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The Walrus Auditory Region and the Monophyly of Pinnipeds

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ABSTRACT

Within the customary tripartite division of pinnipeds a grouping of the Odobenidae (walruses) and Otariidae (sea lions) to the exclusion of the Phocidae (seals) has been almost universally recognized. An anatomical review of features, primarily of the auditory region, however, reveals that odobenids share a significant number of derived characters with phocids. The evidence supporting the traditional otariid/odobenid grouping is examined and is found to consist almost exclusively of primitive, and therefore phylogenetically uninformative, characters. A review of characters that have been proposed as supporting the widely accepted alliance of phocids and mustelids reveals that they fail to provide compelling evidence for

pinniped diphyly; the arguments for diphyly are further weakened by acceptance of a phocid-walrus relationship. Some aspects of the cranial morphology of several putative early Miocene otarioids are reviewed, and it is suggested that *Pinnarctidion* and *Allodesmus* are actually better regarded as members of a group including phocids and odobenids. Thus, the major morphological gap between the highly derived phocids and their presumed sister group may largely be filled. A cladogram depicting a sister-group relationship between odobenids and phocids, the monophyly of pinnipeds, and the tentative relationships of these fossil taxa is presented.

INTRODUCTION

Historically, the relationships of odobenids (walruses) have generated little controversy. Pinnipeds are generally divided into three groups of coordinate rank, otariids

(eared seals or sea lions), phocids (true seals), and odobenids. During the past century there has been strong agreement that odobenids are little more than highly divergent otariids and

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that consequently these two groups share a more recent common ancestry than either does with phocids.

Alban Doran's (1878) masterful survey of the mammalian auditory ossicles bears directly on the phylogenetic relationships of the walruses. His landmark study is remarkable both in terms of the breadth of its coverage and in the detail of its description and comparison. Motivation for the analysis presented here, and much of its substance, derives directly from his careful observations.

My intent is to expand Doran's discussion of odobenid ear ossicles specifically, and pinniped ear ossicles generally, and to consider this information, as well as additional information concerning the pinniped otic region and other anatomical provinces, in a phylogenetic context. This yields some potentially important observations that suggest a major departure from currently held views of walrus relationships.

Among mammals, the ear ossicles of aquatic forms show by far the highest degree of modification; in contrast, the three middle ear bones of terrestrial mammals are, by and large, rather conservative in form. Because highly modified auditory regions have arisen at least three times in aquatic mammals (pinnipeds—perhaps twice within this group, see below—cetaceans, and sirenians), one might argue that this area of the basicranium shows a tendency toward parallelism and is therefore (at least among these forms) an unreliable indicator of phylogenetic affinities. Nevertheless, because many of these modifications are completely dissimilar in the three eutherian groups in question, and because many of their anatomical details are restricted to certain aquatic mammals, I see no reason to consider, *a priori*, these modifications of diminished phylogenetic importance.

DISCUSSION

"FISSIPED" MALLEUS AND INCUS

Doran (1878) prefaced his discussion of carnivoran ear ossicles by noting the remarkable uniformity within the families, genera, and species of the "fissipeds" (an almost certainly paraphyletic assemblage of all terrestrial carnivores, but a term used here for the sake of convenience) of the malleus

and incus. Several derived features of the pinniped ossicular chain are seen in these elements. The mallei of *Canis* and *Ursus* are shown in figure 2 as representative "fissiped" mallei (ossicular terminology is shown in fig. 1). The "fissiped" malleus is characterized by a small anteriorly convex head (except ursids and some procyonids), a long thin manubrium, a well-developed processus muscularis (site of insertion for the tensor tympani) (except ursids), a well-developed lateral process (process brevis), and a broad thin lamella (except *Herpestes* and allies; Doran, 1878) extending between the slender processus gracilis (anterior process, goniale, process folii, processus longus) and the region of the head and neck.

Whether these features represent primitive or derived characters within Eutheria is difficult to assess and fortunately is not critical to this discussion. What is of interest is whether such a malleus may be considered as the morphotypic or "ancestral" carnivoran malleus. For this to be the case it must be shown that pinnipeds, whose ear ossicles differ markedly from those of "fissipeds," are related to a particular "fissiped" subgroup—in other words it must be demonstrated that pinnipeds are not the sister group of all other carnivores. There is ample evidence that this is indeed the case. Pinnipeds are more closely allied to arctoids (ursids, mustelids, and procyonids) than they are to the feliforms (felids, hyaenids, viverrids) or cynoids (canids) as shown by several features of the dentition and basicranium (Tedford, 1976). (As elaborated later, this is only the most general expression of Tedford's scheme.)

PINNIPED MALLEUS AND INCUS

Phocid ear ossicles are characterized by a number of modifications (e.g., extreme expansions of the incus to form a head, and, in some, extra articulations on the malleus) not seen in either otariids or odobenids nor in all other carnivorans. Even the earliest phocid ear ossicles known, a late Miocene incus and malleus of *Monotherium? wymani*, are already exceedingly derived (see Ray, 1976, pls. 3 and 4). Otariids retain ear ossicles that are rather typical for mammals of their size, but those of phocids are greatly enlarged. As Re-

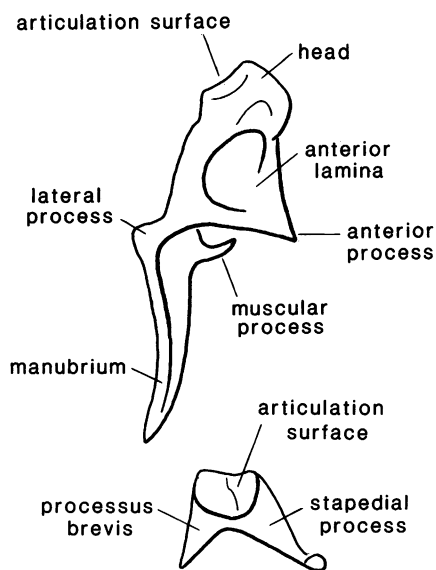


Fig. 1. Generalized "fissiped" malleus (top) and incus (bottom) demonstrating ossicular nomenclature.

penning (1972, p. 319) points out in his superb functional analysis of the pinniped ear, phocid auditory ossicles are "many times larger than those of other carnivores *except the odobenids*" [emphasis mine]. Odobenid ear ossicles are larger than those of otariids (Doran, 1878, p. 401; Repenning, 1972) but this enlargement is not so extreme as in phocids (table 1). Except for this great difference in relative size, phocid, odobenid, and otariid mallei are extremely similar.

The malleus of the only living member of the family Odobenidae, *Odobenus rosmarus*, and representatives of this element in phocids and otariids are presented in figure 3. There are several conspicuous resemblances between the ossicles of all three families. In mammals, the globular malleolar head (caput mallei) supports the malleolar surface of articulation contributing to the incudomalleolar joint. The *Odobenus* malleolar head is greatly enlarged and bears a triangular vestige of the anterior lamina. Doran (1878) reported that the region of the head anterior to the articulating surface is marked by a deep concavity. Of the several mallei I have examined, however, I have only been able to identify faint indications of such an excavation in os-

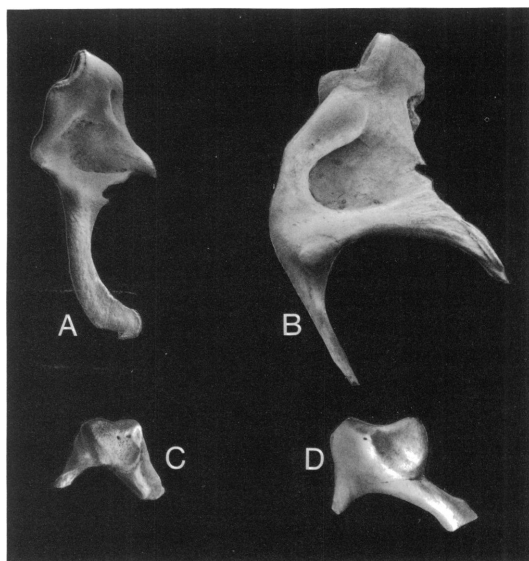


Fig. 2. A, C *Ursus* and B, D *Canis* malleus and incus (right). Note well-developed anterior lamina, size of malleolar head, and length of manubrium (approx. $5\frac{1}{4} \times$ natural size). Muscular process on *Canis* malleus not visible in this view.

sicles from juvenile individuals (otherwise the heads are typically convex).

The odobenid malleus lacks a muscular process, the manubrium is shortened, the processus gracilis—if it can even be considered present—is reduced to a low blunt ridge. The broad lamina extending between the head region and the manubrial base, so characteristic of "fissipeds," is represented only by the vestige mentioned above, and the lateral process is short, broad, and rounded.

As in *Odobenus*, the phocid malleus is characterized by an enlarged head (table 1).

