northern elephant seals. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **293**, R2376–R2381.

Iverson, S. J., Hamosh, M., and Bowen, W. D. (1995). Lipoprotein lipase activity and its relationship to high milk fat transfer during lactation in grey seals. *J. Comp. Physiol. B* **165**, 384–395.

Keith, E. O., and Ortiz, C. L. (1989). Glucose kinetics in neonatal elephant seals during postweaning aphagia. *Mar. Mamm. Sci.* **5**, 99–115.

Lang, S. L. C., Iverson, S. J., and Bowen, W. D. (2005). Individual variation in milk composition over lactation in harbour seals (*Phoca vitulina*) and the potential consequences of intermittent attendance. *Can. J. Zool.* **83**, 1525–1531.

Mellish, J. E., Iverson, S. J., Bowen, W. D., and Hammill, M. O. (1999). Fat transfer and energetics during lactation in the hooded seal: the roles of tissue lipoprotein lipase in milk fat secretion and pup blubber deposition. *J. Comp. Physiol. B* **169**, 377–390.

Nordoy, E. S., Stijfhoorn, D. E., Raheim, A., and Blix, A. S. (1992). Water flux and early signs of entrance into phase-iii of fasting in gray seal pups. *Acta Physiol. Scand.* **144**, 477–482.

Nordøy, E. S., and Blix, A. S. (1991). Glucose and ketone body turnover in fasting grey seal pups. *Acta Physiol. Scand.* **141**, 563–571.

Ortiz, R. M., Wade, C. E., and Ortiz, C. L. (2001). Effects of prolonged fasting on plasma cortisol and TH in postweaned northern elephant seal pups. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **280**, R790–R795.

Ortiz, R. M., Wade, C. E., and Ortiz, C. L. (2003). Body water handling in response to hypertonic-saline induced diuresis in fasting northern elephant seal pups (*Mirounga angustirostris*). *Comp. Biochem. Physiol. A* **134**, 423–428.

Ortiz, R. M., Crocker, D. E., Houser, D. S., and Webb, P. M. (2006). Angiotensin II and aldosterone increase with fasting in breeding adult male northern elephant seals (*Mirounga angustirostris*). *Physiol. Biochem. Zool.* **79**(6), 1106–1112.

Pernia, S. D., Costa, D. P., and Ortiz, C. L. (1989). Glomerular filtration rate in weaned elephant seal pups during natural, long term fasts. *Can. J. Zool. (J. Can. Zool.)* **67**, 1752–1756.

Sharp, J. A., Cane, K. N., Lefevre, C., Arnould, J. P. Y., and Nicholas, K. R. (2006). Fur seal adaptations to lactation: Insights into mammary gland function. *Curr. Top. Dev. Biol.* **72**, 276–308.

Sharp, J. A., Lefevre, C., Brennan, A. J., and Nicholas, K. R. (2007). The fur seal—a model lactation phenotype to explore molecular factors involved in the initiation of apoptosis at involution. *J. Mammary Gland Biol. Neoplasia* **12**, 47–58.

Tedman, R. A. (1983). Ultrastructural morphology of the mammary-gland with observations on the size distribution of fat droplets in milk of the Weddell seal *Leptonychotes weddelli* (Pinnipedia). *J. Zool.* **200**, 131–141.

Tedman, R. A., and Bryden, M. M. (1981). The mammary-gland of the Weddell seal, *Leptonychotes weddelli* (Pinnipedia) 1. Gross and microscopic anatomy. *Anat. Rec.* **199**, 519–529.

Worthy, G. A. J. (1991). Insulation and thermal balance of fasting harp and gray seal pups. *Comp. Biochem. Physiol. A* **100**, 845–851.

P

Pinnipedia, Overview

Annalisa Berta

Pinnipeds have always been understood to represent a group distinct from other aquatic mammals. They are recognized as members of the mammalian order Carnivora and include three monophyletic lineages, Otariidae (fur seals and sea lions), Odobenidae (walruses), and Phocidae (true or earless seals). Pinnipeds comprise slightly more than one-fourth (26%) of the species diversity of marine mammals (approximately 128 species currently recognized). Thirty-three living species of pinnipeds are distributed throughout the world: 18 phocids, 14 otariids, and the walrus. One additional species of phocid (Caribbean monk seal) and one subspecies of otariid (Japanese sea lion) are reported extinct in historical time.

I. Systematics and Distribution

A. Otariidae: Fur Seals and Sea Lions

Of the two groups of seals, the otariids are characterized by the presence of external ear flaps or pinnae, and for this reason they are often called "eared" seals (Fig. 1). Otariids (and the walrus) can turn their hindflippers forward and use them to walk (discussed further under Adaptations). The Otariidae traditionally are divided into two subfamilies Otariinae (sea lions) and Arctocephalinae (fur seals) although recent molecular studies have revealed that neither fur seals nor sea lions are monophyletic. Five living genera and species of sea lions are recognized, occurring in both the northern and southern hemispheres: *Eumetopias jubata* (northern or Steller's sea lion), *Neophoca cinerea* (Australian sea lion), *Otaria byronia* (Southern sea lion), *Zalophus californianus* (*Z. c. californianus* California sea lion, *Z. c. japonicus* Japanese sea lion, and *Z. c. wollebacki* Galapagos sea lion), and *Phocarctos hookeri* (New Zealand sea lion; Fig. 2). The fur seals, named for their thick, dense fur, include two genera, the monotypic Northern fur seal (*Callorhinus ursinus*) and the southern fur seals (*Arctocephalus*), consisting of eight species: *A. australis* (South American fur seal), *A. forsteri* (New Zealand fur seal), *A. gazella* (Antarctic fur seal), *A. galapagoensis* (Galapagos fur seal), *A. philippii* (Juan Fernandez fur seal), *A. pusillus* (*A. p. pusillus* South African fur seal and *A. p. doriferus* Australian fur seal), *A. townsendi* (Guadalupe fur seal), and *A. tropicalis* (Subantarctic fur seal). All of the fur seals except the northern and Guadalupe fur seals are found in the southern hemisphere. The northern fur seal is found in subarctic waters of the North Pacific, with the exception of a small population on San Miguel Island off California (Fig. 3).

