



FAUNA *of* AUSTRALIA

56. OTARIIDAE AND PHOCIDAE

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Australian Sea-lion—*Neophoca cinerea* [G. Ross]



Southern Elephant Seal—*Mirounga leonina* [G. Ross]



Australian Sea-lion—*Neophoca cinerea* [G. Ross]



Ross Seal, with pup—*Ommatophoca rossii* [J. Libke]



Weddell Seal—*Leptonychotes weddellii* [P. Shaughnessy]



New Zealand Fur-seal—*Arctocephalus forsteri* [G. Ross]



Crab-eater Seal—*Lobodon carcinophagus* [P. Shaughnessy]

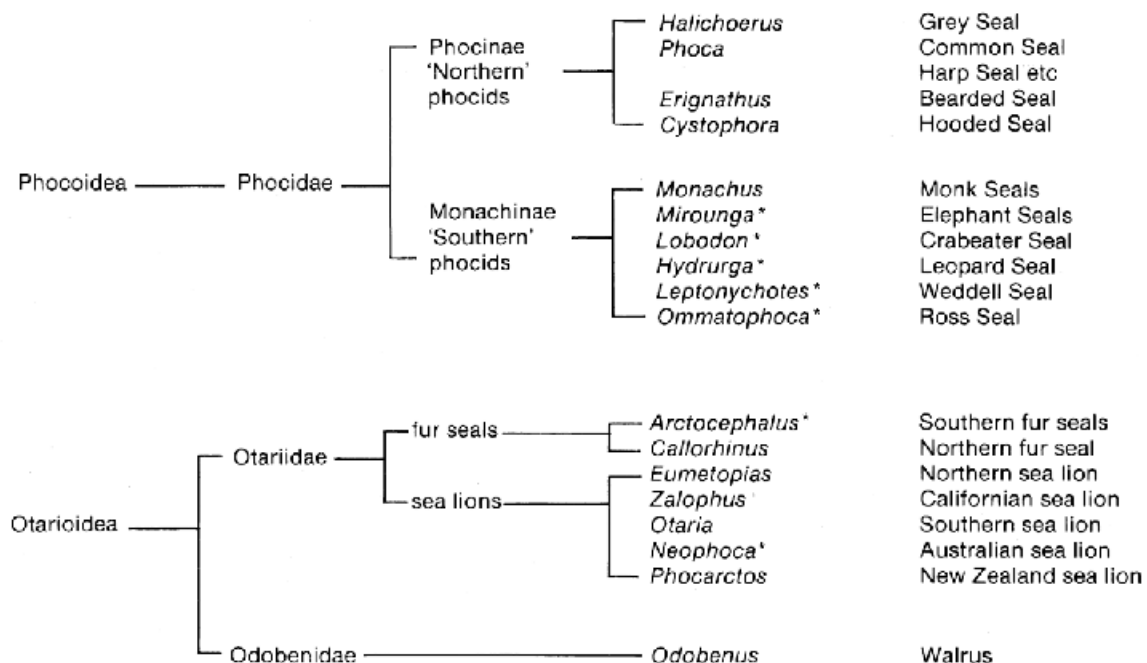
DEFINITION AND GENERAL DESCRIPTION

Pinnipeds are aquatic carnivores. They differ from other mammals in their streamlined shape, reduction of pinnae and adaptation of both fore and hind feet to form flippers. In the skull, the orbits are enlarged, the lacrimal bones are absent or indistinct and there are never more than three upper and two lower incisors. The cheek teeth are nearly homodont and some conditions of the ear that are very distinctive (Repenning 1972).

Both superfamilies of pinnipeds, Phocoidea and Otarioidea, are represented in Australian waters by a number of species (Table 56.1). The various superfamilies and families may be distinguished by important and/or easily observed characters (Table 56.2). King (1983b) provided more detailed lists and references. These and other differences between the above two groups are not regarded as being of great significance, especially as an undoubted fur seal (Australian Fur-seal *Arctocephalus pusillus*) is as big as some of the sea lions and has some characters of the skull, teeth and behaviour which are rather more like sea lions (Repenning, Peterson & Hubbs 1971; Warneke & Shaughnessy 1985).

The Phocoidea includes the single Family Phocidae – the ‘true seals’, distinguished from the Otariidae by the absence of a pinna and by the position of the hind flippers (Fig. 56.1). The two subfamilies within the Phocidae are the Phocinae, frequently referred to as Northern phocids (there are no members in Australia), and the Monachinae or Southern phocids, to which belong all the phocids found in Australian territories. Characters distinguishing Phocinae and Monachinae are mainly skeletal (Burns & Fay 1970; King 1966; 1983b).

Table 56.1 A summary of the present classification of pinnipeds. Genera occurring in Australian waters and Australian Antarctic Territory are marked with an *



The placement of pinnipeds in the Carnivora means that the detailed relationships and classification of both groups have to be reconsidered. This is not a matter that need concern us here; it is usually sufficient to use the family names Otariidae, Odobenidae and Phocidae.

Ten genera of phocids are recognised, one of which (*Phoca*) has seven species and a number of subspecies. Otariids comprise five genera of sea lions; two genera of fur seals, one of which (*Arctocephalus*) has eight species; and one genus of walrus (*Odobenus*). The total is 34 different species of pinniped (not including fossils), though this does vary a little according to different authors (King 1983b).

Adult male seals are called bulls, immature males are bachelors. Adult females are cows and the young are pups until they are about 5 months old. After this, until their first birthday they are yearlings. The pups may gather in groups or pods and a group of breeding animals is a rookery. The young of Walruses (*Odobenus rosmarus*) are calves.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The general external shape of a seal is well known (Fig. 56.1). The plump body is spindle-shaped, streamlined with few protuberances for an aquatic life. An external pinna is very small in otariids and absent in phocids. The testes are scrotal in otariids, but inguinal and invisible externally in phocids, the teats are retracted and the penis is withdrawn into a pouch.

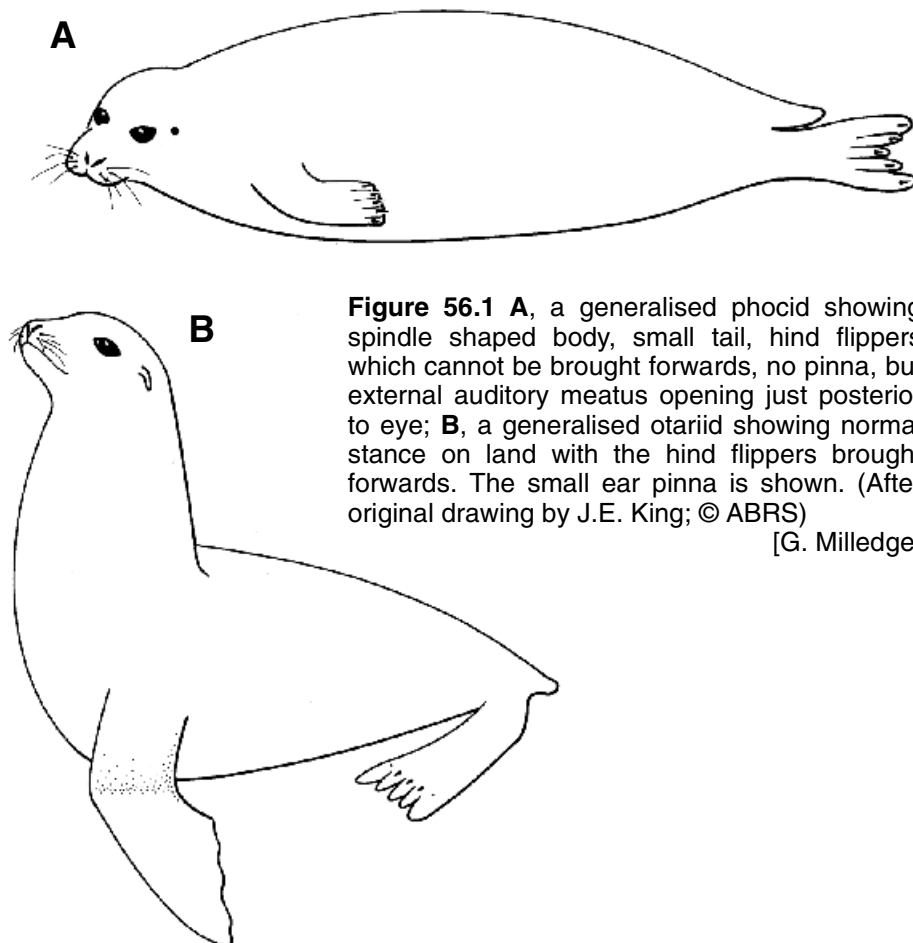


Figure 56.1 A, a generalised phocid showing spindle shaped body, small tail, hind flippers which cannot be brought forwards, no pinna, but external auditory meatus opening just posterior to eye; B, a generalised otariid showing normal stance on land with the hind flippers brought forwards. The small ear pinna is shown. (After original drawing by J.E. King; © ABRS)

[G. Milledge]

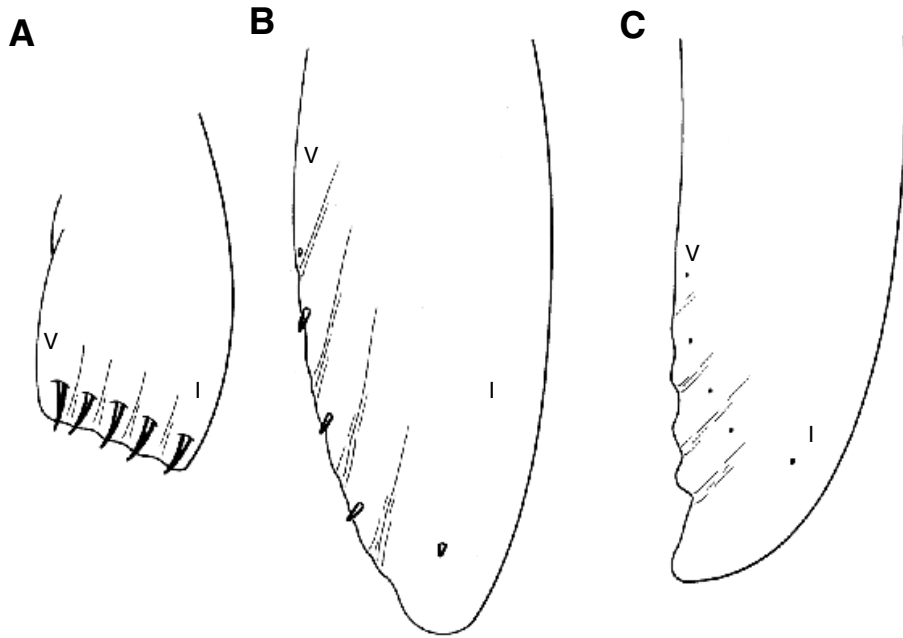


Figure 56.2 Right fore flippers (not to scale) of pinnipeds. **A**, the Harbour Seal, *Phoca vitulina*, showing the short, square, large-clawed flipper typical of northern phocids; **B**, the Leopard Seal, *Hydrurga leptonyx*, a southern phocid, in which the flipper is long, digit V is much shorter than the others and the claws are reduced; **C**, the Californian Sea-lion, *Zalophus californianus*, an otariid, in which the fore flippers are also long with a short digit V and rudimentary claws. Digits I and V are marked. (After original drawing by J.E. King ; © ABRS) [G. Milledge]

Flippers are perhaps the most obvious way in which seals differ from land mammals. The leg and arm bones are short and lie within the body outline. The axilla in otariids is level with the middle of the forearm and in phocids is at the wrist. In both groups the hind flipper is free only from the ankle. The flippers themselves, the manus and pes, are proportionally larger than these parts in a terrestrial mammal, to facilitate swimming. The whole flipper is encased in integument. The surface area is increased by the skin stretching between the digits and, in otariids, by a cartilage-supported extension of tissue beyond the claws of the hind digits.