In phocids and otariids the anterior portion of the malleolar head usually bears a deep concavity (absent in adult *Zalophus* but distinctly present in juveniles—personal observ.). It is notable that ursids (and to a lesser degree some procyonids) show a similar, but smaller, excavation in this region (see fig. 2). Phocids and otariids share a greatly reduced or absent processus gracilis and associated lamina. Most otariids maintain a vestige of the lamina and, in this regard, bear a plesiomorphous resemblance to odobenids. A reduced processus gracilis and lamina are, however, sometimes present in phocids, par-

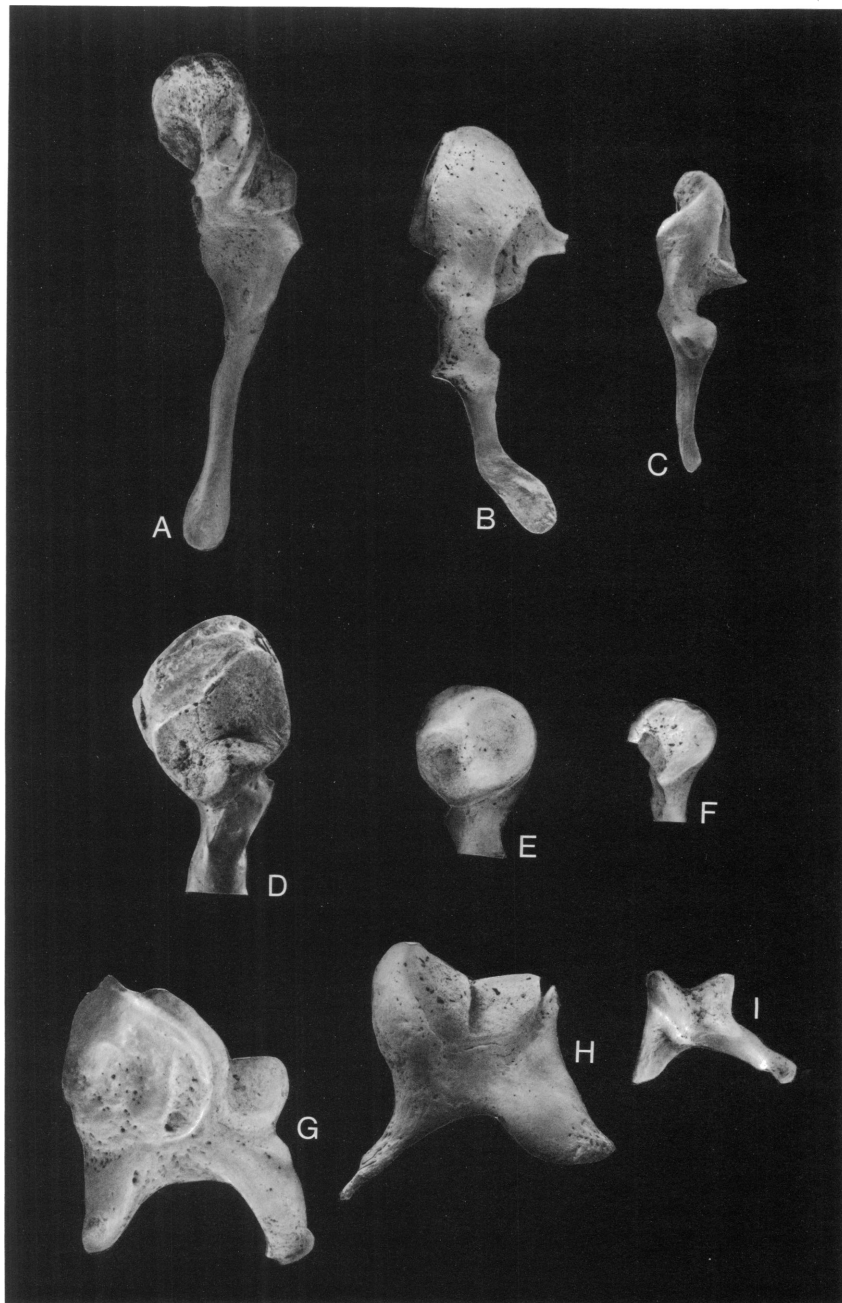


Fig. 3. Right malleus, malleal articulation surface, and incus of: **A, D, G** *Phoca*, **B, E, H** *Odobenus*, **C, F, I** *Callorhinus* (otariid). The view in (A) is internal to demonstrate the lack of a muscular process, thus the anterior concavity is at the upper left (approx. $5\frac{1}{4}\times$ natural size).

ticularly juveniles. Relative to other carnivores, all pinnipeds are characterized by proportionally shorter manubria (see table 1).

In addition to this general enlargement of

the ossicles, a distinctive feature allying odobenid and phocid mallei is a specialization of the articulation surface. In most carnivores (including otariids) the articulation

TABLE 1

Measurements of the Incus and Malleus for Selected Carnivores (in millimeters)

1. manubrium, 2. head + neck, 3. head, 4. relative manubrium size—manubrium/head + neck, 5. relative head size—head/head + neck + manubrium, 6. maximum dimension (end of stapedial process to top of incudal head), 7. maximum thickness, 8. size of incus relative to malleus maximum—incus/head + neck + manubrium.

	Malleus					Incus		
	1	2	3	4	5	6	7	8
<i>Odobenus</i>	5.47	7.71	4.65	0.71	0.35	7.33	3.62	0.56
<i>Odobenus</i> juv.	5.41	7.17	3.87	0.75	0.31	8.09	3.07	0.64
<i>Lobodon</i>	5.66	7.53	5.89	0.75	0.45	10.72	5.35	0.81
<i>Phoca</i>	6.72	7.07	4.13	0.95	0.30	8.67	4.89	0.66
<i>Phoca</i> sp.	4.72	6.70	4.26	0.70	0.37	7.40	4.38	0.65
<i>Erignathus</i>	6.72	7.94	4.59	0.85	0.31	8.30	4.21	0.57
<i>Zalophus</i>	3.62	3.70	2.29	0.98	0.31			
<i>Eumetopias</i>	3.98	4.12	2.04	0.97	0.25			
<i>Callorhinus</i>	4.05	4.08	2.37	0.99	0.29	4.62	1.97	0.57
<i>Ursus</i>	6.18	4.75	2.37	1.30	0.22	3.98	2.03	0.36
<i>Canis</i>	5.40	3.34	1.72	1.62	0.20	2.88	1.50	0.33
<i>Felis</i>	5.67	3.55	1.86	1.60	0.20	2.91	1.38	0.32

surface is vertically broad and occupies most of the posterior region of the malleolar head. In phocids and odobenids the articulation is more discrete (perhaps owing to the increased size of the head), dorsoventrally narrow, and horizontally broad. It is composed of two closely appressed facets forming a surface that is shaped roughly like a figure 8 that has been folded about its midpoint (fig. 3) (this feature is, however, less sharply defined in the walrus). Nevertheless, at this juncture it is appropriate to note Doran's (1878, p. 401) concluding assessment of the walrus malleus; it is, he states, "plainly a mere modification of the seal type of malleus It far less resembles the Otarian malleus."

Regarding the ossicles of *Potamotherium*, a fossil arctoid often implicated in the ancestry of phocids, Savage (1957, pp. 175–176) reported that the malleus is larger than that of the otter *Lutra*, that a muscular process is well developed, and that the lamina appears to have been short and narrow. Also, the incus is larger than that of *Lutra*, but otherwise the two are very similar structurally. From Savage's figure 12 it would seem that the malleolar articulation is of the primitive "diffuse" type and that the incus is not greatly expanded as it is in the walrus and phocids. Further, the incus and malleus of *Lutra* are

thoroughly "fissiped" in their character; the anterior lamina is well developed, the muscular process is present, and the incus is not enlarged (see Segall, 1943). This description also pertains to the lutrines *Pteronura*, *Enhydra*, and *Aonyx* (personal observ.).

As in other pinnipeds, the incus of *Odobenus* is much larger relative to the malleus (or stapes) than it is in "fissipeds" (see table 1). (Often in pinnipeds the incus is actually larger than the malleus, a condition never seen in "fissipeds"). Taking into account scaling differences, the walrus incus is enlarged and inflated but not (as was the case for the malleus) as greatly as in phocids; otariids retain a small, uninflated incus. The thin process brevis (posterior crus) is slightly longer than the rather broad stapedial process (processus longus) but relative to its typical carnivoran form, the walrus incus is greatly inflated.

It is noteworthy that the great increase in phocid ossicular size occurs extremely early in ontogeny. Enlargement of all three ossicles has been shown in a 27 mm (crown-rump length) *Leptonychotes* (Fawcett, 1918) and a 103 mm *Mirounga* (Kummer and Neiß, 1957). Unfortunately no comparable developmental information exists for *Odobenus*.

Although odobenid and some otariid os-

sicles bear a superficial resemblance, this is due strictly to the retention of a suite of pinniped features here inferred to be primitive. Odobenid ossicles are distinguished simply by the lack of most derived uniquely phocid attributes. Therefore, while I would agree with Repenning's (1972, p. 326) conclusion that odobenid ossicles are "except for size," like some otariids in form, I would not attribute any phylogenetic significance to this resemblance. The inflation of odobenid and phocid ear ossicles, the specializations of the malleolar articulation, and the shortened manubrium described above, can be viewed as attributes inherited from a common ancestor rather than as instances of parallelism.

It is of course widely known that other marine mammals have highly derived ossicular chains. This raises the specter that convergence might account for the similarity of these bones among pinnipeds or between odobenids and phocids. It should be emphasized, however, that the ossicles of cetaceans and sirenians, on the one hand, and pinnipeds, on the other, are not even remotely similar. Cetaceans and sirenians retain, for example, a muscular process on the malleus, they lack an anterior concavity on the malleolar head, and their mallei (including the manubrium) are several times more massive than those in even the most derived phocids. The issue of convergence is addressed further below.

OTHER FEATURES OF THE AUDITORY REGION

Associated with their greatly enlarged ear ossicles, phocids and odobenids naturally show equally enlarged epitympanic recesses. In contrast, the otariid epitympanic recess is similar in dimension to that of comparably sized "fissipeds," although otariids appear to be specialized in having a reduced tympanic membrane. Odobenids fall within the range of tympanic membrane/oval window area ratios seen in phocids (Repenning, 1972) but this is most likely a shared primitive character.