Otariid monophyly is well supported based on a both morphologic as well as molecular data. Morphologic and molecular studies consistently position *Callorhinus* as the earliest diverging extant otariid (Fig. 4). Extinct otariids *Pithanotaria*, *Thalassoleon*, and *Hydractos* are sequential sister taxa to *Callorhinus*. Molecular results strongly support a branch containing the Guadalupe, South American, and New Zealand fur seals and the Australian and New Zealand sea lion. Good support was also found for South African fur seals as sister to this clade. The relationship between Northern + California sea lions, Southern sea lion and remaining sea lions and *Arctocephalus* species is not conclusively resolved. In support of fur seal and sea lion paraphyly is evidence for hybridization of various sympatric species (e.g., *Arctocephalus gazella*/*A. tropicalis*/*A. forsteri*, *Zalophus californianus*/*Otaria byronia*). Additionally, the violent sexual behavior by male sea lions toward females of different species my have resulted in more hybridization and introgression than has been typically recognized for the evolutionary history of otariids.

B. Odobenidae: Walruses

Although tusks are arguably the most characteristic feature of the modern walrus a rapidly improving fossil record indicates that these unique structures evolved in a single lineage of walruses and "tusks do not a walrus make" (Repenning and Tedford, 1977). The living walrus is the sole survivor of what was once a diverse radiation of at least 11

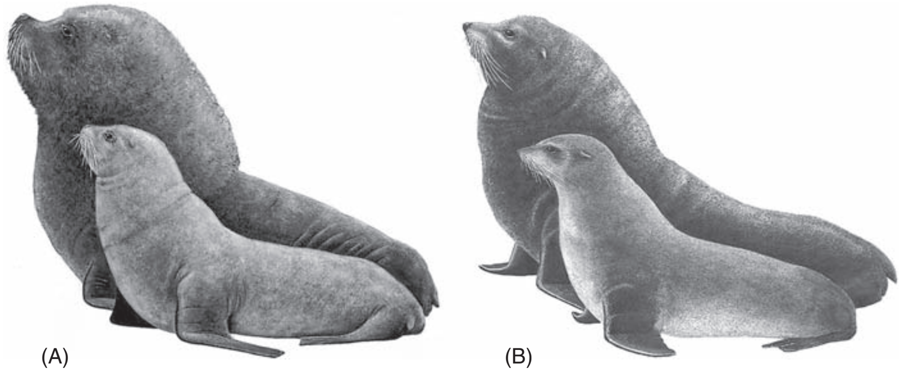

Figure 1 *Representative otariids (A) southern sea lion,* Otaria byronia *and (B) South African fur seal,* Arctocephalus pusillus, *illustrating pinna. Note also the thick, dense fur characteristic of fur seals. Illustrations by P. Folkens. (From Berta* et al., *2006.)*

Figure 2 *Distribution of sea lions. Based on Riedman (1990). (From Berta* et al., *2006.)*

Figure 3 *Distribution of fur seals. Based on Riedman (1990). (From Berta* et al., *2006.)*

P

genera and 14 species of walruses that lived from the early Miocene to the end of the Pliocene (see also PINNIPED EVOLUTION). Two subspecies of the modern walrus *Odobenus rosmarus* are usually recognized: *O. r. rosmarus* (Atlantic walrus) and *O. rosmarus divergens* (Pacific walrus) although a population from the Laptev Sea has been described as a third subspecies *O. rosmarus. lapteevi* but this has not been substantiated. Pacific walruses are more abundant, are larger, and have longer tusks than Atlantic walruses (Fay, 1981). Walruses inhabit the northern hemisphere in areas with pack ice over shallow water of the continental shelf (Fig. 5). Like phocids, walruses lack external ear flaps. A unique feature of members of the modern walrus lineage are enlarged upper canine tusks that function primarily in breeding and social contexts. Walrus locomotion combines elements of phocid and otariid locomotion (discussed further under Adaptations).

Monophyly of the walrus family is strongly supported although controversy continues regarding whether walruses are more closely related to otariids or to phocids. Although there is morphologic evidence to ally walruses and phocids recent total evidence and molecular studies provide consistent, robust support for an alternative alliance between otariids and odobenids. A survey of genetic variation among Atlantic and Pacific populations of the walrus suggests separation of the subspecies about 500,000–750,000 years ago, supporting the suggestion that *Odobenus* evolved in the Pacific and reached the North Atlantic early in Pleistocene time (Cronin *et al*., 1994).