Phocids have five large claws on all digits, though the flippers of Southern phocids tend to have reduced claws (King 1983b) (Fig. 56.2). Otariid foreflippers are elongated and the claws reduced to small nodules. On the hind flippers, the claws of the three middle digits are longer and used for grooming when the tissue extension is folded back. The two outer claws are very small (Fig. 56.3).

Body Wall

The integument of seals is comprised of three layers: an epidermis and a dermis which forms the skin and the hypodermis beneath forming the blubber. In phocids, or at least in the Southern Elephant Seal (*Mirounga leonina*) where much work has been done (Ling 1968), a pliable waterproof horny layer is formed by the solid keratinised cells of the stratum corneum. This layer is lubricated by sebaceous glands and shed only at the annual moult. The continuous shedding of the cells of the outer layer of the epidermis, such as occurs in humans, would soon lead to a seal becoming waterlogged.

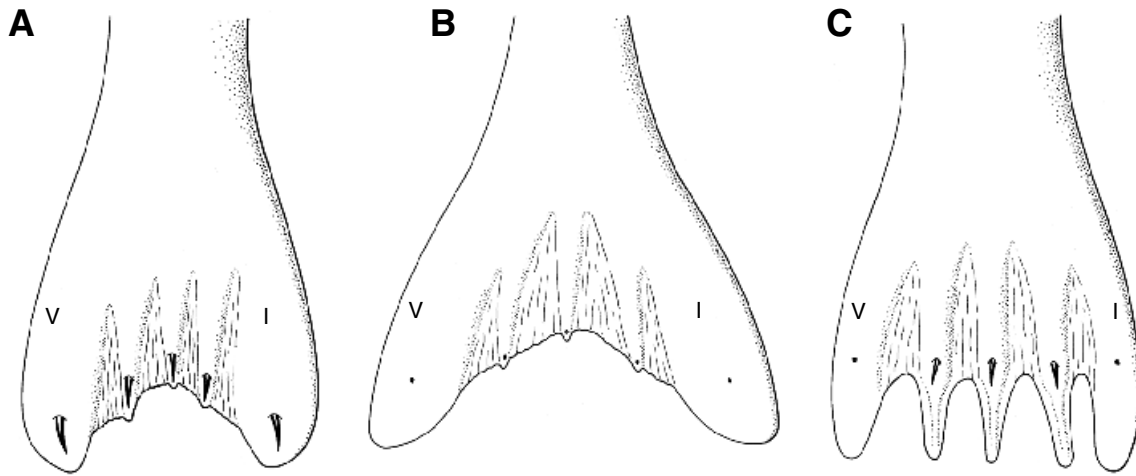


Figure 56.3 Right hind flippers (not to scale) of pinnipeds. **A**, the Harbour Seal, *Phoca vitulina*, in which the five equal sized large claws are typical of northern phocids; **B**, the Southern Elephant Seal, *Mirounga leonina*, showing the reduced nodular claws typical of southern phocids; **C**, the otariid, Hooker's Sealion, *Phocarctos hookeri*, in which the two outer claws are reduced, while the other three claws are longer, for grooming. The cartilage-supported tissue extensions on the otariid flippers can be seen. On all three flippers the thin expansile skin between the digits is indicated. Digits I and V are marked. (After original drawing by J.E. King; © ABRS) [G. Milledge]

The dermis bears the hair follicles and is well supplied with blood vessels. The hypodermis or blubber is closely connected to the dermis, but only loosely connected to the underlying muscle layer, so that the 'skinning' of a seal results in the removal of the hypodermis, dermis and epidermis. The thickness of the blubber depends on the age and size of the seal. An adult male Southern Elephant Seal may have blubber up to about 100 mm thick. When these seals were used commercially, about 400 litres (90 gallons) of oil could be extracted from the blubber of one seal.

The hairs grow in groups, each group consisting of a larger flattened guard hair lying anterior to a number of finer wavy underfur hairs. All the hairs grow from separate follicles, but those of each group emerge to the surface through one pilary canal whose walls grip the hairs and prevent the entry of water. The number of underfur hairs per unit varies. It is low in phocids and sea lions (ca 1 to 5), but higher in fur seals (17+), giving rise to a soft fur of commercial value.

Moult is annual in adult seals, but this is a relatively slow affair so that each seal is adequately covered at all times. The curious moult of the Southern Elephant Seal has been studied (Ling & Thomas 1967). The hair and the outermost layer of the skin fuse, so that when the hair is shed the stratum corneum is shed as well. Patches of moulted skin, about 20 cm², with the hairs attached can be found around a moulting animal. This type of moult may be present in some other seals as well, but is noticeable particularly in elephant seals as they relieve the irritation by lying in muddy wallows with their peeling skin hanging in strips.

Skeletal System

The skull and skeleton of seals is of the basic mammalian plan, with modifications. The skull, while varying from genus to genus, is characterised by a large rounded cranium, abruptly delimited from an elongated interorbital region, a short snout and large orbits. Phocid skulls have an inflated tympanic

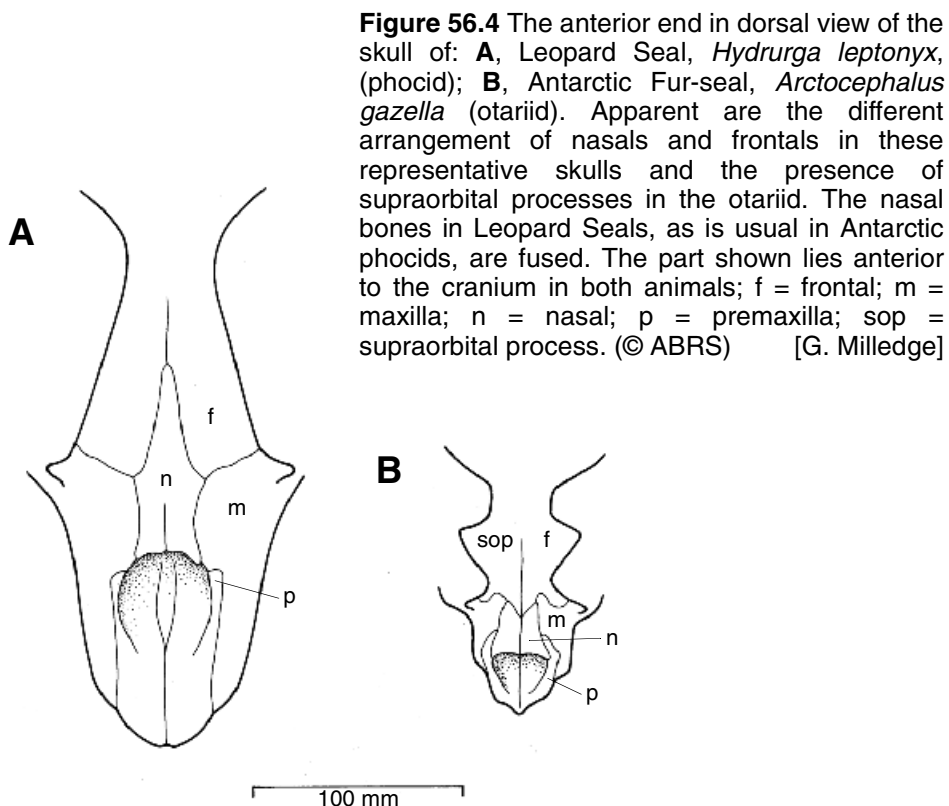
bullae, but no alisphenoid canal or supraorbital processes and the nasal bones extend posteriorly between the frontal bones. Otariid skulls have a smaller, less inflated bulla, an alisphenoid canal, supraorbital processes and the frontal bones project anteriorly between the nasal bones. (Fig. 56.4) More detailed characters may be found in King (1983b).

Pinnipeds never have more than three upper and two lower incisors in each side and some have fewer. There are no carnassial teeth in living forms and, as a reflection of their diet, the cheek teeth are nearly homodont. Four premolars and one or two molars are present, but their similarity in shape makes it easier to refer to them as postcanines (PC) or cheek teeth.

The dental formula of otariids is $I \ 3/2$, $C \ 1/1$, $PC \ 5 \text{ or } 6/5$, the number of cheek teeth varying according to the seal involved. The first two upper incisors have a deep transverse groove, the third incisor is larger and caniniform. The canines are well developed and the cheek teeth are relatively simple, slightly flattened, cone-like structures, sometimes with small cusps.

All phocids have $C \ 1/1$, $PC \ 5/5$ but the incisors may be $3/2$ (most Phocinae), $2/2$ (most Monachinae) or $2/1$ (*Cystophora* and *Mirounga* – though this does not imply a relationship). There is no transverse groove in the incisors. The shape of the cheek teeth shows more variability than in the Otariidae, ranging from the relatively simple teeth of *Mirounga* and *Leptonychotes*, for example, to the decorative and functional cusping of *Hydrurga* and *Lobodon* (Fig. 56.5).