In his excellent osteological survey of the mammalian auditory region, Fleischer (1973), noted several interesting features of the pinniped petrosal. The following is an emendation of his discussion.

Fleischer observed that, relative to other mammals, the cochlear aqueduct (canaliculus cochleae) and the fenestra rotunda (fenestra cochleae) of pinnipeds are greatly enlarged and only narrowly separated. Typically, in carnivores the cochlear aqueduct is an exceedingly narrow canal that passes about half the width of the promontorium through the petrosal itself. Its extracochlear aperture lies in the posteromedial petrosal wall nearly in line with the round window (e.g., *Canis*) or actually on the dorsal (cerebellar) petrosal surface along its posteromedial edge (e.g., *Ursus*). Laterally, the cochlear aqueduct opens directly into the scala tympani anterior to the aperture of the round window. In pinnipeds, however, this arrangement is considerably modified. As Fleischer (p. 187) noted:

Innerhalb der Pinnipedia wird die knöcherne Begrenzung des Canaliculus cochleae immer mehr verkleinert in der Form, daß die knöcherne Begrenzung zur Fenestra cochlea immer dünner und schließlich aufgelöst wird. Hier ist also zu verfolgen, wie der (bei allen Pinnipedia sehr große) Canaliculus cochleae langsam in die Fenestra cochleae aufgenommen wird (vrl. Sirenia). So besitzen die Otariidae (hier: *Arctocephalus* und *Zalophus* einen völlig selbständig durch den Knochen verlaufenden Canaliculus, bei *Odobenus* sind Fenestra cochleae und Canaliculus cochleae nur noch durch ein flaches Knochenblatt voneinander getrennt, bei *Phoca* und *Halichoerus* schließlich ist der Canaliculus in die Fenestra cochleae aufgenommen und sein Verlauf ist dort nur noch eine Rinne markiert.

Thus in pinnipeds the bony division between the cochlear aqueduct and fenestra rotunda is progressively reduced, and in phocids at least the canal for the aqueduct, strictly speaking, does not exist. Otariids retain a more primitive condition than other pinnipeds in that the cochlear aqueduct still pierces the petrosal (clearly seen in the poorly macerated juvenile *Zalophus* AMNH 5514).

In phocids the entrance of the cochlear aqueduct into the cochlea coalesces with the foramen rotunda and thus the aqueduct loops into the cochlea across the posteromedial rim of the round window. The course of the canal into the scala tympani is marked on the ventral petrosal surface at the medial edge of the round window by a shallow groove. Similarly, in *Odobenus* the cochlear aqueduct enters

the cochlea through the round window, although I have not observed the thin osseous separation noted by Fleischer. Even if the thin division Fleischer noted is present in some individuals, the course of the walrus cochlear aqueduct closely approximates that seen in phocids. To sum, the pinniped cochlear aqueduct is greatly enlarged and shortened; in phocids and *Odobenus* its connection to the cochlea is via the round window.

The cetacean cochlear aqueduct, like that of pinnipeds, is greatly enlarged; sirenians lack a bony canal altogether (Fleischer, 1973). Otherwise the petrosals of these orders are both highly modified, each in its own regard, and they bear little resemblance to the condition seen in pinnipeds. It can be observed in *Potamotherium* (MNHN SG 690) and from Savage's (1957) figures that the cochlear aqueduct is not enlarged and that it pierces the petrosal in the typical "fissiped" fashion.

Consideration of the pinniped external ear yields an obvious derived character shared by phocids and odobenids: the loss of pinnae. The external ear of phocids is formed by a faint wrinkling of skin. Unlike otariids, however, there is no supporting cartilage in either phocids or odobenids (Walker, 1968). [Additional otic features common to the walrus and phocids are discussed in a later section concerning *Potamotherium*.]

OTHER CRANIAL FEATURES

Odobenids and phocids share several additional conspicuous cranial features outside of the auditory region. Unlike most carnivores (including otariids), odobenids and phocids lack a supraorbital process (a supraorbital process is present but not prominent in *Potamotherium*—Savage, 1957, p. 164). There is some degree of ontogenetic and phylogenetic variation in the shape of the process within the various pinniped families (Fay, personal commun.). The "process" may be developed faintly in some phocids, particularly the Antarctic genera, but it usually almost completely disappears with age. Similarly, what could be called supraorbital processes are present in the fetal walrus as low parallel ridges, but again these are lost in the adult. The important distinction to be made here is that the small bumps present in this

region in some phocids and the young walrus do not at all resemble the sharply developed supraorbital processes of the great majority of otariids.

Similarly, odobenids and phocids share a unique modification of the snout region. The nasal processes of the premaxillae in these two groups are greatly narrowed, and contact between the premaxillae and nasals occurs only along a short suture. Conversely, in otariids and other carnivores, the premaxillae remain dorsally expanded and form a broad contact with the long, unretracted nasals (compare figs. 5A, B, C). In some phocids (e.g., *Erignathus*) the degree of premaxilla-nasal contact approaches that seen in otariids, but, significantly, the converse is not true (i.e., the phocid condition is not seen in otariids).

The premaxilla configuration in *Odobenus* differs from that of phocids. In the walrus this element forms a broad suture with the nasals inside the nasal cavity (this suture is occasionally manifest on the surface) whereas in phocids no such internal contact occurs. The structure of the rostrum in the living walrus is obviously highly modified to accommodate the enlarged tusks. It is hoped that eventually fossils of a less highly modified odobenid will clarify the arrangement of these bones, but in the meantime I tentatively regard this character as a phocid plus odobenid synapomorphy. The more important role of this feature, however, is in allying some already well-known fossil forms to a clade including phocids (see below).

Moving to the ventral surface of the skull, the odobenid and phocid basioccipital is short, broad, and widened posteriorly; in many carnivores (e.g., aeluroids) this bone is generally long and narrow and its edges bordering the auditory region tend to be parallel. In other carnivores where the element broadens posteriorly (e.g., arctoids) it is not so shortened that it is broader than it is long as in phocids and *Odobenus*. The primitive fossil otariid *Thalassoleon* has a basioccipital that widens posteriorly but this feature does not appear to be accompanied by the extreme shortening of this element seen in phocids and the walrus (see Repenning and Tedford, 1977, pl. 20).

Finally, the deciduous dentition of phocids

is rudimentary in that the milk teeth are usually resorbed before birth or are shed very soon thereafter (King, 1983). Similarly, the milk teeth of the walrus are minute and are largely resorbed before birth (Owen, 1853; Cobb, 1933; Fay, 1982); the otariid deciduous dentition is typically less reduced (King, 1983), although it is reduced relative to that of other carnivores (see below).

OTHER ANATOMICAL FEATURES

A cursory examination of literature dealing with pinniped postcranial osteology and "soft" anatomy yields several derived characters that support the close alliance of odobenids and phocids.

The testes of phocids and *Odobenus* are inguinal and lie lateral to the penis (Harrison et al., 1952; Fay, 1981, 1982). In otariids, as in other carnivores, the testes lie outside the inguinal ring (ibid.; Davis, 1964, p. 222).

Odobenus shares with otariids several primitive features of the circulatory system such as the lack of well-developed pericardial plexus, the lack of a prominent stellate plexus over the surface of the kidneys, and the presence of a single azygous vein (Fay, 1981). It has been reported, however, that in several other respects (which appear to me to be plausibly derived), walruses resemble phocids. These include a greatly inflated hepatic sinus, a well-developed caval sphincter, a large intervertebral sinus, a duplicate posterior vena cava, and a venous return from the hind limbs primarily by the gluteal route (Fay, 1981).

Pinnipeds share several specializations of the vertebral column. Some of these (e.g., reduced zygapophyses) are common to other aquatic mammals, but phocids and otariids each maintain distinctive structural patterns. In *Odobenus*: "As in the Phocidae, the cervical vertebrae are slightly smaller than the thoracic and lumbar vertebrae, the spinal canal in each of those regions is nearly as large in diameter as the centrum, and the transverse processes of the lumbar vertebrae are two to three times as long as they are wide (in otariids, the cervicals tend to be largest, the spinal canal less than half the diameter of the centrum, and the transverse processes of the lumbar about as wide as long)" (Fay, 1981, p. 10). Although the morphology of the

vertebral column is clearly in need of a detailed comparative treatment in pinniped outgroups, it is interesting to note King's (1983) summarizing assessment of the *Odobenus* vertebral column; she states, (p. 154) "that the walrus is, in most respects, intermediate though rather more like the phocids."

King (1983) correlated the differences in the phocid and otariid vertebral column with their different means of locomotion. In this context it is of particular interest that phocids and odobenids share a similar mode of swimming; they both propel themselves principally by alternating strokes of the hind flippers and otherwise employ their limbs very similarly (Backhouse, 1961; Gordon, 1981; Fay, 1982). For example, phocids and *Odobenus* both rotate the hind flippers during the power stroke (Gordon, 1981).

Conversely, "The hind limbs play no apparent active role in aquatic thrust production in sea lions" (English, 1976, p. 348). This corresponds closely to the swimming methods of both the brown and polar bears and *Procyon*, all of which brachiate in the water and drag their hind limbs immovably tensed and together (Fay, personal commun.). When swimming, canids, badgers, and skunks use all four limbs, freshwater otters all four but principally the hind limbs, and *Enhydra* only the hind limbs (ibid.). Noteworthy also is the shape of walrus hind flippers; they are triangular in outline, "similar to those of the Phocidae" (Fay, 1981, p. 3).