C. Phocidae: Seals

The second major grouping of seals, the phocids, often are referred to as the "true" or "earless" seals for their lack of visible ear pinnae, a characteristic which readily distinguishes them from otariids as well as the walrus (Fig. 6). Among the most distinguishing phocid

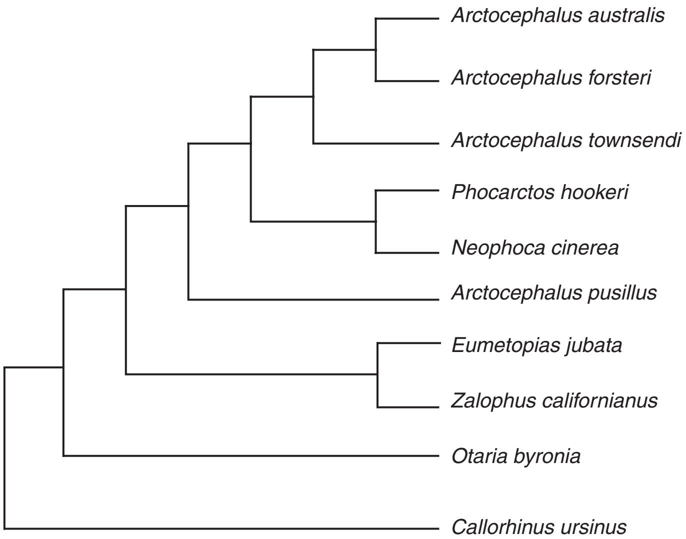

Figure 4 *Phylogeny of the Otariidae based on molecular data. (From Arnason* et al.*, 2006.)*

Figure 5 *Distribution of modern walrus subspecies,* Odobenus rosmarus divergens *(Pacific walrus) and Odobenus rosmarus rosmarus (Atlantic walrus).*

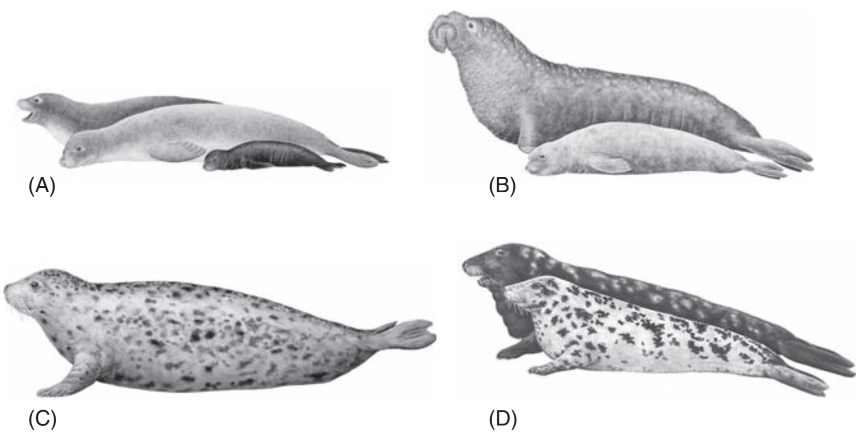

Figure 6 *Representative monachines (A) Hawaiian monk seal,* Monachus schauinslandi *and (B) northern elephant seal,* Mirounga angustirostris *and phocines (C) Harbor seal,* Phoca vitulina, *and (D) gray seal,* Halichoerus grypus. *Males are shown behind smaller females. Illustrations by P. Folkens. (From Berta* et al.*, 2006.)*

characteristics is their inability to turn the hindlimbs forward to support the body, resulting in a peculiar crawling locomotion on land (discussed further under Adaptations). Phocids inhabit both northern and southern hemispheres, although they are largely restricted to polar and subpolar regions (Fig. 7). Among pinnipeds, phocids are unique in their ability to survive in estuarine and freshwater habitats (e.g., Caspian and Baikal seals inhabiting landlocked lakes).

Traditionally phocids have been divided into two to four major subgroups (including the Monachinae, Lobodontinae, Cystophorinae, and Phocinae). Recent molecular studies strongly support monophyly of both the Monachinae and Phocinae (Davis *et al.*, 2004; Arnason *et al.*, 2006; Fig. 8).

The Monachinae clade of "southern seals" includes Monachini (monk seals), Miroungini (elephant seals), and the Lobodontini