The vertebral column reflects the different modes of swimming. Otariids use the front end of the body and there are strong processes on cervical and thoracic vertebrae. Phocids use the hind end and the lumbar vertebrae have strong transverse processes. The tail in both groups is short. There is no clavicle in pinnipeds. The otariid scapula is divided into three areas by a spine and a bony ridge, a structural arrangement which provides greater attachment for swimming muscles. The phocid scapula has a more centrally placed spine which is much reduced in the Southern phocids. The humerus, radius and ulna are short and stout. There is no fused pubic symphysis and the post-acetabular part of the



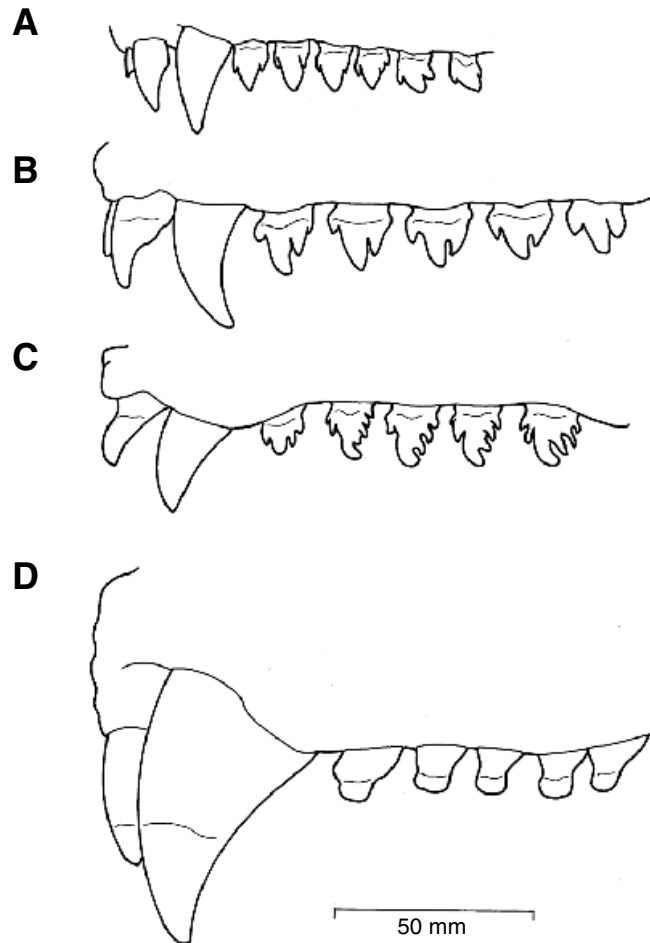


Figure 56.5 Lateral view of the teeth in the left side of the upper jaw. **A**, Australian Fur-seal, *Arctocephalus gazella* (otariid); **B**, Leopard Seal, *Hydrurga leptonyx* (phocid); **C**, Crab-eater Seal, *Lobodon carcinophaga* (phocid); **D**, Southern Elephant Seal, *Mirounga leonina* (phocid). (After original drawing by J.E. King; (© ABRS) [G. Milledge])

pelvis is elongated. The femur is short and flattened. The tibia and fibula are long and fused at their proximal ends. More details may be found in King (1983b).

Locomotion

Phocids and otariids use different methods of locomotion. In water, phocids flex the hind end of the body when swimming. Alternate strokes of the hind flippers are assisted by lateral swinging of the hind end of the body and there is, thus, great development of the spinal musculature. The foreflippers are held close to the body, but are used when changing direction. Otariids use their large foreflippers as oars and 'fly' through the water. The hind flippers are not used in swimming. In water, phocids and otariids may reach speeds of about 19 km / hour and 28 km / hour respectively.

On land, phocid progression appears clumsy, but nevertheless they can move well over rocky or icy ground. The hind flippers are held up off the ground and the animal takes its weight alternately on the sternum and on the pelvic area, achieving a humping or hitching method of movement. The foreflippers may sometimes be used to give balance or a certain amount of traction. Crab-eater

Seals (*Lobodon carcinophagus*) may reach speeds of about 25 km / hour on ice while using a sinuous movement of its body assisted by the foreflippers making pushing strokes against the ice.

Otariids are more agile on land. The weight of the body is supported by the foreflippers which extend laterally with a right angle bend at the carpal region and by the hind flippers which bend forwards at the ankle. The foreflippers are moved forwards alternately. The whole of the manus is placed on the ground. The hind flippers also are moved alternately, the pes is raised with only the heel on the ground. The heavy head and neck region are swung over the weight-bearing foreflipper so that the other one may be raised. At higher speeds, both foreflippers are moved together, resulting in a gallop.

Feeding and Digestive System

The digestive system of seals is uncomplicated and of the normal mammalian pattern. The stomach is of simple shape, the caecum is barely 30 mm in length and frequently almost indiscernible. There is no internal fat; it is restricted to the blubber. The small intestine, however, is remarkable for its great length. That of herbivorous mammals may be up to 28 times the length of the body, but the small intestine of carnivores is only about five or six times the body length. In seals, there is enormous variation, even within the same species. Two Southern Elephant Seals, both with a nose to tail length of 4.8 m, had a small intestine length of 122 m (25 times body length) and 201 m (42 times body length) (Laws 1953). Small intestine lengths of 34 m (adult female Hooker's Sea-lion – *Phocarctus hookeri*), 32 m (adult male Californian Sea-lion – *Zalophus californianus*), 42 m (adult male Walrus) and 29 m (adult female Crab-eater Seal) are among those that have been recorded (in King 1983b). Amongst the adult seal intestines that have been measured, that of the Ross Seal, *Ommatophoca rossi* is among the shortest (11.2 m, female adult, 4.9 times body length). The metabolic rate of seals is high and their rate of digestion is fast, but it is interesting that the seals with the longest and the shortest intestines (Southern Elephant Seals and Ross Seals feed predominantly on squid. The passage of food through the gut, as shown by a dye-marked meal, has been shown to be 5 hours or less, a considerably shorter time than in most other animals (Helm 1984). Apparently, the length of the intestine has little bearing on the rate of food passage and the speed of transit observed in seals is attributed to the high metabolic rate and the high water content of the food.

The most usual food of seals is fish and many sorts of local fish are eaten by most seals. Inevitably, this causes competition with fishermen. Some damage to nets and gear does occur, but often a higher proportion of non-commercial fishes is eaten. Lampreys are eaten, often in large quantities and in areas where lampreys are parasitic on salmon the seals do the fishermen a service (Jameson & Kenyon 1977; Street 1964). Cephalopods, such as squid and octopus, are a common source of food. Crustaceans, including crabs, crayfish, amphipods, prawns and krill also are taken.

Quantities of stones are found very frequently in seal stomachs. Up to 11 kg have been found in a single stomach. Pups pick up anything while they are exploring their environment and it is probable that stones are acquired this way. A good explanation for the stones in adult stomachs has yet to come forward, but theories from the grinding up of parasites to ballasting and the allaying of hunger pangs have been propounded.

Many seals, and other animals such as polar bears and husky dogs, store such large amounts of vitamin A in their livers that even reasonable amounts of such livers, if eaten by travellers, cause headache, vomiting and other symptoms of hypervitaminosis (Fay 1960; Rodahl 1949). Livers of Australian Sea-lions (*Neophoca cinerea*) have caused sickness to fishermen and wrecked sailors on

Kangaroo Island and are reported to have even caused death to Aborigines in the mid-19th Century (Cleland & Southcott 1969). The liver of the Australian Fur-seal also has a high level of vitamin A, particularly that of the bigger individuals (Southcott, Chesterfield & Warneke 1974). Some of the Antarctic phocids, such as Weddell Seals (*Leptonychotes weddelli*), seem to have less vitamin A in their livers. About 2250 g would have to be eaten at a sitting to achieve toxicity (Southcott, Chesterfield & Lugg 1971), whereas 500 g of Australian Sea-lion liver would cause ill effects.

Humans, in the early days, hunted many seals almost to extinction and even now cause considerable disturbance to the seals' environment. This may take the form of tourist pressure or the sheer bulk of marine traffic and the subsequent pollution. Organochlorine pesticides, polychlorinated biphenyls and mercury are found in tissues of seals the world over. Some of these products may be involved in high abortion rates of seals, but not enough is known about this yet (Holden 1978). In this respect humans are a predator of seals. The other main predators of seals are sharks, Killer Whales (*Orcinus orca*) and, in the Arctic, the Polar Bear (*Ursus maritimus*). Depending on the seal, local animals may also be predators. In South Africa, for example, Black-backed Jackals (*Canis mesomelas*) and Brown Hyenas (*Hyaena brunnea*) may take pups and carcasses. Vampire Bats (*Desmodus*) have been seen taking blood from the hind flippers of the Southern Sea-lion (*Otaria byronia*), on the Peruvian coast (Andrew 1985).

Circulatory System

The pinniped heart is of normal mammalian construction, though it tends to be broader and flatter than hearts of terrestrial mammals. Both ventricles contribute to the apex of the heart and they frequently are separated by a groove so that the apex appears to be bifurcated. The ascending aorta increases rapidly in width by about 40% to form an aortic bulb which, after all the great vessels have left, continues posteriorly as a relatively slender aorta (Drabek 1975; 1977; King 1977). The significance of this bulb is virtually unknown, but may be correlated with diving, as the deepest diving seal (the Weddell Seal) has the greatest bulb.

The arterial system of pinnipeds is very much as in the dog. Most of the modifications are to be found in the venous system and most of these have some correlation with diving. The following are the main venous modifications of phocids and the interested reader should consult King (1977; 1983b) where details and references will be found.

1. Venous system complex, thin walled, almost no valves, connects via anastomosing networks with all other parts of the system.
2. Large extradural vein lying dorsal to spinal cord receives blood from brain.
3. Stellate plexus of veins on surface of kidney draining into posterior vena cava, but also connected with extradural vein.
4. Large, usually duplicated posterior vena cava.
5. Hepatic veins enlarge to form capacious hepatic sinus just posterior to diaphragm. Present at birth.
6. Immediately anterior to diaphragm, vena cava has a surrounding muscular caval sphincter.
7. Pericardial plexus of anastomosing veins and brown fat forms ring round base of pericardium and sends branches into pleural cavities.

The otariid venous system is less specialised and has fewer modifications, but some differences from phocids are noted.

1. Cranial drainage normal mammalian pattern most blood returned by external jugular.
2. Extradural veins paired and ventral to spinal cord, normal mammalian arrangement.
3. No obvious stellate plexus on kidney.
4. Hepatic sinus present in adults, but not in pups.
5. Caval sphincter present, but muscular arrangement different from phocids.
6. No pericardial plexus.

The normal heart rate of seals varies considerably. Rates of between 60 and 120 beats per minute have been recorded in different animals. The rate in pups is slightly faster and the reduction in rate while diving will be mentioned later. The blood volume of seals is very high, about 12% of body weight (compare with 7% in humans). This means that Weddell Seals—which have a particularly high volume—have about 55 litres (12 gallons) of blood, while Southern Elephant Seals have 59 litres (humans 4.5–6 litres). The diameter of the red cells is large. They have a high haemoglobin concentration which gives great oxygen storage capacity.

Respiration

The nostrils are closed when relaxed. The trachea divides into bronchi immediately outside the lung in phocids, but much higher, at the level of the first rib in otariids. Support for the trachea is in the form of cartilaginous rings that may be complete, overlap dorsally or, as in some Southern phocids, be present as ventral bars only. The lungs are slightly larger, but, with a few exceptions, are lobulated approximately as in terrestrial mammals.

Within the lung of phocids, the muscle layer of the small airways runs right up to the alveolated endings which occur in groups of about 10, surrounded by a thin tissue layer. In otariids, the cartilaginous rings extend right up to the alveoli, but there is less muscle (Denison & Kooyman 1973). The alveolated sacs occur in pairs. It may be that the strengthening of the terminal airways in otariids assists the animal in taking in a lot of air in a short time. When swimming, they tend to surface briefly and frequently. Phocids stay under longer, but also remain on land longer between dives.

The subject of respiration leads naturally to diving, a complicated subject that can only be dealt with very briefly here.