Fay's account of walrus locomotion contains several interesting observations. He noted (p. 14) that often, when on ice, walruses drag their hindquarters with flippers directed posteriad (phocids always hold their flippers in this manner), and that although walruses progress mainly quadrupedally, they do so much less capably than otariids. Gordon (1981), noted in his detailed account of walrus locomotion that its walk consists of a series of forward lunges. Unlike most tetrapods (including *Zalophus*) where the limbs support the weight of the animal and are used to propel it forward, in the walrus the animal's weight is borne by the venter and the limbs are used for propulsion only during the lunge phase. Phocids do not use their hind limbs in moving over land or ice; thus, they

resemble the walrus in that the limbs play little or no role in supporting the body weight (O'Gorman, 1963).

Related to the subject of ice, it deserves mention that only (but not all) phocids and *Odobenus* inhabit and give birth on pack ice—otariids do not (Stirling, 1975). (It is of course entirely possible that the modern walrus is an exception in its pagophilic habits since some fossil walruses were nonpagophilic.) Walruses generally conform to the social behavioral, and reproductive characteristics (e.g., short synchronized mating periods, reduced disparity in sex ratio, loose social organization, copulation in water) of other pagophilic pinnipeds, except that they do not have a short weaning period (ibid.). "In this aspect," Stirling (1975, p. 209) suggested, "the walrus betrays its phylogenetic relationship to the otariids. The long weaning period of up to 2 years was a legacy from its ursid-like ancestor, and apparently *O. rosmarus* has not been able to shorten it." This statement is self-contradictory in my thesis, however. If a long weaning period is indeed a primitive holdover from an ursine ancestry, then this character has no validity in identifying a relationship between odobenids and otariids.

Pinnipeds are characterized by elongated manubria but again there are interfamilial differences. The otariid modification is primitive and is effected by a bony anterior extension at the point of attachment of the first pair of ribs, whereas, "In phocids and walrus the length of the manubrium is increased by cartilage" (King, 1983, p. 157).

Scheffer and Kenyon (1963) noted a strong correlation between the occurrence of copulation in water and relative baculum size. In phocids—the great majority of which copulate in water—the weight of the baculum as a percent of total body weight (with the exception of *Mirounga* which copulates on land) exceeds, often greatly, that found in otariids. An only slightly broader overlap between otariids and phocids is seen in Scheffer and Kenyon's (1963, table 2) comparison of baculum length as a percent of body length. *Odobenus*—which is strongly suspected of copulating in water (Fay, 1981, 1982)—has a baculum that is almost twice as heavy (relatively) as that of the nearest phocid *Phoca groenlandicus* (see Scheffer and Kenyon,

1963). Lest the condition of an enlarged baculum of phocids and *Odobenus* be dismissed as an obvious adaptive (and therefore phylogenetically insignificant) correlate of copulation in water, it is telling that a baculum is entirely absent in cetaceans (ibid.) and in sirenians. With regard to its form, the adult walrus baculum most resembles that of early juvenile otariids (Mohr, 1963, pp. 22–23). The apex of the adult otariid baculum is marked by a distinct flaring (as it is in other arctoids), usually with the appearance of distinct dorsal and ventral lobes that become exaggerated with age. This distal expansion is much less marked in *Odobenus* (lobes are absent) and is usually entirely absent in phocids (ibid.). The ontogenetic criterion (Nelson and Platnick, 1981) dictates that the juvenile-adult *Odobenus*/juvenile otariid similarity in baculum shape be considered a primitive retention. Either or both the large degree of distal bacular flaring seen in otariids, or the absence of such flaring seen in phocids should be regarded as the apomorphic condition(s); the condition of reduced flaring in the walrus stands somewhere intermediate.

The relative positions along the hair canal of the ducts of the apocrine sweat gland and its associated sebaceous glands reveals an interesting ontogenetic and phylogenetic pattern. In his exemplary review of walrus biology and ecology, Fay (1982) discovered that along the pilary canals of the fetal walrus the sweat ducts always open distal to the openings of the sebaceous ducts; in calves and adults, however, the openings of both types of ducts occur at approximately the same level. In otariids the sweat duct is the more distal (Ling, 1965) as in the fetal walrus. [This is also the case in the sea otter (Kenyon, 1969).] In most phocids, however, the situation is reversed and the openings of the sweat duct tend to be more proximal (Ling, 1965). For functional reasons (see references in Fay, 1982, p. 54) it has been proposed that proximally positioned sweat ducts are correlated with sparse pelage. Fay reasoned, therefore, that the observed ontogenetic shift of the relative position of these ductal orifices was to be expected in the walrus, the most sparsely haired pinniped (Scheffer, 1964). He suggested that the consistent distal placement of the sweat duct orifices in otariids and fetal

Odobenus supported his assumption that these two groups are each other's nearest relatives. He further regarded the ontogenetic shift seen in the walrus as possibly "a pre-adaptation to the sparsely haired condition later in life."

I offer an alternative interpretation that does not invoke convergence. The ontogenetic transformation Fay so clearly documents indicates that the distal position of the opening of the sweat duct is likely the primitive pinniped condition. Otariids simply maintain this primitive arrangement. I would consider the proximal migration of this orifice in the walrus, and its proximal position in phocids (as well as the sparse pelage of both groups) to be phocid/odobenid synapomorphies. [Scheffer's (1964) data show, with the exceptions of three of the antarctic seals *Lobodon*, *Ommatophoca*, and *Hydrurga*, and the sea lion *Eumetopias*, this trend toward less dense pelage in phocids and *Odobenus*.]

Correlated perhaps to this decreased hair density are thick layers of subcutaneous fat (less developed in otariids) and a lack of grooming (otariids are known to groom) in phocids and walruses (Tarasoff, 1972). As do other "fissipeds," lutrines lack these thick layers of fat, they are densely haired, and they groom (*Enhydra* intensively) (ibid.).

It is also of significance that the primary hairs of otariids have a medulla but those of phocids and *Odobenus* do not (Scheffer, 1964). Noback (1951) concluded that the presence of a medulla was correlated with large hair diameter and therefore dismissed the phylogenetic importance of this character. There is considerable overlap of the mean basal widths of otariid and phocid primary hairs, but as Scheffer's (1964) data show the distribution specified above (medulla absent only in the walrus and phocids) holds true without exception. Medullated hair has been recorded elsewhere in the Carnivora in both the dog and weasel (fide Noback, 1951); therefore, the lack of a medulla in *Odobenus* and phocids can reasonably be regarded as a derived attribute.

There is one additional feature of the pelage that, although in need of broad modern treatment, offers a curious distribution. In otariids the pelage units (a primary hair and its surrounding secondaries) are spaced uni-

formly "like trees in an orchard" (Scheffer, 1964). In the walrus and in all members of the Phocinae the units are arranged in groups of two to four or in rows. Scheffer (1964) reported that in "Cystophorinae" and Monachinae the patterns are not consistent with other phocids, but judging from his figure 3 (p. 298), *Cystophora* appears to agree much more closely with the arrangement seen on *Odobenus* (his fig. 4, p. 300) than it does with the regular spacing of *Zalophus* (his fig. 1, p. 296). De Meijere (1894, p. 327) noted that the pelage units of *Canis* and *Ursus* occur in alternating rows of linearly arranged groups of three, thus it seems that the otariid pattern alone is derived among pinnipeds. *Lutra* (ibid., p. 329) shows an arrangement completely unlike that of pinnipeds. In the adult, a cluster of normal pelage units is surrounded by numerous hair bundles comprising exclusively secondary hairs. It is also of note that all pinnipeds have lost the musculature associated with raising hair (Scheffer, 1964).

The configuration of the astragalus is further evidence supporting the linkage of phocids and odobenids. It is well known that the phocid astragalus is characterized by a strong caudally directed process (calcaneal process) over which passes the tendon of the flexor hallucis longus. As Howell (1929, p. 132) has termed it: "This is perhaps the most significant single detail of the specialization of the Phocidae." In the living walrus there is also at least a slight posterior extension of this element; in otariids there is not (Howell, 1930, personal observ.). More interesting is the astragalus of the late middle and early late Miocene odobenid *Imagotaria* where this process, which extends on the plantar surface posteromedially from the posterior calcaneal articulation (=ectal facet), is enlarged (Repenning and Tedford, 1977), and judging from their figures 23-26, plate 14, considerably more so than in the living walrus. It is equally significant that the middle Miocene "otarioid" (see below) *Allodesmus* appears to be characterized by a similar astragalar protuberance (see Mitchell, 1966, pls. 21 and 22). Hence the astragali seen in odobenids and *Allodesmus* seem at least to approach the hallmark phocid condition.

This similarity pertains to the calcanea of these forms as well. Typically in mammals,

and in all "fissipeds," when the astragalus and calcaneum are in articulation the calcaneal tuber extends far proximal to the astragalar head. This also tends to be the case in otariids but conversely in phocids the calcaneal tuber is shortened and projects posteriorly only as far as the process of the astragalus. Similarly, in odobenids and *Allodesmus* the calcaneal tuber is short and extends only slightly beyond the astragalar head (from Mitchell, 1966, pls. 21 and 22).

EVIDENCE SUPPORTING OTARIOID MONOPHYLY

The evidence presented above suggesting a phocid/odobenid relationship must be judged against that used to diagnose the traditional otariid/odobenid pairing. The characters uniting Otarioidea (odobenids and otariids plus their reported fossil allies)—taken from Repenning and Tedford's (1977) diagnosis (not intended as a cladistic definition) of the group—are listed below.