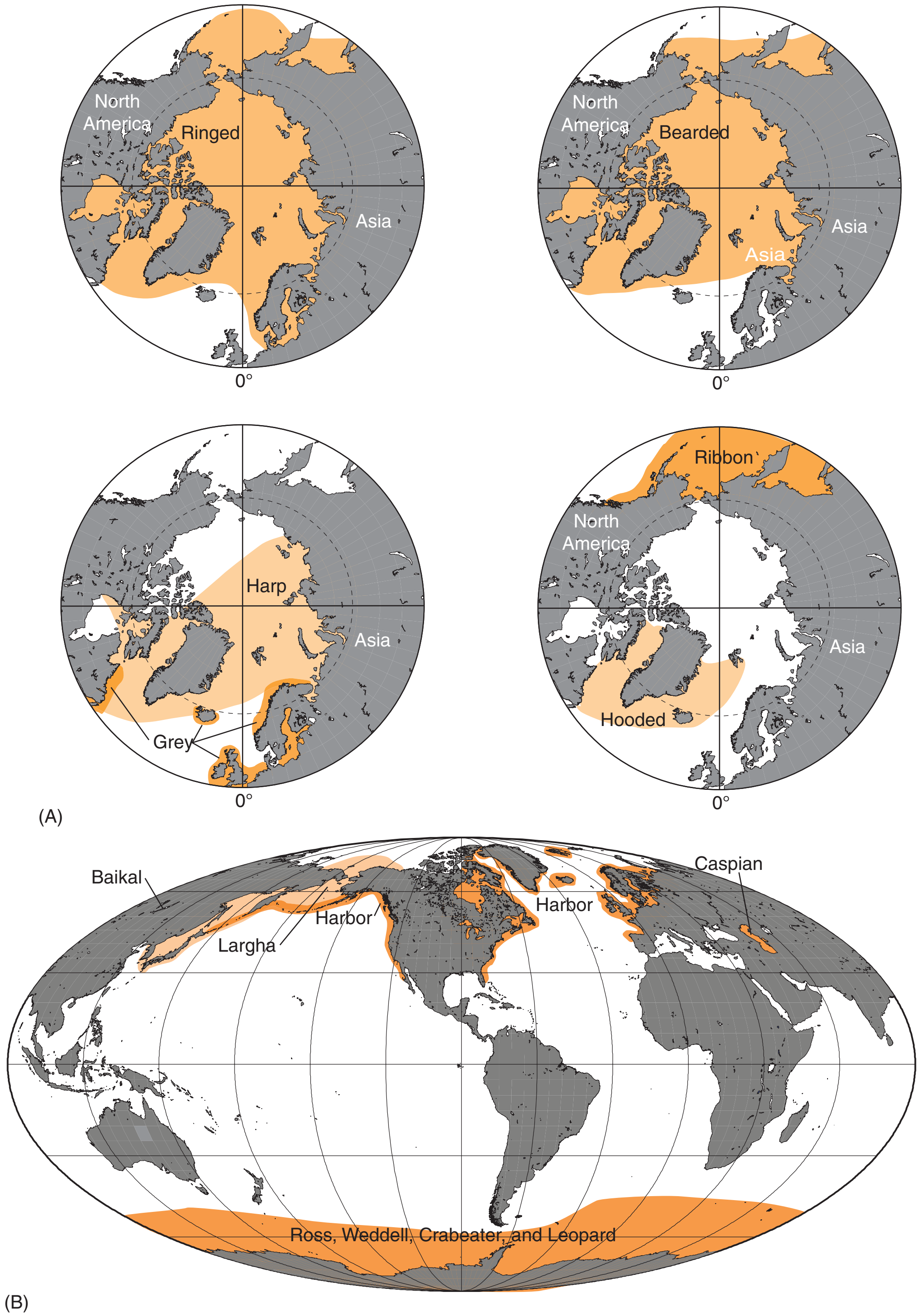

Figure 7 *Distribution of some phocine seals (A), Antarctic phocine seals (B), and monachines (Facing page). Based on Riedman (1990). (From Berta* et al.*, 2006.)*

P

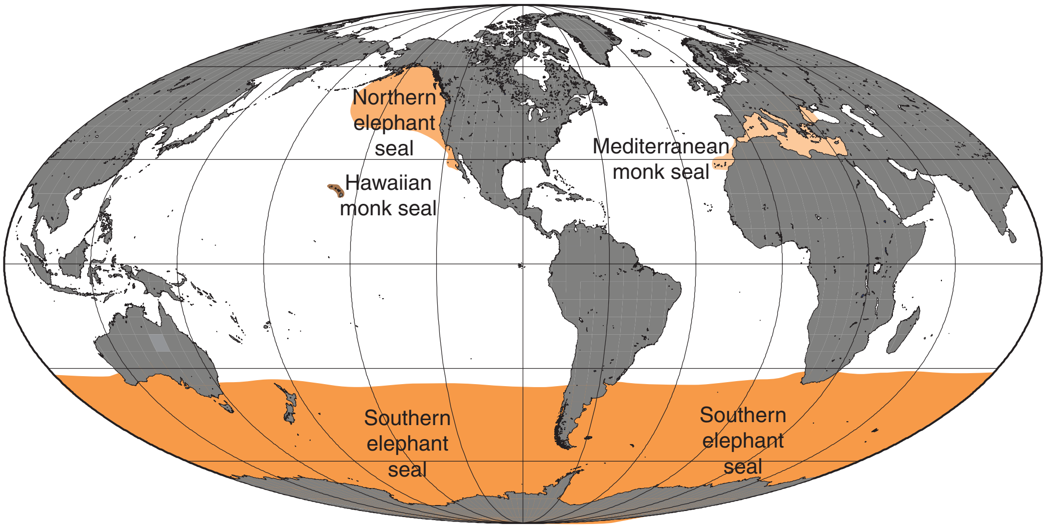

Figure 7 *(continued)*

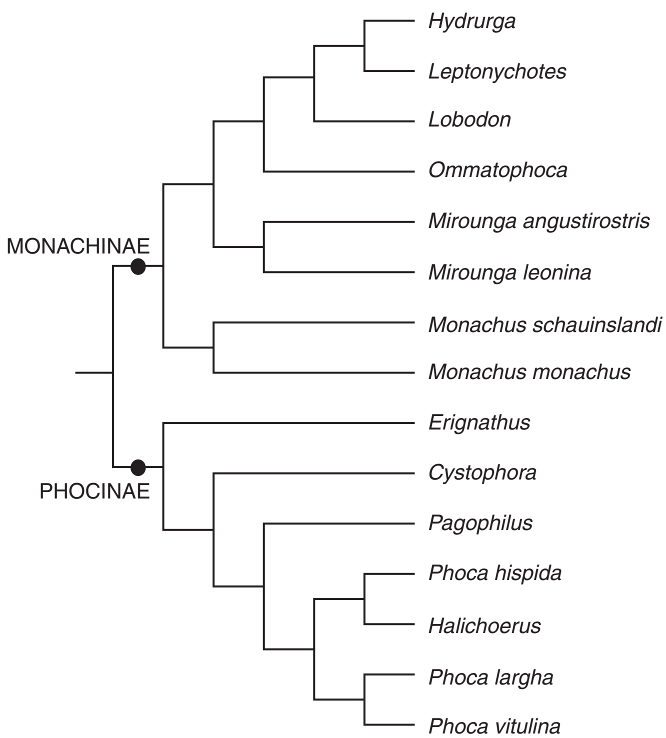

Figure 8 *Phylogeny of the Phocidae based on molecular data (Arnason* et al.*, 2006).*