Modern techniques allow free swimming seals to be monitored with depth recorders. Phocids seem to be good divers (Table 56.2); Harp Seals (*Phoca groenlandica*), dived to 300 m under experimental conditions. The depth record is held by the Weddell Seal which can go down to 600 metres. Most of its dives, however, are between 200 and 400 metres. Although this species is capable of staying under water and thus not breathing for 70 minutes, it rarely dives for longer than about 30 minutes at a time (Kooyman 1981a; Kooyman *et al.* 1980; 1981). In fact, over 95% of its dives are shorter than 26 minutes, probably the limit for many phocids. The diving capabilities of otariids are less known than those of phocids, but are less extensive (Table 56.2). Northern Fur-seal (*Callorhinus ursinus*) has dived to 190 m for 5.4 minutes although most dives last for less than 5 minutes.

Table 56.2 Distinguishing characters of pinniped superfamilies and families.

Phocoidea	Otarioidea
Hind flippers cannot be turned forwards see Fig. 56.1	Hind flippers can be brought forwards Animal can raise body off ground on fore- and hind flippers. see Fig. 56.1
Nails on hind flippers same size on all five digits	Nails on hind flippers larger on middle three digits, rudimentary on outer digits
	Otarioidea
	Odobenidae
Walruses - not in Australia	Sea lions and fur seals
No external ear pinna	Small external ear pinna
Internal testes	Scrotal testes
Enlarged upper canines	Normal upper canines
	Otariidae
	Sea lions
Blunter nose	Pointed nose
Sparse underfur	Thick underfur
Larger body size (usually)	Smaller body size (usually)
3rd upper incisor larger, with circular cross section	3rd upper incisor smaller, with oval cross section
Usually five upper cheek teeth on each side	Usually six upper cheek teeth on each side
	Fur seals

Seals do not suffer from caisson sickness, or the ‘bends’ as human divers may. While diving, gaseous nitrogen under pressure goes into solution in the blood. If the pressure is released too suddenly, as happens if the diver ascends too rapidly, the nitrogen comes out of solution as bubbles in the blood. This can be very painful and even fatal. Seals, however, exhale before diving, and thus take down very little nitrogen, and obviously are not supplied with any extra air while below. The smaller airways of the lungs are reinforced with cartilage, so nitrogen from the small remaining amount of air in the lungs is not absorbed into the blood system.

To stay under water for so long, a seal must conserve the oxygen taken down in its blood. Seals have a high blood volume. The large red corpuscles have haemoglobin concentration and oxygen capacity amongst the highest in mammals. The oxygen stored in a given amount of blood in Weddell Seals is nearly twice that in Harbour Seals (*Phoca vitulina*) and five times as much as in a man (Lenfant, Johanson & Torrance 1970). The very high concentration of myoglobin gives a very dark red colour to the muscles.

Most important in conserving O_2 is the constriction of the arteries to the peripheral parts of the body. Blood continues to flow to the brain and there is some evidence that the seal brain tolerates a certain oxygen lack, but the flow to viscera, skeletal muscle, skin and flippers is reduced by about 90%.

There is enough O_2 stored in a resting animal for short dives of about 15 minutes. For another 10 minutes the O_2 comes from the reduction of the blood flow to non-essential areas. After this, for really long dives, the ‘non-essential’ areas start functioning anaerobically. A series of short dives means that the animal can replenish its O_2 supply quickly and be ready to dive again.

When diving, the heart rate decreases quite dramatically. From about 120 beats a minute, the rate slows to five or six beats (bradycardia). This low level continues until the seal surfaces, when it beats more quickly for a while before returning to normal. The function of bradycardia is probably to reduce the amount of blood that flows, still at normal pressure, through the restricted parts of the body.

The parts of the circulatory system that are modified particularly for diving are the extradural veins, caval sphincter, the hepatic sinus and large size of all abdominal veins. On diving, the plexuses in the neck become occluded, so blood from the brain travels through the rest of the body and is stored in the capacious hepatic sinus and abdominal veins. The caval sphincter controls the flow of blood back into the heart.

Pregnancy does not appear to affect diving. The blood of the seal foetus has, as in other mammals, a higher affinity for O_2 than that of its mother, but is different from other mammals in that the foetal blood has a lower haemoglobin concentration and thus a lower O_2 capacity, which reduces the necessity for blood to go to the uterus during diving.

Excretion

Kidneys are present and are reniculate. Such kidneys are found only in cetaceans and pinnipeds. Each kidney is made up of small units, the reniculi. Each reniculus is like a simple kidney in miniature, with cortex, medulla and calyx, with its duct joining the others, eventually to form the ureter. A single kidney of a Southern Elephant Seal may have 300 reniculi, although they are not all visible on the surface. The reniculate kidney is thought to be correlated with the large size of the animals and the ability to concentrate urine.

Table 56.3 Comparative physiological adaptations for diving in the two families of seals

Phocid	Otariid
Deep divers	Shallow divers
High Hb concentration in blood	Lower Hb concentration in blood
Large O_2 capacity	Lower O_2 capacity
Little O_2 in lungs when diving	More O_2 in lungs when diving
More time spent breathing between dives	Surface frequently for quick breath
Cartilaginous support of airways not up to alveoli	Cartilaginous support right up to alveoli keeps airway open for quick breath
Pericardial plexus	No pericardial plexus
Large extradural vein	'Normal' extradural vein

Normally, seals get all the water they need from their food and do not drink. Breakdown of blubber may also provide water when necessary. Experimentally administered sea water caused stomach upsets, but some seals (otariids, and all in warmer climates) have been seen drinking sea water. These have all been adult males, fasting during the breeding season. In hot weather they may not have produced enough water for body needs. Presumably, they do not drink enough sea water to cause upset.

Sense Organs and Nervous System

Touch. Some seals are strongly thigmotactic and crowd together with bodies touching, even when there is plenty of space. Elephant seals and sea lions are thigmotactic, but many phocids are not. Mystacial whiskers are tactile organs and the presence of erectile tissue round the base of the follicles could increase the sensitivity of the whiskers to water vibrations (Stephens, Beebe & Poulter 1973).

Smell. The olfactory lobes of the brain are small, but smell plays an important part in the life of seals. It is the final important link in the recognition by its mother of the correct pup from among others on a crowded beach. The odour of a female is also very important to the male in the breeding season.

Sight. Seals have large eyes, even the smallest of them (Baikal Seal – *Phoca sibirica*, 1.3 m long) has eyes about the size of those of a domestic ox. Southern Elephant and Ross Seals seem, according to the few measurements available, to have the largest eyes with a diameter of 60 mm. The cornea is strongly keratinised and slightly flattened in the vertical plane. The tapetum is more developed in seals than in any other animal, indicating a very light-sensitive eye. Rods dominate the retina, giving increased sensitivity in dim light, while the cones function best in bright light to give the seal effective daytime vision. There is no good evidence of colour vision in seals.

The two curvatures of the cornea give the seal astigmatism, so on land the seal will see most clearly in bright light when the pupil is contracted. In water, the astigmatic effect of the cornea is lost as water has the same refractive index. In dim light under water the pupil opens wide and the tapetum and photo-receptors in the retina give the seal the benefit of all the available light. There also is increased sensitivity to green wavelengths (Lavigne & Ronald 1972). The visual acuity of a seal in water is good and is at least as good as that of a cat on land. There is no lacrimal duct, so tears run down the face.

Hearing. To appreciate fully the complications of the seal ear and hearing, the reader should consult Repenning (1972). In air, seals can hear well, as well as man, but not as well as many fissipeds. In water, however, seals hear better than fissipeds and have good directional hearing.

Voice. Some seals, for example, Californian Sea-lions are very noisy, but others, for example, Harbour Seals, hardly vocalise. Reasonably enough, polygynous species tend to make the most noise, as communication within the rookery is necessary. A bleating sound is produced by most pups.

Adults make various barking, coughing and roaring sounds. Underwater, clicks, whistles, warbles and trains of pulses are produced by various seals.

Echolocation. Blind seals remain well fed in the wild. Although experiments in captivity have shown that seals discriminate in the dark between objects of the same size and that a blind seal can follow the contours of an irregular wall by barking, there is yet no totally convincing evidence that seals use echolocation (Schusterman 1981).

Nervous System. The pinniped brain has not been the subject of much research. The brain is more spherical than in a terrestrial carnivore and highly convoluted. In general form, the otariid brain has resemblances to that of bears, while the phocid brain is dog-like. The olfactory area is reduced, the auditory area is large and the trigeminal sensory area is well developed.

The spinal cord is short and reaches only to points between the eighth and 12th thoracic vertebrae with the cauda equina continuing past this. In humans, the spinal cord reaches the first lumbar vertebra and in dogs it reaches the last (seventh) lumbar vertebra.

References for further study of the nervous system may be found in King (1983b).

Endocrine and Exocrine Systems

Endocrine Glands. As far as is known, seals possess the normal complement of carnivore endocrine glands performing similar functions. The pineal body is probably the largest among mammals and is particularly large in seals of polar regions. The pineal body of the Weddell Seal is 25 x 10 mm and weighs about 1 g

(Cuello & Tramezzani 1969) (the human pineal is about 8 mm long). It is a very active organ with, probably, a rhythmic activity correlated with light and the reproductive cycle (Griffiths & Bryden 1981).

The pituitary gland is secreting actively at birth. The secretion contains a large amount of cystine which may be correlated with the production of antidiuretic hormone and the need for water conservation by a pup feeding on very rich milk with a high fat content. Other hormones in the foetal pituitary may cause the increase in size of the gonads of newborn phocids (Amoroso *et al.* 1965; Cannata & Tramezzani 1971; Leatherland & Ronald 1976).

In Harbour Seals at least, the thyroid gland increases in weight very rapidly and starts to function about 3 months before birth. There is also a second period of intense activity in the lactating female. Little detail is known about the functioning of the gland, but there is an association between the thyroid gland and the fat content of milk. The active adult thyroid may be correlated with the high fat content of seal milk (Harrison *et al.* 1962; Leatherland & Ronald 1979).

The adrenal gland reaches its greatest weight in young pups, reflecting its importance in the rapidly growing animal (Amoroso *et al.* 1965; Bourne 1949).

Exocrine Glands. Sebaceous glands open into the pilary canals and the secretions probably serve to keep the epidermis pliable. Only apocrine sweat glands are found in seals, one to each guard hair follicle. Their viscid secretion is not thought to have any role in thermoregulation. There is increase in the activity of the sweat glands during moulting and in the breeding season. They may provide sexual scent signals. The glands are small in phocids, but larger in otariids and Walrus. The largest ones are between the mystacial vibrissae of Walrus where the secretion may aid in recognition between mother and calf (Ling 1974).

Reproduction

Chromosomes. Otariids have 36 chromosomes, Walrus have 32. The monachine phocids have 34 and most phocines have 32 derived from the 34 type by fusion of two chromosome pairs. Two phocines (Bearded (*Erignathus barbatus*) and Hooded (*Cystophora cristata*) Seals) have 34, but the relationships of both these animals are not certain at the moment (Arnason 1974).

Male Reproductive System. The penis is retractable, within a cutaneous pouch, and is supported by a baculum. The testes are inguinal in Phocidae and Walrus, lying outside the abdominal muscles and covered by skin and blubber. In spite of being under the blubber, the testes may be up to 7°C cooler than the body temperature. The venous plexuses outside the testes have extensive connections with the veins of the hind flippers and so could be cooled by the passage of cool blood from the flippers (Blix, Fay & Ronald 1983; Bryden 1967). The testes of otariids are scrotal.