1. legs capable of being turned forward, used in terrestrial locomotion
2. neck lengthened
3. skull with mastoid process large and salient
4. skull with distinct alisphenoid canal
5. basal whorl of cochlea directed posterolaterally
6. anterior process of malleus present
7. no head developed on incus
8. internal acoustic meatus present
9. auditory bulla $\frac{3}{4}$ ectotympanic, entotympanic confined largely to formation of carotid canal
10. jugular process of exoccipital (=paroccipital process) fused to the mastoid
11. sexual dimorphism great

At first glance this might suggest rather strong support for otarioid monophyly. A closer examination reveals, however, that most of these features do not represent convincing evidence for this suggested relationship. The majority of these characters are primitive (i.e., they diagnose more inclusive groups) or are otherwise problematic and are, therefore, of little relevance to the question of relationship addressed here. A detailed evaluation of each of these features follows in the sequence presented.

1. *Legs capable of being turned forward.* This feature is primitive at least at the level of Tetrapoda. The phocid condition of the feet oriented posteriorly, represents the derived condition.

2. *Long neck.* King (1983, p. 156) noted that the length of the cervical vertebrae in phocids "is very little less than that of an otariid." This conclusion is supported by the work of Bisailon et al. (1976) who have shown that actually the neck of *Odobenus* is relatively shorter than that of most phocids. Moreover, a long neck is undoubtedly primitive for arctoids and probably primitive for carnivores (ibid., table 3). Therefore, a long neck cannot be used to support otarioid monophyly both because it is primitive for pinnipeds and because it does not occur in odobenids. In fact, a short neck might be viewed as evidence for a close odobenid/phocid relationship.

3. *Mastoid process large, etc.* Relative to other carnivores the mastoid is well developed in arctoids. It is particularly prominent in ursids but is also well developed in the majority of phocids. Against the greatly inflated phocid auditory bulla, however, the mastoid process may have the deceiving appearance of being smaller than that of otariids, but the two are often not greatly different in size. Due to the pachyostosis of the region in phocids, the mastoid process assumes a more rounded form than its angular condition seen in otariids. The mastoid process of the living walrus is greatly enlarged, but this is autapomorphic. The mastoid processes of the fossil odobenids *Imagotaria* and *Aivukus* are more typical; they are angular knobs much like those of ursids and otariids (see Repenning and Tedford, 1977). In ursids and other arctoids the mastoid process does not form a complete ventral ridge that extends back to the paroccipital process as it does in otariids and odobenids. A ridge joining the paroccipital and mastoid processes is present in the Miocene *Enaliarctos* (Mitchell and Tedford, 1973) (see section on fossils) and thus this condition may possibly be primitive for pinnipeds.

4. *Alisphenoid canal.* Although an alisphenoid canal is present in otariids and odobenids, it is also present in canids, ursids, a few procyonids, some viverrids, fetal felids,

and some fossil felidlike forms (nimravids), thus rendering the polarity of this character ambiguous (if not primitive) for the group in question.

5. *Posterolaterally oriented basal whorl of cochlea.* This is primitive for mammals. The transversely oriented basal whorl of phocids (Repenning, 1972) represents an autapomorphy of that group. In all pinnipeds the basal whorl of the cochlea is greatly enlarged in width and internal diameter. This expansion appears to be most marked in phocids and in odobenids (see Repenning, 1972, fig. 2). Interestingly, Repenning and Tedford (1977) point out that this modification in *Imagotaria*, a middle to late Miocene odobenid, is greater than in living otarioids and parallels that of phocids. [This implies, as does the astragalar feature discussed above, that *Odobenus* has secondarily reversed in some characters, or that *Imagotaria* is closer to phocids than is *Odobenus*.] Pending a quantified survey of carnivoran basal whorl volumes, inflation of the basal whorl can be regarded as a tentative odobenid/phocid synapomorphy.

6. *Presence of an anterior process of the malleus.* This is probably primitive for mammals and is certainly primitive for carnivores and is present in all "fissipeds." Its absence in phocids, again, is an autapomorphy.

7. *Lack of head developed on incus.* Once more, this is primitive for mammals. Within carnivores it is developed only in phocids.

8. *Presence of an internal acoustic meatus.* This is a mammalian feature. It is lacking, "properly speaking" (Gray, 1905), only in phocids, where the vestibulocochlear nerve enters the petrosal through a pit on its dorsal surface and the facial nerve enters through a separate canal lateral to this pit which represents the medial portion of the former internal acoustic meatus. (Vestiges of the lamina delimiting the roof of the former true internal acoustic meatus are clearly present in the three species of *Monachus*—see Repenning and Ray, 1977.) In otariids, as in other mammals, these nerves enter the petrosal through separate openings within a common depression, the "internal acoustic meatus." In odobenids, however, the internal acoustic meatus is wide and shallow and, as Repenning (1972, p. 326) notes, there is "almost complete separation between the canal

for the facial nerve and the fossa for the vestibulo-cochlear nerve." The otariid internal auditory meatus is also dorsoventrally flattened, but the degree of division between these nerves (although it occurs) does not appear to be as extreme. I agree with Repenning's conclusion (1972, p. 326) that the general condition of the odobenid meatus is "suggestive of a morphological stage between fissipeds and phocids." It follows that the complete or nearly complete separation of the entrances of cranial nerves VII and VIII within the acoustic meatus might be regarded as a phocid/odobenid synapomorphy (fig. 4). Moreover, a broad shallow internal auditory meatus with at least incipient division between cranial nerves VII and VIII appears to be a uniquely derived feature of pinnipeds—the completely divided phocid condition being the most extreme manifestation of this feature. A potential problem with this interpretation is that Repenning and Tedford's (1977) plate 10, figure 2 shows a latex mold of the dorsal basicranium of *Pontolis magnus*, a dusignathid odobenid, with what they interpret as a common opening for these two nerves. If this is not simply an artifact of preservation, it would argue that the separation between these nerves may have been independently acquired in phocids and odobenids. It is also noteworthy that the division between the passages for the facial and vestibulocochlear nerves is more extreme in the late Miocene odobenid *Aviukus cedrosensis* than in the living *Odobenus* (compare Repenning and Tedford, 1977, pl. 1, figs. 5, 7, and 9).

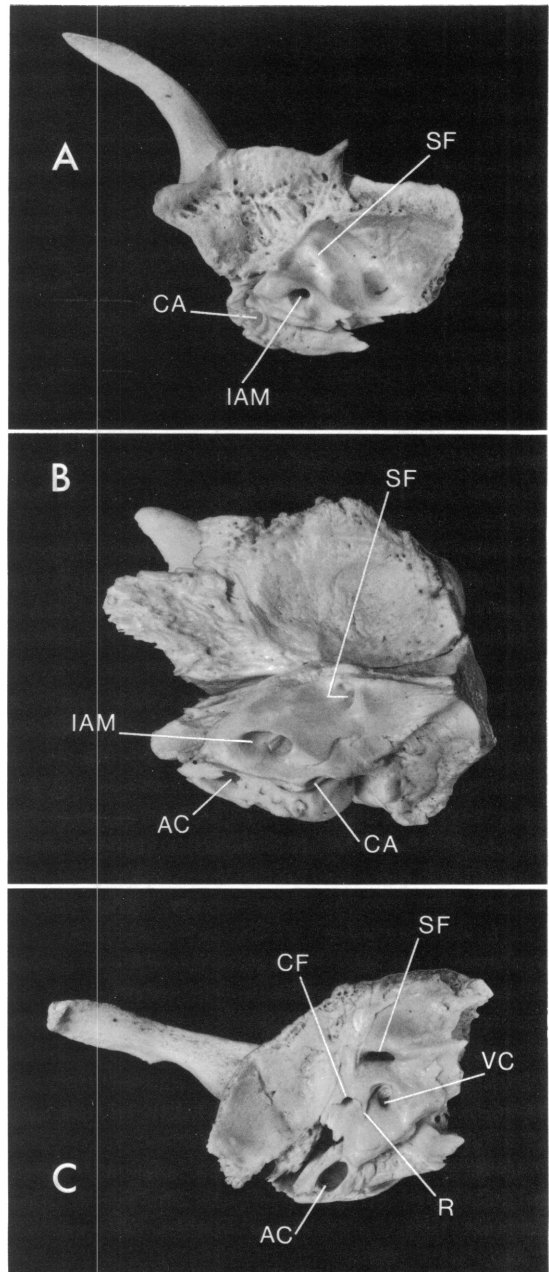
In *Potamotherium* the arrangement of cranial nerves VII and VIII within the internal auditory meatus and the shape of the meatus itself are decidedly primitive and unlike the condition seen in pinnipeds (personal observ.).

9. *Auditory bulla $\frac{3}{4}$ ectotympanic, etc.* This also pertains to ursids and closely agrees with what could be considered a primitive arctoid bulla. Moreover, it can easily be seen (particularly in posterior view) that the entotympanic of *Odobenus* is more inflated and makes a significantly greater contribution to the bulla than it does in ursids or otariids. In the walrus the ratio of contribution to the bulla of the entotympanic and ectotympanic is

closer to $\frac{1}{3}$ to $\frac{2}{3}$ with the entotympanic contributing slightly more to the bulla than simply forming the tube for the carotid artery as it does in ursids and otariids (personal observ.).