(Antarctic seals). Within the Monachinae there is strong support for a split between Monachini, the deepest branching lineage and Miroungini and Lobobontini. Three species of *Monachus* have been described, *M. schauinslandi* (Hawaiian monk seal), *M. monachus* (Mediteranean monk seal), and the recently extinct *M. tropicalis* (Caribbean monk seal). Molecular sequence data for extant species of *Monachus* supports a sister group relationship between the Hawaiian and Mediterranean monk seals (Davis *et al.*, 2004; Fyler *et al.*, 2005). Elephant seals, named for their enlarged proboscis, are represented by two species, *Mirounga angustirostris* (northern elephant seal) and *Mirounga leonina* (southern elephant seal).

The Lobodontini which include *Leptonychotes weddelli* (Weddell seal), *Lobodon carcinophagus* (Crabeater seal), *Hydrurga leptonyx* (Leopard seal), and *Ommatophoca rossi* (Ross seal). Molecular studies consistently position the Ross seal as sister to the other three Antarctic seals.

The Phocinae clade of "northern seals" includes *Erignathus barbatus* (bearded seal), *Cystophora cristata* (hooded seal), *Halichoerus grypus* (gray seal), *Phoca* (including among others harbor and spotted seal), *Pusa hispida* (ringed seal), *Histriophoca fasciata* (ribbon seal), and *Pagophilus groenlandica* (harp seal). A basal divergence between the bearded seal and the hooded seal + Phocini (*Pusa*, *Histriophoca*, *Pagophilus*, *Halichoerus*, and *Phoca*) is strongly supported by molecular studies (cited above). Disagreement about relationships among the Phocini, attributed to their rapid radiation, have resulted in taxonomic uncertainty regarding their classification. There is general agreement that the Phocini are divided into an earlier diverging lineage of spotted + harbor seals and remaining seals. It is acknowledged that relationships among the latter group are poorly resolved.

The harbor seal (*Phoca vitulina*) has the most extensive geographic distribution of any seal, with a range spanning over 16,000 km from the east Baltic, west across the Atlantic and Pacific Ocean to southern Japan. The population structure of the harbor seal studied by Stanley *et al.* (1996) revealed that populations in the Pacific and Atlantic Oceans are highly differentiated. The mitochondrial data are consistent with ancient isolation of populations in both oceans coincident with the development of continental glaciers and extensive sea ice. In the Atlantic and Pacific Oceans populations appear to have been established from west to east, with the European populations showing the most recent common ancestry.

II. Anatomy and Physiology

Pinniped aquatic specializations include their streamlined shape, reduced external ear pinnae, paddle-like limbs and feet, small tail, and genital organs and mammary glands that are retracted beneath the skin. In comparison to most terrestrial carnivorans, pinnipeds are large which helps to conserve warmth. Pinnipeds, particularly phocids show tremendous diversity in size ranging from the smallest pinniped, the Baikal seal reaching a length of just over a meter and a weight of 45 kg to the largest pinniped, the elephant seals nearly 5 m

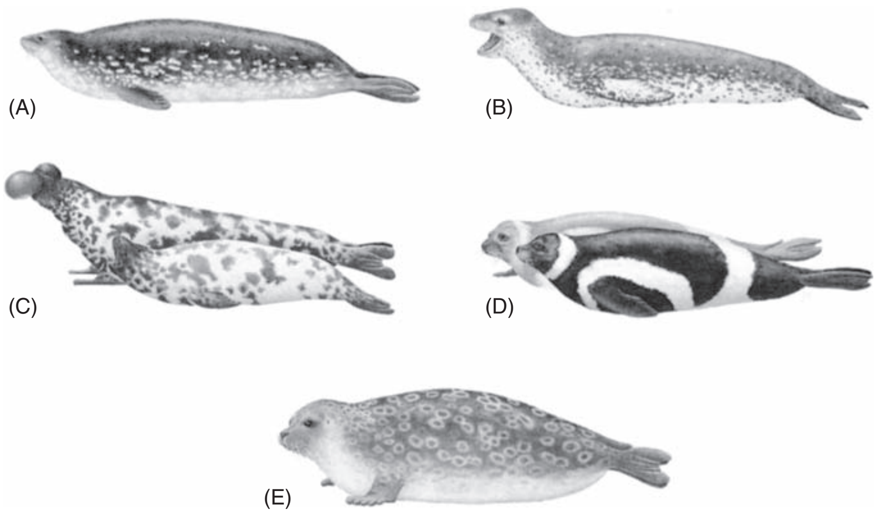

Figure 9 *Examples of phocid pelage patterns (A) Weddell seal,* Leptonychotes weddellii, *(B) leopard seal,* Hydrurga leptonyx, *(C) hooded seal, Cystophora cristata, (d) ribbon seal* Histriophoca fasciata, *and (E) ringed seal,* Phoca hispida. *(Illustrations by P. Folkens, in Berta and Sumich, 1999.)*