Female Reproductive System. The ovary is surrounded by a fold of peritoneum to form a bursa into which the fallopian tube opens. The ovaries usually function alternately. Within the body of the uterus, the two cornua are separated by a thick medial partition and the common area which traverses the cervix is small. Sometimes the two cornua remain separate and each opens separately into the vagina (Harrison *et al.* 1952). The vagina is long and is separated from the vestibule into which the urethra opens by a fleshy hymeneal fold. The vestibule opens to the exterior just ventral to the anus, but both open into a common furrow surrounded by muscle fibres which act as a sphincter. An os clitoridis occurs irregularly in all seals.

There are four mammary teats in Otariidae, Walrus and the phocids Bearded and Monk (*Monachus* species) Seals. All other phocids have two teats. When not in use the teats lie retracted beneath the body surface. The mammary glands in

phocids are distinct, each enclosed in a connective tissue sheath and communicating with the appropriate teat. In otariids, the glands coalesce to form a sheet over the ventral surface of the body.

Seal milk is very rich in fat and protein and low in water. Lactose is virtually absent. For this reason the seal gut is not very tolerant of the lactose found in cow's milk, and some of the problems of rearing orphan pups may be attributed to this. Special feeding formulae have been evolved by Keyes (1968) and Geraci (1975). The fat and protein levels may be correlated with the fast rate of growth of the pup and the need to lay down a layer of insulating blubber as soon as possible. Concentrated milk would also facilitate its storage by lactating females while feeding at sea. The proportions of the milk constituents change during lactation, the fat content rising and the water content falling, but this has been investigated in very few animals (Bryden 1968; Kooyman & Drabek 1968; Riedman & Ortiz 1979).

On this concentrated diet, weight increases of phocid pups have been recorded as 2.5 kg daily in Harp Seals (Stewart & Lavigne 1980) and 5–6 kg daily in Southern Elephant Seals (Laws 1953). There is some correlation between a short lactation period, the mother remaining with her pup throughout this period, and the fast growth rate. Otariids have a slightly lower level of fat in the milk, a longer lactation period and a smaller daily weight gain; New Zealand Fur-seals (*Arctocephalus forsteri*) pups gain about 40–60 g per day. The two otariids with the shortest lactation periods—Northern Fur-seal and Antarctic Fur-seal (*Arctocephalus gazella*)—however, have faster growth rates, the male pups increasing by 93 g and 98 g a day, respectively (Payne 1979).

The length of the lactation period varies enormously in pinnipeds from the 2 years of Walruses to the eight to 12 days of Harp Seals. In all sea lions and in all fur seals of the genus *Arctocephalus* (where known and with one exception), there is a 12 month lactation period. Antarctic Fur-seals lactate for only four months and Northern Fur-seals for three months. The time varies in the northern phocids from 8–12 days in Harp Seals and 21 days in Grey Seals, to 6–7 weeks in Bearded Seals and 2.5 months in Baikal Seals. Few definite details are known for the Southern phocids, but the lactation period varies from 12–18 days in Weddell Seals, 23 days in Southern Elephant Seals and about 4 weeks in Crab-eater, Leopard and Ross Seals.

The placenta is of the zonary endothelio-chorial type. The maternal blood vessels dilate to form sinusoids and the barrier between maternal and foetal circulation may be as little as 1 μ (Harrison & Kooyman 1968; Harrison & Young 1966).

The total gestation period varies from about nine months in Harbour Seals, 11.5 months in Grey Seals, nearly 12 months in otariids and 15 months in the Walrus. This difference depends on the time lapse between pupping and mating. The actual time during which the embryo is growing (the active gestation period) depends on the delay between fertilisation and the attachment of the blastocyst. This delay varies according to the species of seal and may be between 6 weeks and 5 months, but the average is about 3.5 months.

Detailed work on the British Grey Seal has shown that 8–10 days after fertilisation the blastocyst has developed. For the next 100 days (approximately 3 months), it remains lying dormant in the uterine horn. After this, it recommences development, becomes attached via the placenta to the uterine wall and normal growth continues for 240 days. Including the 10 days immediately after fertilisation, this gives 250 days (about 8 months) of active gestation and a total gestation of around 350 days (11.5 months) (Hewer & Backhouse 1968).

A single young usually is produced at birth, though twins are known for almost every species of seal. These have been recorded from twin blastocysts or foetuses, as well as twin births, but are not the normal situation. Hybrids have occurred, mainly in captivity, between various genera of seals, but they have not lived beyond about 6 months. Hybrids occurring in the wild are less easy to determine though attempted copulations between animals of different genera have been seen. Probable hybridisation occurs between Subantarctic Fur-seals (*Arctocephalus tropicalis*) and Antarctic Fur-seals—see Section on Macquarie Island—but more confirmatory observations are needed.

For the behaviour of seals during the breeding season, accounts of individual seals should be seen (both here and in King 1983b).

Table 56.4 Composition of the milk of various seal species and other mammals.

	% Fat	% Protein	% Water	% Lactose
Phocidae				
Harp Seal	53.2	6.0	40.2	0.32
Harbour Seal	45.0	9.0	45.8	0.20
Southern Elephant Seal	49.0	8.5	-	-
Northern Elephant Seal (<i>Mirounga angustirostris</i>)	54.4	9.0	32.8	-
Otariidae				
Australian Fur-seal	49.0	12.0	-	-
Antarctic Fur-seal	26.4	22.4	51.1	-
Bovine	3.4	3.3	88.0	4.40
Human	3.5	1.0	88.8	6.50

NATURAL HISTORY

Phocidae

The only breeding colonies of phocids in Australian waters (excluding the Antarctic Territory) are those of Southern Elephant Seals on the islands of Macquarie, Heard and McDonald. There are historical records of Southern Elephant Seal breeding colonies in Australia and stragglers sometimes reach our shores. Occasional phocid visitors from the Antarctic to the above islands and also to Tasmania and the Australian mainland include Leopard, Crab-eater, Weddell and Ross Seals.

Scientific and meteorological stations are maintained by ANARE (Australian National Antarctic Research Expedition) at Casey (66°17'S, 110°32'E) opened in 1969, Davis (68°35'S, 77°58'E) opened in 1956-57 in the Vestfold Hills area and Mawson (67°36'S, 62°53'E), the first ANARE station on the Antarctic Continent, opened in 1952 in MacRobertson Land. Other ANARE stations are on Macquarie and Heard Islands (Ingham 1960; Johnstone 1972). The phocids occurring in the vicinity of these stations are detailed.

Southern Elephant Seals (*Mirounga leonina*) are, because of their size and shape, one of the better known seals of the world. Breeding colonies are found on most of the subantarctic islands such as the South Shetlands, South Georgia, Gough Island, Marion Island and Kerguelen. The only Australian breeding colonies are on Macquarie, Heard and McDonald Islands. Of the total world population of approximately 6–700 000 animals, the largest colonies are on South Georgia (310 000) and Kerguelen (100 000), but Macquarie ranks third

with about 95 000 and there are about 85 000 animals on Heard Island. South of the regular breeding grounds stragglers are found frequently in the pack ice and round the Antarctic Continent. There is a regular summer hauling out ground in the Vestfold Hills, near Davis, where several hundred seals come to rest and moult. Although Southern Elephant Seals may be seen there at all times of the year, the majority are absent between August-October, presumably returning to the nearest breeding ground at Heard Island (Ingham 1957; Johnstone, Lugg & Brown 1973).

Some 8000 years ago Tasmanian Aborigines on the north-western coast made great use of Southern Elephant Seal pups in their diet, as the contents of their middens show (Jones 1967). There is, however, no evidence that the seals bred on Tasmanian shores and the Aborigines probably scavenged dead or stranded seals from the nearby breeding colonies on King Island and Hunter Island (Stockton 1982). These colonies suffered early in the sealing fever of Bass Strait and may have been wiped out, probably before about 1805 (Abbott & Nairn 1969; Warneke 1966). Elephant seal oil was in demand in the 19th Century as it burned clear, without smell or smoke. It has no rancid taste and could be used in food and to soften cloth fibres. Four hundred tons of this oil, taken from Macquarie Island to London, earned John Raine a large silver medal in 1823 (Abbott & Nairn 1969). After the discovery of Macquarie Island in 1810 and the immediate exploitation of the fur seals which lasted only 10 years, the sealers then turned their attention to the elephant seals. In another 10 years even this resource was uneconomic. Sealing continued intermittently, the oil being supplemented with that from King and Royal Penguins, until licenses were stopped in 1919 (Carrick 1957; Carrick & Ingham 1962; Cumpston 1969).

At the present time, occasional Southern Elephant Seals reach our shores. There are records of less than a dozen reaching Tasmania, but two of these gave birth to pups at about the same time as the animals on the regular breeding colonies (Guiler 1978; Tyson 1977). Over about the last 15 years there have been less than 10 recorded strandings on the Australian mainland coast, all between Coffs Harbour, New South Wales, and Encounter Bay, South Australia.

An adult male Southern Elephant Seal is, at 4–5 m nose to tail length and 3–6 tonnes, the largest of living pinnipeds. The proboscis, an enlargement of the nasal area, starts developing when the male is about 2 years old and reaches its full size at about 8 years. In the breeding season it can be erected by a combination of muscular action, blood pressure and inflation to form a high cushion on top of the snout with the nostrils at the tip hanging down in front of the open mouth. A harsh, rattling roar is produced and the proboscis acts as a resonator. The roar of a big bull may carry for several kilometres (Laws 1956). Females are smaller at 2–3 m length and 900 kg weight and do not develop the proboscis.

On Macquarie Island the females mate for the first time at 3–6 years old. While bulls may be sexually mature at 5 years, they are not sufficiently powerful to hold a harem until they are at least 12 years old. On South Georgia, where controlled commercial sealing stopped only in 1964, the removal of many bulls appeared to result in a diminution of the disturbance to the rookeries caused by very large numbers of adult males, with subsequent earlier maturation of the pups. On Macquarie Island, there has been no recent commercial sealing and the large numbers of bulls disturb the harems, causing discomfort and injury to the pups. This disturbance decreases the amount of milk taken by the pups and stunts their growth (Bryden 1968).

Bulls start coming ashore in September, followed by the pregnant females which gather in groups or harems. The harem bull defends the territory on which his harem lies, but has less success in preventing the females from moving about. The pups are born about a week after the cows haul out. They are 1.2 m long,

weigh about 35 kg and are covered in black woolly hair. Their mothers feed them for 3 weeks, but then must fend for themselves going to sea when 10 weeks old, but in the interim they must learn to swim in small coastal pools (Bryden 1983). The females mate again about 18 days after the birth of the pup, but there is a delay of 4 months from about the beginning of March before the blastocyst becomes implanted. As soon as the pups are weaned the cows return to sea to feed and, as the cows disperse, the bulls become less aggressive, and soon they, too, end their fast and return to sea. Between December and February the adults return to land again to moult (Laws 1953; 1956).