Phocids share with procyonids and some mustelids an enlarged caudal entotympanic. In phocids the entotympanic is usually pinched off posteriorly due to the presence of the external cochlear foramen, a feature unique to phocids, through which the round window opens external to the skull (Burns and Fay, 1970). However, in procyonids and mustelids the entotympanic is inflated and the bullar cavity, unlike that seen in phocids, extends well posterior of the promontorium. *Monachus schauinslandi*, which is in many respects the most primitive (i.e., could be considered the outgroup of the rest of the group) known bona fide phocid (Repenning and Ray, 1977), retains a bulla more wholly composed of ectotympanic and a less inflated caudal entotympanic. In addition, it displays a more posterior position of the caudal opening of the carotid canal, a condition also seen in *Mirounga*. In *Monachus*, especially, the posterior aperture of the carotid canal closely approaches the jugular foramen; this condition is seen in ursids, otariids, and odobenids and is primitive for arctoids. Several fossil forms that I suspect are close phocid allies are characterized by a very ursidlike (i.e., primitive arctoid) bulla (see below).

Whether or not the similarity between most phocids and procyonids plus some mustelids (exclusive of mephitines and lutrines) is regarded as a true synapomorphy, a strong case can be made that otariids and odobenids simply retain the primitive arctoid bullar configuration (e.g., Van Kampen, 1905). Further, if pinnipeds are regarded as monophyletic (see discussion below), then the phocid condition must be viewed as an autapomorphic, if convergently acquired, modification. Even if phocids are considered to be allied with mustelids (as McLaren, 1960; Tedford, 1976; and



C the complete separation of the entrances of nerves VII and VIII typical of phocids in *Monachus tropicalis*. AC = anterior opening of carotid canal, CA = opening of cochlear aqueduct, CF = canal accommodating facial (VII) nerve, IAM = internal auditory meatus, SF = subarcuate fossa, VC = fossa accommodating vestibulocochlear nerve. Anterior is to the left except in (C) where it is to the lower left. Approximately $\times 0.66$.

Fig. 4. Dorsomedial view of the right temporal regions showing A the internal auditory meatus in its undivided condition in an otariid, *Arctocephalus*, B its incipient division in *Odobenus*, and

de Muizon, 1982a, 1982b have suggested) then the condition seen in otariids and odobenids still does not support a close relationship between these two groups as it is primitive for arctoid carnivores.

As was noted above, the phocid bulla is inflated, often greatly. It is of some interest that the odobenid bulla is also (although only slightly) inflated; externally this inflation is obscured by expansion of the mastoid (Repenning, 1972). (This inflation does not approach that seen in *Monachus* or in other phocids however.) Possibly this is simply primitive in odobenids.

10. *Jugular process, etc.* This character was presented with the qualification that it does not strictly apply to odobenids. When fusion between the jugular process and the mastoid does occur in odobenids, it takes place only in old age (Repenning and Tedford, 1977). Moreover, the jugular process is commonly fused in other arctoids, therefore, I would question its significance.

11. *Sexual dimorphism.* This is also strongly manifest in the phocid *Mirounga*. Moreover, the dimorphism of the walrus has been cited as actually being reduced (see Stirling, 1975), as it is in some otariids, thus this feature, like many of the others discussed above, does not offer clear support for the monophyly of otarioids.

PINNIPED MONOPHYLY

Until this point I have largely avoided an idea that has gained considerable attention in recent years, namely the possibility of a diphyletic origin of pinnipeds (e.g., McLaren, 1960; Tedford, 1976; de Muizon, 1982a, 1982b). Proponents of this view hold that otariids (along with odobenids) and ursids form a clade, while phocids share a more recent common ancestry with mustelids. If this theory is correct, then the question of odobenid relationships does not simply reduce to whether walruses are more closely allied to seals or to sea lions, but to whether they are related to a group including ursids, or to a group including mustelids.

It is difficult to deny that pinnipeds are remarkably similar, that they are clearly distinct from other carnivores, and that they are uniquely modified among marine mammals.

There has been, however, a tendency among pinniped workers to overlook the profound morphological resemblances of these aquatic carnivores because of the assumed susceptibility of these features to convergence. Whether such extreme caution regarding potential convergent evolution is justified or not, the challenge to a systematist supporting monophyly has been to discover features uniting pinnipeds that cannot directly be construed as aquatic adaptations, or to discover features that might well be aquatic adaptations but are unlike those of other aquatic mammals.

As far as characters of the former category are concerned, there is an obvious difficulty here. Pinnipeds are so highly modified that there is scarcely an element of their anatomy that could be considered untouched by the potential effects of aquatic adaptation. From a phylogenetic standpoint, if one is willing to dismiss all such resemblances (including biochemical similarities, see below) as independently derived, the multiple origin (it needn't be only twice) of aquatic carnivores becomes an almost irrefutable proposition.

It must be kept in mind that a decision to accept convergence must be based on assumptions of relationship, that is, convergent characters can only be identified as such within the context of a phylogenetic arrangement specifying that the taxa in question are not in fact closely related. The central issue regarding diphyly reduces, therefore, to the following questions: How well has the relationship of phocids to some nonaquatic taxon been established? Does the evidence supporting such a relationship outweigh the otherwise overwhelming evidence for pinniped monophyly?

Although this study only tangentially addresses the issue of diphyly, in the interest of completeness, a discussion of the merits of this hypothesis is unavoidable. Although at this point I am not prepared to give an exhaustive treatment of the broader questions of pinniped relationships, I think it is useful to reiterate below some well-known characters [e.g., those of Doran, 1878 (numbers 1–5); and Repenning, 1972 (numbers 5–12)], others reported above, and one new character that may be regarded as supporting pinniped

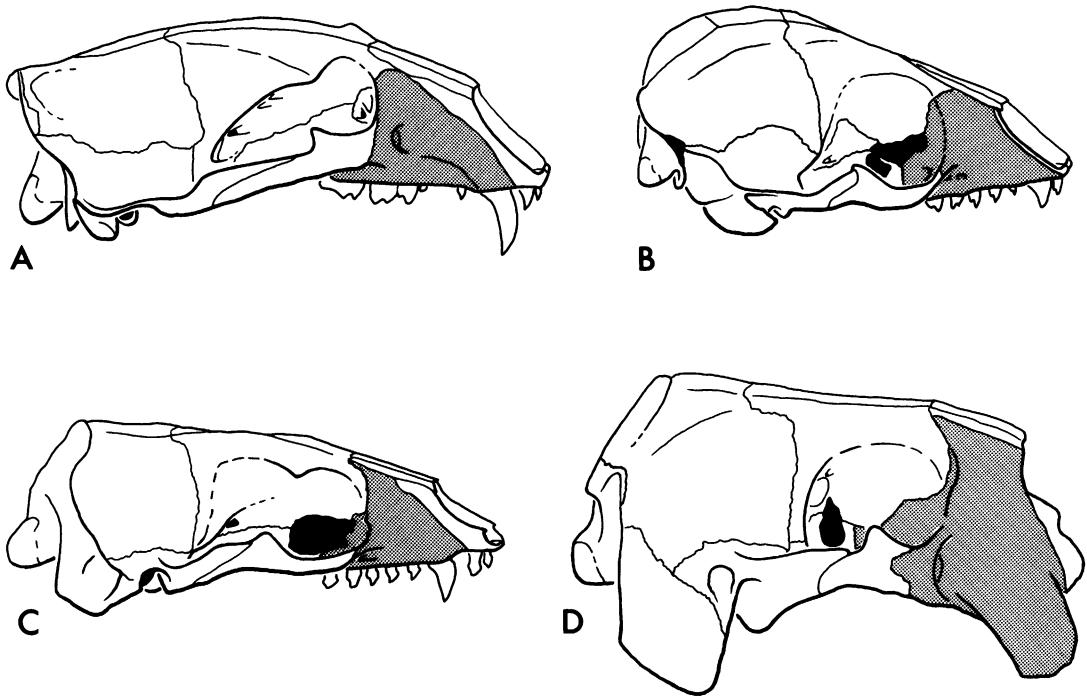


Fig. 5. Orbital regions representing **A** *Ursus* and the three families of extant pinnipeds: **B** *Phoca*, **C** *Zalophus*, and **D** *Odobenus*. Extent of maxilla marked by stiple; note its intrusion into the orbit in pinnipeds. 5B also displays the mortised jugal-squamosal contact typical of phocids, *Allodesmus*, and *Pinnarctidion*, reduced maxilla-nasal contact, and nasals penetrating frontals (compare with A, C, D: not to scale). Orbital vacuities are marked in black.

monophyly. (Additional features appear in the text.)

1. loss of muscular process on malleus (also in ursids)
2. reduction of processus gracilis and anterior lamina of malleus
3. tendency toward anterior concavity on malleolar head
4. marked ossification of stapes, stapedia foramen reduced or lost
5. malleolar manubrium shortened
6. isolation of petrosal from surrounding bones
7. jugular foramen (posterior lacerate foramen) greatly enlarged
8. round window large with development of round window fossula
9. basal whorl of scala tympani enlarged
10. large petrosal apex
11. lack of pit for insertion of tensor tympani
12. distensible cavernous tissue lining mid-

dle ear cavity and external auditory meatus

13. internal auditory meatus wide and shallow
14. lacrimal fuses to surrounding bones early, is greatly reduced, or absent; does not contact jugal
15. maxillary contribution to anterior orbital rim and orbital wall
16. cochlear aqueduct large (Fleischer, 1973)

Most of these have received ample discussion above, some are self explanatory, and three deserve further comment.

