. Comp. Zool., 122:129–142.

————. 1975. The relationships of *Hemicaulodon effodiens* Cope 1869 (Mammalia:Odobenidae). Proc. Biol. Soc. Washington, 88:281–304.

RAY, C. E., A. WETMORE, D. H. DUNKLE, AND P. DREZ. 1968. Fossil vertebrates from the marine Pleistocene of southeastern Virginia. Smithsonian Misc. Coll., 153(3):1–25.

RAY, [G.] C. 1963. Locomotion in pinnipeds. Nat. Hist., 72:10–21.

————. 1973. Underwater observation increases understanding of marine mammals. Marine Technol. Soc. J., 7:16–20.

RAY, [G.] C., AND F. H. FAY. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). II. Evidence from physiological characteristics. Zoologica, 53:19–32.

RAY, [G.] C., AND M. S. R. SMITH. 1968. Thermoregulation of the pup and adult Weddell seal, *Leptonychotes weddelli* (Lesson), in Antarctica. Zoologica, 53:33–46.

RAY, G. C., AND W. A. WATKINS. 1975. Social function of underwater sounds in the walrus, *Odobenus rosmarus*. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 169:524–526.

REEVES, R. R. 1978. Atlantic walrus (*Odobenus rosmarus rosmarus*): a literature survey and status report. U.S. Fish Wildl. Serv., Wildl. Res. Rept., 10:1–41.

REPENNING, C. A. 1976. Adaptive evolution of sea lions and walruses. Syst. Zool., 25:375–390.

REPENNING, C. A., AND R. H. TEDFORD. 1977. Otarioid seals of the Neogene. U.S. Geol. Surv. Prof. Paper, 992:1–91.

REPENNING, C. A., C. E. RAY, AND D. GRIGORESCU. 1979. Pinniped biogeography. Pp. 357–369, *in* Historical biogeography, plate tectonics, and the changing environment (J. Gray and A. J. Boucot, eds.). Oregon State Univ. Press, Corvallis, 500 pp.

RUTTEN, L. 1907. On fossil trichechids from Zealand and Belgium. Koninkl. Akad. van Wettenschappen, Amsterdam, 10:2–14.

SCHEFFER, V. B. 1958. Seals, sea lions and walruses, a review of the Pinnipedia. Stanford Univ. Press, Stanford, California, 179 pp.

SCHEFFER, V. B., AND K. W. KENYON. 1963. Baculum size in pinnipeds. Z. Saugetierk., 28:38–41.

SLEPTSOV, M. M. 1940. On the adaptations to swimming in pinnipeds. Zool. Zhurnal, 19:379–386.

SMIRNOV, N. A. 1929. A review of the Pinnipedia of Europe and northern Asia. Izv. Otd. Priklad. Ikhtiol., 9:231–268.

STIRLING, I. 1974. An overwintering walrus in the Beaufort Sea. Murrelet, 55:40–41.

TAVROVSKII, V. A. (ED.). 1971. Mammals of Yakutia. Nauka, Moscow, 670 pp.

TOMILIN, A. G., AND A. A. KIBAL'CHICH. 1975. Walruses of the Wrangell Island region. Zool. Zhurnal, 54:266–272.

TSALKIN, V. I. 1937. Materials on the biology of the walrus of the Franz Josef Archipelago. Biul. Mosk. Obsch. Isp. Prirody, Otd. Biol., n.s., 46:43–51.

VIBE, C. 1950. The marine mammals and the marine fauna in the Thule District (northwest Greenland) with observations on ice conditions in 1939–41. Medd. om Grønland, 150(6):1–115.

WARTZOK, D., AND G. C. RAY. 1980. The hauling out behavior of the Pacific walrus. Rept. PB 80-192578. Nat. Tech. Info. Serv., Springfield, Virginia, 46 pp.