Fish and cephalopods form the main food of Southern Elephant Seals. Killer Whales and Leopard Seals are probably their only enemies, but neither is believed to cause much damage.

Leopard Seals (*Hydrurga leptonyx*) are solitary animals and, although frequently seen, relatively little is known of their life history. They live in the outer fringes of the circumpolar pack ice and immature animals disperse widely, reaching south to the coast of the Antarctic Continent in summer and north to many of the subantarctic islands in winter. The most northerly, exceptional record is two animals from Rarotonga in the Cook Islands (Berry 1961), but they have also turned up in South America and South Africa.

In Australian waters, the Leopard Seal is seen occasionally at the ANARE Antarctic stations and is a regular winter and spring visitor to Macquarie and Heard Islands (Ingham 1960). At Macquarie Island its abundance seems to go in cycles with a major peak of over 200 animals followed after 4 years by a minor peak of around 100 animals, then after an interval of 5 years, another major peak (Rounsevell & Eberhard 1980). Most of these animals are immatures up to about 3 years old. Tasmania has an occasional stranding, but the southern coasts of continental Australia receive them almost regularly. The south-eastern corner of Australia, south of 30°S, between Coffs Harbour, New South Wales and Port Lincoln, South Australia has most such visitors. They are known also from Heron Island and Lord Howe Island. They are almost annual visitors to the Sydney region and some have lived for several years in Taronga Zoo. In 1977, one of the peak years at Macquarie, 227 were seen. This was reflected in the greater numbers seen in Australia that year. Of 18 strandings recorded that year in Australia, seven were in Sydney. Most Australian strandings are between August and October, with animals of most sizes and ages represented (King 1983b).

Breeding normally does not occur outside the pack ice and there is little information. There is the possibility of extended pupping so that pups are born between September and January.

Adult male Leopard Seals are about 3 m in nose to tail length and weigh about 270 kg. Adult females are larger and may reach 3.6 m in length. The coat is dark grey dorsally, light grey ventrally, with lighter and darker spots. The long slim body, disproportionately large head with its curiously reptilian appearance, the very wide gape and the distinctive three-cusped teeth make this seal easy to recognise.

The Leopard Seal eats fish and cephalopods and sieves large quantities of krill through its teeth. It is adept at catching many species of penguins. They cruise along the coast near a penguin rookery and catch the birds as they enter the water. Leopard Seals will also take other birds such as giant petrels, attack and feed on young Southern Elephant, Crab-eater and Weddell Seals, and feed on any carrion available.

Weddell Seals (*Leptonychotes weddelli*) are the most southerly of the Antarctic seals, and are normally found on circumpolar fast ice within sight of land. This species breeds at colonies on the Antarctic mainland and at all three ANARE stations (Johnstone 1972; Johnstone *et al.* 1973). South Georgia forms the

northern breeding limit. Young animals wander and occasionally are seen at Macquarie and Heard Islands. Only a single animal is so far known from close to the Australian mainland. It was caught in a fisherman's net in Encounter Bay, South Australia before 1925 (Jones 1925).

Adult male Weddell Seals have a nose to tail length of about 2.5 m. Females are slightly longer. They are greyish-black dorsally with lighter coloured splashes and streaks which increase in number laterally till they meet the predominantly light ventral surface. Most pups are born in the last half of October. This species is renowned for being the deepest pinniped diver and much work has taken place on its physiology (see Section on respiration and diving).

Crab-eater Seals (*Lobodon carcinophagus*) are probably the most abundant seal in the world, but the numbers of Antarctic animals are notoriously difficult to estimate. An appraisal of the different estimates, which vary from 2–15 or 30 million animals, is given by Kooyman (1981b).

Crab-eater Seals are found on the drifting pack ice, moving north with the pack ice in winter and further south in summer as the ice breaks up. The pups are born in spring (October), but remarkably little is known of the details of this seal's life history.

The Crab-eater Seal is not common on the Antarctic mainland, though occasional animals are seen at the ANARE stations and also on Heard Island. Over the last century there have been 11 recorded strandings on the more southern coasts of Australia. These have been at Nambucca Heads, Manly and Port Hacking in New South Wales; St Kilda (two), Sandringham and Portland in Victoria; Denial Bay, South Australia; Cheyne Beach and Safety Bay, Western Australia and Ralph's Bay, Tasmania. All except one of these were in late autumn, winter and early spring (May–October) with the largest number (six) in winter.

In spite of their common name Crab-eater Seal, these seals do not eat crabs, but feed almost exclusively on krill. They take these shrimp-like animals into the mouth and dispose of the water through the gaps in their elaborately cusped cheek teeth. Adult seals are about 2.6 m in length, silver-brown-grey dorsally, shading to a pale ventral surface. During the year the coat colour fades to a cream-white, from which comes the other common name—White Seal.

The Ross Seal (*Ommatophoca rossi*) is the least known of the Antarctic seals. It is circumpolar, occurring mainly in pack ice of medium to high concentration. Local concentrations have been found in the Ross Sea and King Haakon VII Sea, though there are records from all the way round the Antarctic Continent. Although not rare, Ray (1981) believed there is insufficient information to make a reasonable estimate of numbers.

Ross Seals have not been recorded from Australian Antarctic stations though they have been seen in dense pack ice in Prydz Bay by ANARE voyages on the way to Davis (Johnstone *et al.* 1973). A single young female was recorded from Heard Island in September, 1953 (Ingham 1960) and a single young male came ashore at Beachport, South Australia in January, 1978 (Ling & Aitken 1981). A single lower jaw ramus of early Pleistocene age has been found at Napier, New Zealand (King 1973).

Ross Seals grow to about 2.5 m in length, are dark grey above and silver-grey below. The body is plump, the head short and wide. Food is mainly large cephalopods and the seal is a strong and efficient swimmer. The eyes are large. Though the cheek teeth are small and appear weak, the canines and incisors have delicately recurved points which would help hold slippery food. A variety of bird-like chirps and trills is produced. The large trachea and very long soft palate probably act as resonators (Ray 1981).

Little is known of the biology of these seals, as they are solitary and live in difficult terrain. The pupping season is believed to be in early November (Tikhomirov 1975).

Otariidae

The Australian and Tasmanian mainlands and their associated smaller islands are home to Australian Sea-lions, and Australian and New Zealand Fur-seals. Occasional visits of Subantarctic Fur-seals have been reported.

On Macquarie Island, the otariids present are New Zealand, Subantarctic, and Antarctic Fur-seals, and an occasional Hooker's Sea-lion. Heard and McDonald Islands house the Antarctic Fur-seal.

Australian Sea-lions (*Neophoca cinerea*), found on many of the offshore islands of Western Australia and South Australia, are exclusively Australian. In Western Australia, sea lions are present, though not abundant, on Houtman Abrolhos Islands and on some of the islands between Geraldton and Perth. On the southern shore they occur on Eclipse Island and on some of the islands of the Recherche Archipelago. About 700 animals have been estimated to live in Western Australian waters (Abbott 1979; Marlow & King 1974).

Greater numbers occur in South Australia. The islands of Nuyts Archipelago, the Investigator Group and those islands in and around the southern end of Spencer Gulf, including Kangaroo Island, probably support between 3000 to 5000 animals (Inns, Aitken & Ling 1979). Counts at any place vary enormously according to the time of year and the number of animals away at sea. Seal Bay on Kangaroo Island and Dangerous Reef, a rocky island off Port Lincoln, may have the largest populations with about 500 each. There is also a mainland breeding colony on Point Labatt.

Although the present distribution of the Australian Sea-lion does not extend further east than Kangaroo Island, apart from stragglers, there is evidence that the species had a slightly wider distribution in recent historic times. Matthew Flinders, while going to rescue the crew of the wrecked Sydney Cove in 1798, recorded sea lions on some of the islands in the Furneaux Group in Bass Strait. He also saw them on Waterhouse Island off the northern coast of Tasmania (Marlow & King 1974). Another Tasmanian record, from King Island, Bass Strait before 1900, is based on a juvenile skin now housed in the Tasmanian Museum.

Sea lions, occurring within their modern range, figure in the history of Australia. In 1629, after the Batavia was wrecked on the Abrolhos, Pelsaert named one of the islands there 'Robben-eiland'. In 1727, when the Zeewyk was also wrecked there, over 100 sea lions were killed for food (in Marlow & King 1974). Matthew Flinders made frequent reference to hair seals seen on Kangaroo Island and the islands of the Recherche Archipelago in 1802 and also used them for food (Flinders 1814). In 1803, François Péron reached Kangaroo Island and seeing there a seal new to him, named it *Otaria cinerea*. These were probably females or young males, as a little later in the same voyage, when he reached St Peter Island, Nuyts Archipelago, Péron saw the adult male sea lions with their distinctively pale heads and named them *Otaria albicollis*. In 1844, Captain (later Sir) George Grey, Governor of South Australia, led an exploring party in south-eastern South Australia. While at Rivoli Bay they met 'seals as large as donkeys' and the Governor quickly despatched one with a shot through the head. The young George Angas (then 21) sketched the animal and made notes on it. This is a well-documented and illustrated early record, slightly outside the modern range of distribution. The skull of this sea lion is in the British Museum (Natural History) as is a watercolour of a group of sea lions painted by Angas (Ray & Ling 1981).

The fossil history of Australian Sea-lions is virtually unknown. A skull from Queenscliff, Victoria, at the mouth of Port Phillip Bay has been dated to the last Interglacial (Gill 1968). This is outside the modern range, but could easily have been a straggler from perhaps King Island or Tasmania. It was originally described as *Arctocephalus williamsi*, but is undoubtedly *Neophoca cinerea*. A skull from the middle Pleistocene of Ohope Beach, North Island, New Zealand shows the very wide interorbital region by which the genus *Neophoca* is distinguished, but differences in other characters have led to its description as a new species, *Neophoca palatina* (King 1983a).

Australian sea lions have a nose to tail length of about 2–2.5 m and weigh about 300 kg (males), while females are smaller (1.8 m, 80 kg). In colour, adult males are a rich chocolate-brown. The longer, rough hair over the neck region forms a mane. On the vertex of the head and down the nape of the neck the hairs are white—giving rise to one of the common names of this seal—the White-naped Sea-lion. Adult females are silver-grey to fawn dorsally with a cream ventral surface. They remain much the same colour all their lives, but young males resemble females for about the first 2 years. As the males get older, larger and bulkier, the body darkens and the head lightens until the adult colouration emerges (Marlow 1975).