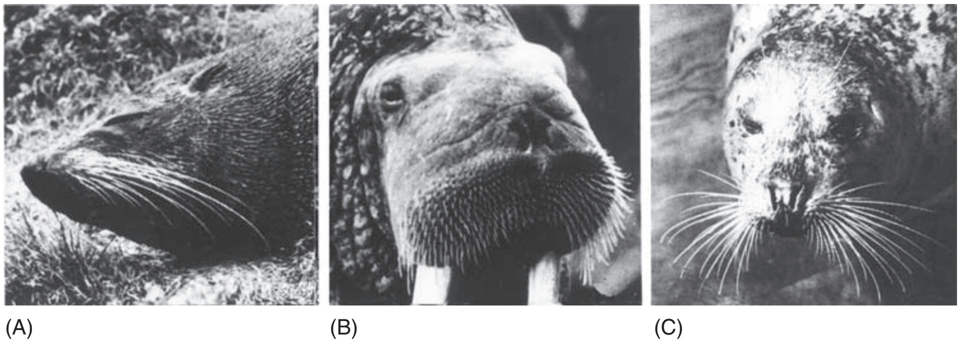

Figure 10 *Heads of various pinnipeds showing facial vibrissae (A) New Zealand fur seal,* Arctocephalus forsteri, *(B) Walrus,* Odobenus rosmarus, *and (C) Pacific harbor seal,* Phoca vitulina richardsi. *(From Ling, 1977 in Berta et al., 2006.)*

in length (adult males) and up to 3200 kg (Bonner, 1990). Pinnipeds are ecologically diverse with habitats ranging from shelf to surface waters in tropical and polar seas, with some species living in fresh water lakes, while others freely move between rivers and the ocean.

Phocids and the walrus have lost much of their hair (fur) and are characterized by thick layers of blubber under the skin. Otariids, especially the fur seals, have retained a thick fur coat. Color patterns in the pelage of pinnipeds occur almost exclusively among phocids. Ice breeding seals (e.g., ribbon seal, harp seal, hooded seal, ringed seal, crabeater seal, Weddell seal, and leopard seal) show contrasting dark and light or disruptive color patterns (Fig. 9). The uniform coloration of some pinnipeds (e.g., white harp seal pups) allows them to readily blend into their arctic environment. Pinnipeds come ashore for birthing and molting. All phocid seals undergo an annual molt. Fur seals and sea lions instead renew their pelt gradually all year.

Vibrissae, or whiskers, are stiff hairs that occur on the face. Most prominent are the mystacial whiskers which range in size from the short stiff bristles of the walrus to the very long, fine bristles of fur seals (Fig. 10). Vibrissae function as sensitive touch receptors. Research on the Baltic ringed seal has shown that they have exceptionally well-developed vibrissae which help them find their way in the dark and often cloudy water beneath the ice. A single vibrissae of the Baltic ringed seal contains more than 10 times the number of nerve fibers typically found in that of a land mammal. Experimental data has also shown that blindfolded harbor seals used vibrations detected by their vibrissae to follow prey (i.e., fish "trails") in the water (Denhardt *et al*., 2001). Evidence of heat conduction in the vibrissae of harbor seals indicates that they also play a role in thermoregulation (Mauck *et al*., 2000).

Pinnipeds, like other marine mammals, have evolved ways to accommodate the immense heat loss that occurs in the water. Among these solutions are a spherical body and a resultant decreased surface to volume ratio and increased insulation (thick blubber or fur). In addition, heat exchange systems occurring in the flippers, fins, and reproductive tracts of pinnipeds conserves body heat (see THERMOREGULATION).

Among modern pinnipeds aquatic and terrestrial locomotion are achieved differently (see LOCOMOTION). Three distinct patterns of swimming are recognized: (1) pectoral oscillation (forelimb swimming) seen in otariids where the forelimbs are used in a "flapping" manner to produce thrust, (2) pelvic oscillation (hindlimb swimming) seen in phocids where the hindlimbs are the major propulsors, and (3) a variant of pelvic oscillation exhibited by the walrus where the hindlimbs are the dominant propulsive force and the forelimbs are used as rudders or paddles. There is a major difference in locomotion on land between phocids on the one hand and otariids and walruses on the other. The inability of phocids to turn the hindlimbs forward results in forward progression by vertical undulations of the trunk which do not involve the hindlimbs. In walruses, as in otariids, the hindlimbs can be rotated forward in terrestrial locomotion.

Pinnipeds are carnivores, most are generalists feeding predominately on fish and squid (see also DIET). Several pinnipeds, notably crabeater and leopard seals have highly modified cheek teeth with complex cusps to trap and strain krill. Leopard seals also possess well-developed canines for preying on birds and other pinnipeds. Walruses are specialists feeding almost exclusively on clams using a suction feeding strategy in which the muscular tongue acts as a piston creating low pressure in the mouth cavity. Some pinnipeds, for example elephant seals, rival gray whales in the distances traveled in migration (18,000–21,000 km) to forage offshore between breeding seasons. The advent of microprocessor-based geographic location time and depth recorders (GLTDRs), satellite telemetry, and crittercams has enabled documentation of details of the foraging behavior of these deep diving seals.

Among pinnipeds are found the most extraordinary of marine mammal divers (see DIVING BEHAVIOR and DIVING PHYSIOLOGY). Average dives of small species such as the Ross seal are just under 10 min in duration increasing to over 1 h for the northern elephant seal and the Weddell seal. Maximum depths vary from less than 100 m in the Guadalupe fur seal to more than 1500 m in northern elephant seal males. Some seals (in addition to sperm whales, sea turtles, and some penguins) are "incredible diving machines" with unique ways of budgeting their oxygen supply and responding to pressure.