A striking osteological feature (that as far as I know has not been previously reported) common to all pinnipeds (including fossil forms, as far as can be ascertained) pertains to the geometry of bones contributing to the orbital region (fig. 5). In mammals the maxilla rarely makes a significant contribution to the bony mosaic forming the orbital wall; this

condition occurs in lipotyphlan insectivores, some primates, some edentates, proboscideans, hyracoids, lutrines, and sirenians. Typically, the maxilla is confined to the facial region and is excluded from contributing to the anterior orbital region by development of the lacrimal, palatine, frontal, jugal, or a combination of these elements. In its usual form the maxilla is limited in its posterior extent by contact of the jugal and lacrimal. Furthermore, the lacrimal in "fissipeds" invariably contacts the palatine.

In pinnipeds, on the other hand, the situation is quite different. Textbook accounts depict the lacrimal as being absent in pinnipeds and initially I considered this a synapomorphy for the group. But, as Wozencraft (personal commun.) has pointed out, this characterization is inaccurate and a lacrimal may in fact occur in some pinnipeds. This bone differs quite distinctly from that seen in other carnivores, however. King (1971) demonstrated the presence of a lacrimal in all extant otariid genera, but unlike the lacrimal in "fissipeds," it tends (with a considerable degree of variation) to fuse relatively early in ontogeny to the maxilla and frontal, thereby obscuring its presence. Although the lacrimal is present, it is small and in no otariid does it contact the jugal or palatine. Through the gap between the lacrimal and jugal, the maxilla laps over the anterior rim of the orbit, thereby making a small contribution to the medial orbital wall.

In the orbital wall of a juvenile walrus Gregory (1920, p. 157) identified "an apparent vestige of a lacrymal . . . represented by an extremely thin sliver of bone covering the maxillo-turbinals." I have observed a similar bone in several additional young specimens, but in later stages it appears to be overlapped by a downgrowth of the frontal so that no trace of it is left to external view. Given its unusual elongate form, its position deep within the orbit, and its coverage during ontogeny, it seems more likely to me that this element represents an orbital exposure of the ethmoid rather than a lacrimal. If a true lacrimal does occur in *Odobenus* it has not been seen by me and it must fuse to surrounding bones very early.

I am aware of only a single report of a lacrimal in a phocid, that of Kummer and

Nei (1957). These authors considered a small, thin ossification fused to the maxilla in the orbital wall of a fetal *Mirounga* (18 mm head length) as a possible lacrimal remnant. Therefore, if a lacrimal is indeed present in early ontogenetic stages of phocids, it is greatly reduced and fuses to surrounding bones exceedingly early. Needless to say, the phocid lacrimal(?) contacts neither the jugal nor the palatine. As do other pinnipeds (King, 1983), phocids lack a nasolacrimal foramen.

Within the walrus and phocid orbit, the maxilla and frontal form a broad suture; in these groups the maxilla makes a proportionally greater contribution to the orbital wall than it does in otariids. Nonetheless, the maxilla forming part of the anterior orbital rim and contributing to the orbital wall is a condition that is unusual among carnivores (see fig. 5). In lutrines the maxilla makes a contribution to the orbital wall and the jugal fails to meet the lacrimal. Otherwise the geometries of the bones comprising the orbital wall are not closely comparable in pinnipeds and lutrines. In lutrines the palatine continues to reach the lacrimal and the lacrimal is large and anteroposteriorly expanded relative to that seen in other mustelids. Likewise, the lacrimal of *Potamotherium* has been described as significantly expanded (Savage, 1957). Of the other eutherian taxa listed above as having significant maxillary contribution to the orbit, only in pinnipeds and proboscideans does this element actually lap over the anterior orbital rim.

Associated with the pinniped configuration of the maxilla is the presence of an unossified space (often termed the "orbital vacuity") in the ventral orbital wall near the juncture of the frontal, maxilla, and palatine bones (see fig. 5). This has the effect of significantly reducing the amount of contact between the frontal and palatine.

Another apparent synapomorphy of pinnipeds is a large round window; the round window fossula is prominent and serves to shield the secondary tympanic membrane from distensible cavernous tissue present in the middle ear cavity of these animals (Repenning, 1972). This fossula is absent in other carnivores except in *Potamotherium* and lutrines where a comparatively very shallow fossula is present (Tedford, 1976; personal

observ.). In these latter forms, however, the round window is not greatly enlarged (in *Potamotherium*, in fact, the round window is nearly equal to or smaller than the oval window). Typically in pinnipeds the round window area is approximately triple that of the oval window (Repenning, 1972). The round window of pinnipeds is expanded most in phocids but is very large in *Odobenus*. The oval window is also larger in the walrus and phocids than it is in otariids (ibid., table 1).

The tensor tympani of "fissipeds" originates from a small pit anterior to the oval window. In pinnipeds, however, this pit is lost and the muscle originates within the osseous Eustachian canal (Repenning, 1972). The pit for the tensor tympani is present in *Potamotherium* (Savage, 1957, p. 174; personal observ.) and in the early Miocene "otarioid" *Enaliarctos* (see below) (Mitchell and Tedford, 1973). In this character then, these two taxa depart from the condition typical of pinnipeds. As mentioned above, *Potamotherium* retains a large unfused lacrimal. *Enaliarctos* is also suspected of maintaining this element (Mitchell and Tedford, 1973, p. 220; but see also p. 261). Thus in this feature as well, these two taxa would appear to be excluded from a group including otariids, odobenids, and phocids.

In addition to the skeletal characters listed above, there are five nonanatomical lines of evidence supporting the monophyly of pinnipeds.

1. The newest and very compelling biomolecular evidence in favor of pinniped monophyly comes from the DNA hybridization work of Árnason and Widegren (1986). In a sample that included the three living pinniped families, as well as *Procyon*, *Ursus*, *Canis*, *Felis*, and several mustelids (including *Lutra*), it was found that pinnipeds shared four highly repetitive DNA components that occurred with identical length either uniquely among pinnipeds or in common with mustelids (with the exception of *Mephitis*). These results are extremely provocative and will almost certainly receive considerable attention over the coming years.

2. The eye lens protein, alpha lens crystallin A (de Jong, 1982), shows two amino acid replacements shared by phocids and otariids that are unique among vertebrates

(at position 51 proline for serine, at position 52 valine for leucine), and a third substitution (position 55 serine for threonine) common to pinnipeds, one of the two cetaceans sampled (*Phocoena*), *Ceratotherium*, and *Gallus* (*Odobenus* was not sampled). Furthermore, among carnivores, the mustelid *Mustela* and the procyonid *Bassariscus* share exclusively two amino acid replacements (at position 7 histidine to glutamine, and at position 61 isoleucine to valine); neither taxon shares a replacement common to any of the other carnivores investigated (*Canis*, *Felis*, *Melursus*, *Halichoerus*, *Zalophus*) (de Jong, 1986). Thus, these data are in accord with Tedford's notion of a procyonid-mustelid sister-group relationship but they do not support the inclusion of phocids within this clade. Note at this point that although DNA and amino acid sequence data agree on the monophyletic grouping of pinnipeds, they differ on the question of the affinities of this clade to other carnivores.

3. Hopkins (1949) argued (with ample supporting character information) that all three families of pinnipeds share closely related ectoparasites. In particular, they are parasitized exclusively by a tightly knit group of genera of the louse family Echinophthiiniidae (Kim, 1985). Hopkins (ibid., p. 546) regarded the extremely close relationship of the lice as "an exceedingly strong indication that the infestation is primary" (see also Kim, 1985). With the exception of the primary parasite of *Lutra canadensis*, *Latagophthirus*, which is the sister group of the pinniped louse *Antarctophthirus*, there is no indication that the lice of any particular pinniped are more closely related to the lice of any other carnivorous family than they are to those of other pinnipeds (other lutrines are infested by the ischnoceran *Lutridia*). McLaren (1960) argued that although *Antarctophthirus* is present on all three pinniped families, because it is absent on phocines plus *Monachus* and *Mirowonga*, it could be concluded that the genus has shown cross-infestivity between otariids and phocids. Therefore, he suggested (p. 21), that the "interchange of parasites was likewise possible in the past, and we cannot be sure that this peculiar group of lice was present in the ancestors of all the pinnipeds." Although interchange can never be ruled out,

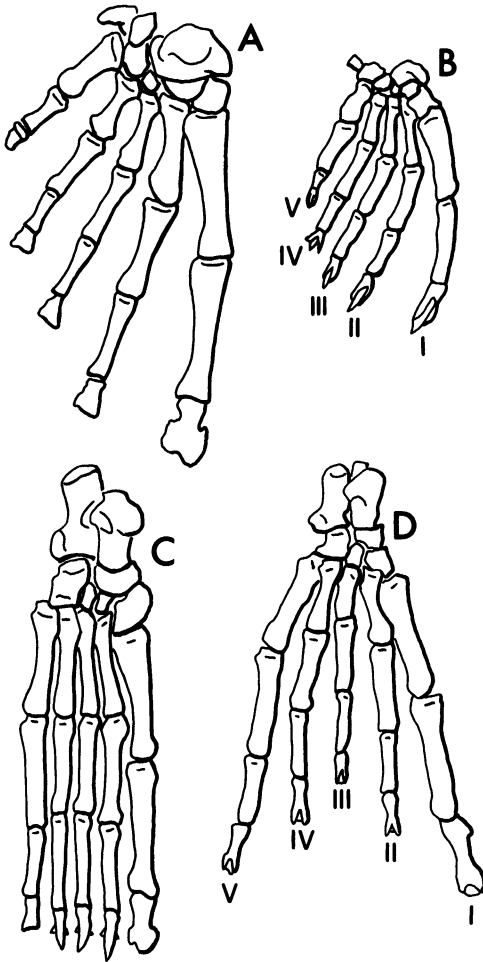


Fig. 6. Manus and pes of A, B *Monachus monachus* and C, D *Eumetopias jubatus* showing the emphasis of digit I in the pinniped manus and digits I and V in the pinniped pes. Digit III is the longest digit of both the manus and pes in *Potamotherium* (Savage, 1957) and in all other carnivores. Note in (D) the posterior process on the astragalar head and the atypical (for a phocid) rugose digit terminations (after de Blainville).

the monophyly of the group formed by these louse genera strongly argues for pinniped monophyly. McLaren's case could only be strengthened by a demonstration that otariid and phocid lice are each more closely related to the lice of different carnivoran families than they are to each other. This not being the case, and because this genus occurs in no other carnivores (Kim, 1985) these data can

only be construed as evidence for pinniped monophyly.