The Australian Sea-lion does not migrate and, though most animals tend to remain in the same area all year, individuals may move up to 300 km from the breeding ground. They live on rocky terrain (for example, Dangerous Reef, South Australia) or on sandy beaches (for example, Seal Bay, Kangaroo Island). Most pinnipeds produce their pups at the same time each year, some very precisely. The Sea-lion does not seem to follow this pattern. On Dangerous Reef most pups are born in October, but the pupping season may start before the beginning of October and extend to early January (Marlow 1975). On Kangaroo Island and in Western Australia, June seems to be the favoured month, but again pups are produced over several months. In one year the peak fell in October. One must assume that for Sea-lions breeding may take place at almost any time of year and may be correlated with the mild climate (Walker & Ling 1981). Long breeding seasons also are known for other seals, for example, Californian Sea-lions on the Galapagos Islands and Hawaiian Monk Seals (*Monachus schauinslandi*) on the Hawaiian Islands—both places with equable climates (Bonner 1984; King 1983b). An 18 month breeding cycle has been suggested (Ling & Walker 1978). There is much yet to be learnt about the breeding cycle of Australian Sea-lions and research work is continuing. It is interesting though to learn that three Sea-lion females in captivity in Adelaide had gestation periods of 14–15 months (D. Langdon personal communication).

About 3 days before the pup is born, the female comes ashore and joins other females on the beach. The adult bulls actively herd the cows and many territorial fights take place. However, the harem that is so jealously guarded does not always consist of the same cows. Restless twisting and turning by the cow signals the arrival of the pup, which may be born head or hind flippers first. The pup soon vocalises, the two animals establishing recognition patterns. The placenta, produced about 30 minutes later is usually eaten by gulls. The newborn pup is about 700 mm from nose to tail and weighs about 6–8 kg. It is chocolate brown in colour, with thick soft fur which is moulted at about 2 months of age for the grey and cream juvenile coat. The pups start suckling soon after birth and may feed in this way for at least a year. Cows about to give birth have been seen suckling the pup they produced the previous year. The pup has close contact with its mother for 2 weeks before she starts going to sea to feed. The pup is at first left in a sheltered position, but as it matures it starts exploring and practices swimming in shallow pools. When about 3 months old it is able to swim well in the sea (Marlow 1975).

Cows have been seen copulating 4–9 days after the birth of the pup and there is, presumably, a post-partum oestrus. Although the details are not known for Australian Sea-lions, there is presumably a delay in the implantation of the blastocyst, as in other pinnipeds, of about 4 months.

Australian Sea-lions are aggressive animals. Adult and subadult males and adult females will attack wandering pups, sometimes tossing them so that lethal injury is sustained. Predators on Sea-lions are mainly White Pointer Sharks (*Carcharodon carcharias*) which abound in South Australian waters. Many Sea-lions bear large curved wounds or missing hind flippers as evidence of such attack. Parasites include lice, nematodes, acanthocephalans and cestodes.

Local fishes such as whiting and school shark are eaten and also taken from fishermen's nets. Probably many other available sorts of fishes are taken. Cephalopods, crayfish and penguins are also eaten. Stones also are found in the stomach (Walker & Ling 1981).

The Sea-lion is protected in Australian waters, although fishermen kill those they deem to be interfering with their fishing. On Kangaroo Island, however, the sea lions are a tourist attraction and an economic asset to South Australia (Stirling 1972).

The name *Arctocephalus pusillus* covers the South African and Australian Fur-seals. On the basis of geography and one skull character, subspecific separation is maintained (Repenning *et al.* 1971). The South African species is *A. p. pusillus* while the Australian one is *A. p. doriferus*. The separation of the two populations, however, is believed to be comparatively recent as they are virtually identical, both anatomically and biologically (Warneke & Shaughnessy 1985).

The total population of the Australian Fur-seal is about 20 000 to 25 000 and most of these are resident in the waters of Victoria and Tasmania. The two largest colonies are on Lady Julia Percy Island and Seal Rocks, off Phillip Island, the latter producing about 2000 pups a year. There are nine other breeding colonies, including those on Kanowna Island, the Skerries, Reid Rocks, West Moncoeur Island, Moriarty Rocks and Tenth Island. From Bass Strait southwards, smaller groups may occur on any suitable rocky shore or island round Tasmania down to the breeding colonies on the Maatsuyker Group and Pedra Branca (King 1983b; Pearse 1979; Warneke 1979; Warneke & Shaughnessy 1985). Lesser known, non-breeding groups occur on Montague Island and on Seal Rocks, near Port Stephens, New South Wales. There is no migration and the seals remain in the area all year, probably no further than 150 km from their birthplace.

There are, at the moment, no known fossils of the Australian Fur-seal and relatively recent archaeological remains form our first evidence of this seal in Australia. Even then, from the fragments remaining, it is difficult to distinguish between *A. p. doriferus* and *A. forsteri*. Fur seal bones are known from aboriginal middens in north-west Tasmania that have been dated to about 8000 years ago and there are further, less ancient deposits on the south coast (Jones 1966; Stockton 1982).

The Australian Fur-seal is the biggest of the fur seals. The adult male is 2–2.2 m in nose to tail length and weighs up to 360 kg. The adult females are smaller, 1.2–1.7 m in length, 36–110 kg in weight. The males are a dark grey-brown all over. The longer, coarser hair on the shoulders forms a mane. The females are lighter, more silver-grey with a yellowish throat and chest and brown abdomen, but on a breeding rookery where the animals spend much time ashore in dirty conditions, all animals appear the same ginger-brown colour. The underfur is the typical chestnut colour.

The breeding colonies are never deserted completely, but for much of the year the occupants are mostly females and immatures. Towards the end of October the territorial bulls come ashore. Some of them return to the same territory for six successive years. They take up their positions with much fighting and commotion, but do not herd the females who move about freely. The pups are born between the beginning of November and the end of December, with a peak between 20 November and 7 December. At birth they are about 600–800 mm nose to tail length, and weigh 4.5–12.5 kg. Male pups are about 1 kg heavier than females. Pups are dark brown dorsally and grey or light brown ventrally until they are about 3 months old, when they moult and resemble the adults. For about 5–6 days after birth the pup stays close to its mother. The cow then mates and goes out to sea to feed, returning about once a week to feed the pup. For the 8 months or so that she does this, the pups congregate in groups or pods, gradually becoming more independent as they play and practice swimming. At about 8 months old the pups will take a certain amount of solid food and are capable of going to sea with their mothers. Lactation lasts for up to a year until the next pup is born, though if some accident befalls the new pup, the older one may continue to suckle for 2, or even 3 years (Warneke 1979). The breeding males usually do not leave the colony for feeding until the end of the breeding season. Little is known of their whereabouts for the rest of the year, although there are many rocky places where they may haul out to rest.

The blastocyst has the normal delay of about 3 months before implantation so the active gestation period is about 8.75 months. The females are sexually mature when they are 3–6 years old and the males at 4–5 years. The males at this age, however, are not physically capable of maintaining a territory against the bigger bulls. Results from tagging indicate that it is not until they are about 12 or even older that they reach the status of territorial males, a position that even then probably is held only for about three seasons (Warneke 1983).

Many sorts of fish, squid, octopus and rock lobsters are eaten by Australian Fur-seals, taken from the sea surface down to the sea bottom, and it is probable that it can dive to at least 120 m (Warneke 1979; Warneke & Shaughnessy 1985).

White sharks and Killer Whales are probably the main enemies of this fur seal. Nematodes, cestodes and acanthocephalans are parasites in the stomach and intestine and mites live in the nasopharynx.

During the early exploration of Australia, George Bass discovered Westernport, Victoria in 1798, increased his food supplies by eating seal meat and suggested the commercial exploitation of the seals of Wilson's Promontory. Matthew Flinders, on returning from his trip to the Furneaux Group in 1798, commented on the number of fur seals he had seen. This resulted in the *Nautilus* leaving Sydney in October, 1798 for the first sealing expedition in the area. The *Nautilus* obtained a cargo of some 9000 skins. This was the beginning of the sealing industry in these waters (Abbott & Nairn 1969; Marlow & King 1974; Warneke & Shaughnessy 1985). The abundance of seals in Bass Strait, particularly on the Furneaux Group and King Island, attracted sealing vessels from as far away as America, England and India and provided the colony at Port Jackson with its first major export trade (Warneke 1966). Sealing continued in Victorian waters until 1891, when the seals were protected. By 1820, the original herds were very much reduced and many of the sealing ships moved further afield. This fur seal is now protected over all its range.

The New Zealand Fur-seal (*Arctocephalus forsteri*) is also resident in Australia (King 1969), although the bulk of its population occurs in New Zealand. In Western Australia, there are breeding colonies on Eclipse Island and on some of the islands of the Recherche Archipelago. In the latter group, Salisbury Island has the largest colony of fur seals in Western Australia with about 1000 animals estimated on the island (Carhart 1982). The islands near the entrance to Spencer

Gulf, South Australia, form another group, with colonies on Four Hummocks, South Neptune and Cape du Couedic on Kangaroo Island. The South Neptune colony is the biggest with about 1300 animals. There is no geographical barrier between New Zealand and Australian Fur-seals in Australia. The former not infrequently turns up in colonies of the latter, as on Seal Rocks and even tries to hold territories there. Analysis of the vocalisations of these two animals, however, shows that they are different and that the vocalisations of New Zealand Fur-seals are similar to those of Antarctic Fur-seals from South Georgia (Stirling & Warneke 1971).

Occasional stragglers reach the Sydney region and some have been kept in Taronga Zoo for short periods. Further afield, three young animals, only an estimated 8 months old, even reached New Caledonia (King 1976). Weather conditions at the time made an Australian origin for these seals possible, though not certain. Australian New Zealand Fur-seals do not occur normally now east of Kangaroo Island, but in 1925 Le Souef found about 100 on Saltpetre Rocks, west of King Island in Bass Strait (King 1969) and there is archaeological evidence of the presence of these fur seals about 1500 years ago on Hunter Island, closer to the Tasmanian mainland. The voyages of Captain Cook made New Zealand Fur-seals known to the world, as George Forster, the botanist on Cook's voyage made a sketch of a 'sea bear' from New Zealand in 1773. In spite of the tens of thousands of fur seals that were killed for the sealing trade in the first 30 years of the 19th Century, there were no specimens of New Zealand Fur-seals nor any description of the animal until 1871 (Marlow & King 1974).

Adult males of this fur seal reach about 2 m nose to tail length and weigh 200 kg. Females are smaller at 1.5 m and 90 kg. Both males and females are a dark grey-brown dorsally, shading to slightly lighter ventrally. The long guard hairs are coarse and dark grey and the thick underfur is chestnut. Most work has been done on the New Zealand populations, but the life of the Australian animals seems very similar (Stirling 1971a; 1971b). For much of the year outside the breeding season, the rookeries are occupied by cows and immature animals while the bulls are away at sea. From October onwards, the number of adult bulls increases on the rookeries and they establish their territories. Large numbers of cows, replete from intensive feeding, come in to the rookeries in November and December. Birth of the pups takes place between the end of November and 22 January, with the peak at the end of December. The female mates about 8 days after the birth of the pup, but stays with the pup for about 10 days, after which she goes to sea for a few days, then returns for a couple of days to feed the pup, repeating the sequence for a while. At the end of the breeding season, during January, the harem system breaks down and the bulls depart to sea again for their first meal for some 10 weeks.

At birth the pups are about 550 mm long and weigh about 4 kg. They are black, but moult at two months to a silvery colour. They are suckled for about a year.