Sounds produced by pinnipeds include both airborne and underwater vocalizations (see SOUND PRODUCTION). Airborne sounds vary from grunts, snorts, or barks identified as either mother–pup calls or threat calls among seals to the distinctive bell-like sounds produced by male walruses striking throat pouches with their flippers as part of a courting display during the breeding season. Pinnipeds produce a variety of underwater sounds that appear most often related to breeding activities and social interactions. Among these are the whistles, trills, chirps, and buzzes of Weddell seals that are used in territorial defense. These contrast with the soft, lyrical calls of leopard seals that may be related to their solitary social system. In contrast to toothed whales, pinnipeds have not been found to use echolocation in their natural surroundings.

The pinniped eye is adapted for vision both above and under water. The spherical lens, thick retina, and the well-developed tapetum lucidum increase light sensitivity. With the exception of the walrus which has small eyes, seals and sea lions have large eyes in relation to body size. The question of whether pinnipeds have color vision is still debated although behavioral experiments and the presence of both rods and cones in the retina have been documented in some species (e.g., California sea lion, spotted seal, walrus) (see VISION).

III. Behavior

Unlike other marine mammals, pinnipeds differ in their need to return to land (or to ice) to give birth. Many pinnipeds (e.g., elephant seal) are extremely polygynous, with successful males mating with dozens of females in a single breeding season (see BREEDING SYSTEMS). Species that are polygynous tend to breed in large colonies on land where males compete for breeding territories (in otariids) or establish dominance hierarchies (in elephant seals). Because these males must compete for access to females associated with extreme polygyny is the strong sexual dimorphism seen in elephant seals including large body size (adult males as much as five times as large as females), elongated proboscis, enlarged canine teeth, and thick skin on the neck. Other phocids (e.g., Weddell seal, harp, ringed, ribbon, bearded, hooded) mate in the water or on ice and show a reduced level of polygyny, that is explained in part by the difficulty in gaining access to females in unstable environments such as pack ice.

Pinnipeds are characterized by sexual bimaturity with females reaching sexual maturity before males. In polygynous species males require several years of physical maturation following sexual maturity before they successfully compete for access to females. Gestation in most species of pinnipeds averages between 10 and 12 months; walruses have the longest gestation period of 16 months. Most species regulate their reproductive cycle (see REPRODUCTIVE BEHAVIORS) by delayed implantation (from 1.5 to 5 months). Delayed implantation prolongs birth until conditions are more favorable for offspring survival. Pinniped females of all species give birth to a single pup. In most species, pupping occurs in spring or summer when food availability is highest.

The maternal behaviors and lactation strategies of pinnipeds are influenced by their breeding habitat whether on ice or land. Most phocids exhibit a fasting strategy where females fast completely and remain out of water for the duration of a relatively short lactation, ranging from less than 1 week in hooded seals to almost 8 weeks in the Weddell seal. It has been suggested that the unstable nature of pack ice has selected for the extremely short lactation periods of some ice breeding phocid seals. To compensate for the brevity of lactation, the milk produced by these species is energy dense, with a fat content up to 60% in some species (i.e., hooded and harp seals). Rapid pup growth is ensured by the richness of the milk. In the foraging cycle strategy of most otariids, mothers fast for only a few days following the birth of pups. Then the mothers begin foraging trips at sea leaving their pups for a few days at a time. The lactation periods of otariids are longer, ranging from several months to more than 1 year, and milk is generally less energy dense than in phocids (e.g., milk fat content averaging between 24 and 40%). Walruses exhibit a variant of the otariid strategy, termed the aquatic nursing strategy, in which walrus pups accompany their mothers on foraging trips into the water. The length of lactation in walruses is the longest among pinnipeds, lasting 2–3 years.

Among generalizations that can be made about pinniped longevity is that females, especially those of polygynous species, tend to live longer than males. In many cases males do not survive even to the delayed age of sexual maturity. Seals have been known to pup successfully at 24–25 years and live as long as 40 years or more. Significant factors implicated in the natural mortality of pinnipeds include disease (especially morbilliviruses), predation (e.g., white sharks, killer whales), starvation, and parasites.

See Also the Following Articles

Adaptations ■ Diving Physiology ■ Earless Seals ■ Eared Seals

References

Arnason, U., Gullberg, A., Janke, A., Kullberg, M., Lehman, N., Petrov, E. A., and Vainola, R. (2006). Pinniped phylogeny and a new hypothesis for their origin and dispersal. *Mol. Phylogenet. Evol.* **41**(2), 345–354.

Berta, A., Sumich, J. L., and Kovacs, K. M. (2006). "Marine Mammals: Evolutionary Biology," 2nd ed. Elsevier, San Diego, CA.
Bonner, W. N. (1990). "The Natural History of Seals." Facts on File, New York, NY.
Cronin, M. A., Hillis, S., Born, E. W., and Patton, J. C. (1994). Mitochondrial DNA variation in Atlantic and Pacific walruses. *Can. J. Zool.* **72**, 1035–1043.
Davis, C. S., Delisle, I., Stirling, I., Siniff, D. B., and Strobeck, C. (2004). A phylogeny of the extant Phocidae inferred from complete mitochondrial coding regions. *Mol. Phylogenet. Evol.* **33**, 363–377.
Denhardt, G., Mauck, B., Hanke, W., and Bleckmann, H. (2001). Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* **293**, 102–104.
Fay, F. H. (1981). Walrus: *Odobenus rosmarus*. *In* "Handbook on Marine Mammals" (S. H. Ridgway, and R. J. Harrison, eds), Vol. 1, pp. 1–23. Academic Press, New York.
Fyler, C. A., Reeder, T. W., Berta, A., Antonelis, G., Aguilar, A., and Androukaki, E. (2005). Historical biogeography and phylogeny of monachine seals (Pinnipedia: Phocidae) based on mitochondrial and nuclear DNA data. *J. Biogeogr.* **32**, 1267–1279.
Ling, J. K. (1977). Vibrissae of marine mammals. *In* "Functional Anatomy of Marine Mammals" (R. J. Harrison, ed.), Vol. 3, pp. 387–415. Academic Press, London.
Mauck, B., Eysel, U., and Dehnhardt, G. (2000). Selective heating of vibrissal follicles in seals (*Phoca vitulina*) and dolphins (*Sotalia fluviatus guianensis*). *J. Exp. Biol.* **203**, 2125–2131.
Repenning, C. A., and Tedford, R. H. (1977). Otarioid seals of the Neogene. *U.S. Geol. Surv. Prof. Pap.*, 992.
Riedman, M. (1990). "The Pinnipeds. Seals, Sea Lions and Walruses." University of California Press, Berkeley, CA.
Stanley, H., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J., and Wayne, R. K. (1996). Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). *Mol. Biol. Evol.* **13**(2), 368–382.

Playful Behavior

Bernd Würsig

Play consists of actions performed for no other apparent purpose than their own enjoyment. However, it is recognized that play occurs in young animals to learn motor and social skills needed to survive. Play as "enjoyment" may have evolved simply because something enjoyable will be sought after, and if needed actions of learning are enjoyable, they will be done. Tussling sibling brown bears, rolling and cuffing each other, are obviously playing. But it has long been a truism that such play in the proximal sense is vital in learning self-defense and in establishing rules of association. Play tends to decrease in frequency as mammals become older and does not often occur in adults. Obvious exceptions are some primates (including humans!) and cetaceans, although as behavioral studies gather details, researchers are learning that play in adults of other species is actually more common than described previously. Play may also be an attempt to relieve boredom, and we would expect play to be especially well developed in the larger brained, behaviorally flexible, mammals (Goodall, 1990; Marino *et al.*, 2007).

I. Motor Imitations

Many marine mammals seem to be especially good at imitating the actions of their conspecifics or of individuals of other species. Thus, untrained dolphins in oceanaria have been described as performing a colleagues' trained repertoire essentially flawlessly when called upon to do so. Apparently, the dolphins learned the motor actions simply by observation (Pryor, 1995). While this by itself is not play, the capability of imitation is often expressed as play: dolphins have imitated a diver's movements of cleaning the pool; as well as the grooming and swimming movements of seals and other pool inhabitants. The dolphins would generally approach the object of imitation, slow their own travel to approximate that of the slower coinhabitant, and then move their body in exaggerated imitation of movements of the other individual. The human diver, alternately bending and straightening at the waist as he or she cleaned the aquarium tank with a rubber scraper, was imitated by the dolphin bobbing its head and neck up and down in rapid and jerky fashion. At the same time, the dolphin released clouds of bubbles from its blowhole in synchrony with the bubbles of the diver's air regulator and made a squeaking sound in an apparent attempt to reproduce the squeaks of the rubber on glass. The author has seen similar behavior in nature, with a bottlenose dolphin (*Tursiops truncatus*) adult in the Bahamas imitating a particularly clumsy tourist who had difficulty in descending below the water as she propelled herself with her skin dive flippers and by rotating her arms. The dolphin matched her speed, alternately bobbed at the surface and descended in unison with the woman, jerked its peduncle and tail back and forth in unnatural fashion, while at the same time rotating its short front flippers as if they were flailing arms. The effect looked highly hilarious, and it would be difficult to rationalize the behavior as anything but a bit of malicious fun, or play.

II. Vocal Imitation

While motor or physical imitation seems to be mainly in the purview of toothed whales, other marine mammals also practice vocal imitation. This imitation may be an outgrowth of learning one's own species-specific (and perhaps group or pod-specific, as in killer whales, *Orcinus orca*) vocalizations, but the capability can then become a method of play. In the 1970s, a captive male harbor seal (*Phoca vitulina*), named Hoover by his caretakers, was capable of imitating the voice of a human worker who frequented his area, complete with a New England accent and a bit of a drunk-sounding slur (Ralls *et al.*, 1985). Beluga whales (*Delphinapterus leucas*) can also imitate human sound and will at times use these imitations in apparent mischievous play. While dolphins cannot imitate human sounds very precisely (they seem to lack the vocal capability, not the intelligence, to do so), they will easily imitate clicks, whistles, barks, scrapes, and squeaks (as the forementioned window-washing sounds) that can occur in an aquarium with other animals. A particularly readable account of imitation, innovation, intelligence, and cognition can be found in Tyack (1999).

III. Examples of Play

When we meet marine mammals underwater, we are apt to be subjects of intense curiosity. Sea lions, fur seals, and harbor seals will dash around us, pirouette in front of us, and gaze at us. Interestingly, these same animals ignore us or become wary if we approach too close to them when they are hauled out onshore. When in their watery milieu, however, fear is gone. Manatees (*Trichechus* spp.) and dugongs (*Dugong dugon*) are similarly attracted to humans underwater, except in those places where they are hunted. This curiosity can turn to play. Just about every researcher who dives with marine