The food of the adults is mainly squid and octopus, but lampreys, rock lobster, crab and penguins also are taken. Fish is eaten and stomach contents indicate that it is largely non-commercial fish that are taken. The seals are protected.

Subantarctic Fur-seals (*Arctocephalus tropicalis*), also have been reported as an occasional visitor to the Australian mainland. Maybe it occurs more often, but so far only two animals have been identified positively by the distinctive yellow chest and crest of hair on the head of the adult male. These fur seals are noted wanderers (King 1983b). From Gough Island, individuals have wandered to South America, South Africa and South Georgia. The animals reported from Macquarie Island and New Zealand probably came from the breeding grounds on the islands of St Paul and Amsterdam, so their presence in Australia is not unlikely. In 1973 or 74 a male fur seal was found at Evans Head, New South Wales and taken to Sea World, where he remained, known as 'Furry' for eight

years before dying in 1982 (G. Abel personal communication). Photographs confirm his identification by colour. ‘Hamish’ was another fur seal that was found, injured, at Wombarra, New South Wales in 1980. He was taken to Taronga Zoo where he posed problems of identification. As he has matured, however, so his distinctive coat pattern has become obvious (Anon. 1983).

Macquarie Island

Macquarie Island was discovered in 1810 when sealers were looking for new places to exploit. They found what they wanted, removed fur seal skins in vast quantities and in 10 years virtually exterminated the fur seal there (Csordas & Ingham 1965; Cumpston 1969; Shaughnessy & Fletcher 1987). Something in the order of 190 000 skins were taken, but from the sealers’ point of view, one fur seal was as good as another and they did not stop to identify the animal they exterminated. Even today we are not sure.

Elephant seals and penguins were taken for their oil in quickly decreasing numbers for another century, but in 1919 all sealing licences were cancelled. The island was proclaimed a sanctuary in 1933. In 1948, the Australian National Antarctic Research Expedition (ANARE) established a station on the island. At that time a small herd of fur seals (about 170) was present at the northern end of the island, staying only during the summer months. The fur seals gradually increased their range and their numbers on Macquarie, reaching about 1222 in 1982 (Shaughnessy & Fletcher 1984; 1987). These seals now are known to be New Zealand Fur-seals and are present all year round. They do not breed on the island. The population is composed of young males.

In 1955, a fur seal pup was born on Macquarie (Csordas 1958) and very small numbers of pups have been born annually since then. It was assumed at the time that they were New Zealand Fur-seals, but this is considered unlikely. In 1959 an unusual seal, distinguished by its colour, was seen in the middle of a group of New Zealand Fur-seals. The yellow chest and face and the crest on the head identified this animal as a male Subantarctic Fur-seal (Csordas 1962). This species has its headquarters on Gough Island, where there may be 200 000 animals, but also is found on the Prince Edward Islands and the islands of St Paul and Amsterdam, all north of the Antarctic Convergence.

Observations since 1981 have revealed the presence at Macquarie Island of Subantarctic Fur-seal males holding breeding territories in which cows and pups of both Subantarctic and Antarctic Fur-seals occur. The latter’s headquarters is on South Georgia and other circumpolar islands south of the Antarctic Convergence (King 1983b). The numbers of both these fur seals have increased enormously over recent years.

The presence of three different fur seals on Macquarie Island, two of which are breeding, poses an interesting situation. Subantarctic and Antarctic Fur-seals also occur together on Marion Island (Kerley 1983) and on the Crozet Islands (Jouventin, Stahl & Weimerskirch 1982). On Macquarie Island the numbers of the Subantarctic/Antarctic group are still low (five bulls, 30 cows, 20 pups), but the Subantarctic Fur-seal has not previously been reported breeding in Australian waters (Fletcher & Shaughnessy 1984; Shaughnessy & Fletcher 1984; 1987). The apparent absence on Macquarie of bulls of Antarctic Fur-seals suggests the possibility of interbreeding. This situation also occurs on Marion Island where anomalous animals that could be hybrids occur (Condy 1978). The fur seals on Macquarie Island and Marion Island are being observed and research work continues.

The original fur seal inhabitant of Macquarie is not known, but research work under way suggests that the Subantarctic Fur-seal is probably the most likely animal (Shaughnessy & Fletcher 1984; 1987).

An occasional visitor to Macquarie Island is Hooker's Sea-lion. The Auckland Islands form the main breeding centre for this species (Falla, Taylor & Black 1979; Marlow 1975), but stragglers, usually young males, not infrequently reach Macquarie.

On Heard Island, only small numbers of non-breeding Antarctic Fur-seal were known until relatively recently. Five hundred fur seals and two young pups were seen in 1963, but by 1969 there were estimated to be 3000 fur seals. A few pups were seen, but most animals were thought to be visitors (Budd 1970). Another inspection in 1971 showed a further increase in the population, though most were non breeding bulls (Budd 1972). On McDonald Island nearby, in 1971, about 150 adults of both sexes and 46 black pups were seen on the two main beaches visited (Budd 1972).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Phocids occur in marine, estuarine and freshwater situations. Most of the Northern phocids occur in Arctic waters and in the northern parts of the Atlantic and Pacific Oceans. In more temperate waters, Grey Seals and some species of *Phoca* occur in British and North American waters. Some Ringed Seals (*Phoca hispida*), live in freshwater lakes which have connections with the Gulf of Bothnia and some Harbour Seals, Harbour Seals live in lakes close to Hudson Bay. Two phocids restricted to inland freshwater lakes are the Caspian Seal (*Phoca caspica*), in the Caspian Sea and the Baikal Seal in Lake Baikal, the deepest freshwater lake in the world.

Southern phocids (the Northern and Southern imply relationship as well as geography) include the circumpolar seals of the Antarctic—Australian Sea-lion, Crab-eater, Ross and Leopard Seals—and the Southern Elephant Seal, of the subantarctic islands. Belonging to the Southern phocids, even though geographically northern, are the Monk Seals of the Mediterranean and North African coasts and the western Hawaiian Islands and the Northern Elephant Seal (*Mirounga angustirostris*) of California.

Walruses are entirely Arctic. Sea-lions occur on both sides of the Pacific Ocean, south to the tip of South America and the Falkland Islands in the east, to Hokkaido in the west. The hotter regions from Japan to the northern and eastern coasts of Australia have no sea lions, though they are present again on the southern shores of Australia and on the islands south of New Zealand.

The Northern Fur-seal (*Callorhinus ursinus*) lives on both sides of the North Pacific, from Japan to California. Eight species of Southern fur seals (*Arctocephalus*) range from Guadalupe off California, along the coast of South America to the islands of the Scotia Arc, the southern shores of Australia and New Zealand and the islands south of New Zealand. Fur seals also occur on the southern tip of South Africa and on the islands from Tristan da Cunha to Kerguelen and Macquarie, on both sides of the Antarctic Convergence.

In many places, where seals appear to be in very hot climates, such as on the Galapagos Islands, California and South Africa for example, there are cold currents such as the Peru Current, California Current and Benguela Current, respectively, which bring cooler water to these tropical areas.

The two seals, both phocids, which spend their lives in the hottest places, the Northern Elephant Seal and the Hawaiian Monk Seal, seem to cope with the heat in a behavioural rather than a physiological manner. Their behaviour patterns vary, but they survive in the heat by being inactive, sleeping a lot and using wet sand, shade and eventually escaping to the sea.

Affinities with other Groups

Although pinnipeds formerly were placed in the Order Pinnipedia, there really is no doubt that they have come from carnivore stock. They exhibit a diagnostic character of the Carnivora: fusion of two of the carpal bones (scaphoid and lunar). The single-chambered bulla of pinnipeds indicates their affinity with the Canoidea rather than the Feloidea.

Detailed characters of the ear of otarioid pinnipeds (otariids and odobenids) suggested that they evolved from a subfamily of Oligocene ursids (Tedford 1976). The structure of the phocid ear suggests the origin of this group from a stock of primitive mustelids (Tedford 1976; King 1983b). This diphyletic origin of seals has been questioned recently (Wyss 1987) with an interesting and convincing argument. Closer alliance of phocids and odobenids is suggested; characters are given which unite all three pinniped families. In this preliminary paper, future researchers are invited to consider seriously the real possibility of monophyly.

Affinities within the Otariidae and Phocidae

Fossil Record

The fossil history of otariid seals is relatively well known. The ancestral group, the Enaliarctidae, is known from California and Japan and existed at the beginning of the Miocene (about 22.5 mybp). From this group evolved the walrus and the otariids. Early walruses separated about 20 mybp and the otariid seals developed about 14 mybp. *Arctocephalus* is the genus thought to be most like the ancestral otariid. From this line, the Northern Fur-seal diverged in the Early Pliocene and the sea lions relatively recently, about three million years ago (Repenning & Tedford 1977). The otariids dispersed from their place of origin in the northern Pacific, fur seals being more widely distributed in the Southern Hemisphere than sea lions.

Less is known about fossil phocids (Ray 1976), but they originated around the margins of the North Atlantic. The earliest phocids are known from the early Middle Miocene (14 mybp) and are thus some 8 000 000 years younger than the earliest otariids. Even then, the phocids were divisible into their two major groups and both groups probably were present on both sides of the North Atlantic. The monachine group was the dominant seal of the North Atlantic in the Pliocene. From the North Atlantic, monachine seals moved into the Pacific from the Caribbean via the South American Seaway. The Caribbean (*Monachus tropicalis*) and Hawaiian Monk Seals, and the elephant seals arose from these ancestors. Other monachines known from the Pliocene of Peru (Muizon 1981) perhaps may be related to the line that gave rise to leopard seals. From the North Atlantic, more monachines moved down the African coast, across to South America and back to South Africa following the ocean currents and giving rise to *Homiphoca*, fossils of which have been found in both places. *Homiphoca* shows some affinities with Crab-eater Seals, but direct ancestry is not implied (Hendey 1972; Hendey & Repenning 1972).

A few phocid fossils are known from Late Miocene-Early Pliocene levels from near Melbourne (Fordyce & Flannery 1983). The two temporal bones are from monachine phocids, but need to be compared with *Homiphoca* to determine their exact relationships. They are the first positive pre-Pleistocene records of Southern phocids outside Peru, Argentina and South Africa and may suggest that phocids reached Antarctic waters before the Early Pliocene.

The affinities of the four genera of louse found on pinnipeds suggest that they have evolved with their hosts. Primitive lice (*Proechinophthirus*) occur on the most primitive otariids (fur seals), but with a different species on *Arctocephalus*

and Northern Fur-seals. *Echinophthirus* is only known from the Northern phocids. *Lepidophthirus* is known only from Southern Elephant Seals and Mediterranean Monk Seals (*Monachus monachus*). *Antarctophthirus* is the most widely distributed of these lice, but its six species are very restricted in their distribution. *Antarctophthirus callorhini* is found only on Northern Fur-seals, *A. microchiri* only on sea lions, *A. trichechi* only on Walrus, *A. ogmorhini* only on Leopard and Weddell Seals, *A. lobodontis* only on Crab-eater Seals and *A. mawsoni* only on Ross Seals. Further details of these lice and their relationships are described by Kim, Repenning & Morejohn (1975).

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