4. Karyology offers further suggestion of the monophyly of pinnipeds. Pinnipeds and other marine mammals are noted for their karyologic uniformity. Otariids have karyotypes of $2n = 36$, *Odobenus* 32, and phocids either 32 or 34; as a group pinniped karyotypes are extremely conservative in comparison to terrestrial carnivores (Fay et al., 1967; Arnason, 1974, 1977, 1981). Morphological, autoradiographic, and banding patterns argue strongly for the homology of pinniped chromosomes—and by implication the monophyly of the group (ibid.). The precise intrapinniped affinity of *Odobenus* based on karyological evidence is still disputed. Fay et al. (1967) concluded firmly that *Odobenus* was karyotypically intermediate between phocids and otariids, whereas Arnason (1974) perceived a greater correspondence between the karyotypes of otariids and phocids than between either and the walrus. Thus, although data support pinniped monophyly, as they pertain to question of walrus affinities, their phylogenetic utility is limited: clearly a strict cladistic treatment of this information is sorely needed.

5. The three pinniped families are also characterized by a unique bile acid. Phocaecholic acid ($3\alpha,7\alpha,23\xi$ -trihydroxy- 5β -cholan-24-oic acid) has been identified in *Odobenus* and the seven phocids and two otariids thus far examined. Although other mammals (including carnivores) have been well sampled, this acid is unknown "elsewhere in nature" (Haslewood, 1978, p. 112). Therefore, I would regard the presence of this acid as yet another character supporting pinniped monophyly (see also Deuel, 1955). [I am grateful to F. H. Fay (personal commun.) for alerting me to this information.]

These and numerous other features [e.g., suppression of the milk dentition homodonty, emphasis of digits I and V on the pes (fig. 6) (Weber, 1904), elongation of digit I on the manus (fig. 6), incorporation of tail and upper limbs within body wall, and the loss of musculature associated with hair (Scheffer, 1964)] should not continue to summarily be dismissed as "obvious" examples of convergence. Some of the attributes discussed above do occur in other aquatic mammals, but they

should, nevertheless, not be excluded from serious phylogenetic consideration. While we would do well to be mindful of the powers of convergent evolution, we should take care not to overestimate them either.

EVIDENCE SUPPORTING PINNIPED DIPHYLY

The evidence used by Tedford (1976) to include phocids within a clade comprising procyonids and mustelids (placing phocids specifically as the sister group of mustelids) included: (a) large caudal entotympanic, (b) hypotympanic cavity significantly extended behind promontorium, (c) posterior opening of carotid canal separated from posterior lacerate foramen, (d) paroccipital and mastoid processes widely separated, (e) alisphenoid canal absent, (f) postscapular fossa absent, (g) a dental formula of $M\ 1-2/2$.

Characters a, b, and c have been addressed above in the discussion of otarioid character 9. I would add only that Hunt (1974, p. 39) characterized the mustelid bulla as "more heterogeneous than [that of] other carnivore families." Among living carnivores, Hunt (1974, p. 44) regarded ursids, otariids, odobenids, and lutrine plus mephitine mustelids as sharing what he classified as his primitive (Type A) carnivore bulla. Thus to reiterate the discussion above, mustelids (if they can properly be considered a monophyletic assemblage) cannot be categorized as having an expanded caudal entotympanic and inflated bulla. At best this condition can be viewed as a derived similarity between phocids and a mustelid subgroup. Considering, however, the varying expressions of this feature among mustelids (contrast lutrines and mephitines to other members of the group) and phocids (contrast *Monachus* and other phocids), and given the construction of the bulla in what I consider to be close fossil allies of phocids (see below), I do not regard bullar morphology as solid evidence of a phocid-mustelid sister-group relationship.

The wide separation between the paroccipital and mastoid process (character d) in phocids is affected (in my opinion) by the general hypertrophy of the mastoid region and is quite unlike the condition seen in mustelids (see below). This character becomes even more

problematic (as do a, b, and c) if the walrus, with its very nonmustelidlike mastoid region, is accepted as the sister group of phocids.

In reference to the diagnosis of otarioids, the problem of the alisphenoid canal has been discussed on page 11. The postscapular fossa (f) is also absent, according to Tedford (1976, table 1) in otarioids. Within Carnivora, the fossa is present apparently only in ursids and procyonids (Davis, 1949). Its absence in pinnipeds renders it useless for supporting diphyly of this group. Regarding character g, it is generally agreed that for this particular phylogenetic problem, the significance of the dental formula is open to question. [The molar counts in otariids and procyonids are, respectively, $M\ 2/1$ and $M\ 1-2/2$ (Tedford, 1976), thus the $M\ 1-2/2$ condition does not uniquely diagnose a phocid + mustelid clade.]

In advocating pinniped diphyly, de Muizon (1982b) has gone as far as suggesting that phocids are the sister group of some lutrine mustelids. His argument rests largely on four characters: a perceived transformation of the suprameatal fossa, the method of swimming employed, the development of a "lutrine crest" on the upper premolars, and the flattening of the crest joining the mastoid and paroccipital processes. As his principal character, de Muizon (see his fig. 1, 1982b) envisioned a sequential transformation of the suprameatal fossa beginning with the fossa closed ventrally (defining his Musteloida = mustelids + phocids), its extreme reduction in lutrines (exclusive of *Enhydra* and *Enhydriodon*), and finally its closing in *Enhydra*, *Enhydriodon*, Semantoridae (including *Potamotherium*), and Phocidae. As evidence that phocids ever had a suprameatal fossa he noted the presence of a small depression in a juvenile *Leptonychotes* (Phocidae) that he suggested in morphology and position resembled the suprameatal fossa in *Mustela* and *Martes*. Thus, as de Muizon (1982b) suggested, the occurrence of what appeared to be a relictual suprameatal fossa in a juvenile seal was evidence that phocids have actually participated in the musteloid reductional trend of this fossa. Establishment of this condition in phocids is central to de Muizon's thesis because it is the single feature defining his group including Mustelidae and phocids.

As will be outlined below, I do not find de

Muizon's transformational argument to be compelling evidence for a close lutrine-phocid relationship. The small depression de Muizon identified in the juvenile phocid *Leptonychotes* (1982b, p. 265) as a suprameatal fossa can be seen from his figure 2c to reside completely within the posteroventral portion of the ectotympanic. In mustelids (including *Potamotherium*), on the other hand, the suprameatal fossa clearly lies within the roof of the external auditory meatus, part of the squamosal (see de Muizon's figs. 2a, 2b). Therefore, I cannot accept that the small pit in the specimen in question represents the homologue of the mustelid suprameatal fossa. Thus we are left (in my opinion) without evidence of the presence of this fossa in any phocid.

Since one can never be assured that an assumed "loss" character was ever present to be lost in the first place, the use of such characters always involves a certain degree of uncertainty. This is particularly true in a case such as the one presented here, where a phylogeny is based almost exclusively on such a character.

If one insists on accepting the structure seen in the above juvenile *Leptonychotes* as a suprameatal fossa, one must equally accept the homology between the mustelid structure and the distinct pit posterior to the medial aperture of the external auditory meatus seen in adult otariids (e.g., *Zalophus*, personal observ.). This pit in *Zalophus* corresponds more closely to the mustelid suprameatal fossa in position (in the squamosal) and is more greatly developed than the "suprameatal fossa" described for *Leptonychotes*. In my opinion the presence of a suprameatal fossa in phocids and its established absence in other arcetids needs to be more adequately demonstrated before it should be considered a valid phocid-mustelid synapomorphy.

De Muizon's second character concerns the mode of swimming of phocids and the sea otter; I have pointed out above that hind limb propulsion is also common to the walrus. One might wish to consider this feature a synapomorphy of a group including *Odobenus*, phocids, and *Enhydra*, but I should point out that such an arrangement faces massive character contradiction. When other characters are taken into consideration it is vastly more

parsimonious to consider the hind limb propulsion in *Enhydra*, and in the group *Odobenus* plus phocids, to be independently derived.

A third character uniting lutrines and phocids concerns the development of a "lutrine crest" on P4 joining the paracone and "protocone" near the anterior margin of the tooth. By de Muizon's own account, however, this feature is lost or greatly reduced in *Enhydra*, *Enhydriodon*, and in most phocids. As far as phocids are concerned, the crest has only been identified in the fossil *Properiptychus* (see de Muizon's fig. 3f). The distinctness of this crest is not clear from this illustration, however. (On a P1 or P2—fig. 4 of de Muizon—of the same genus, this crest is more apparent, but unlike its anterior placement on P4 of *Potamotherium* and *Lutra*, it occurs medially.) At this point (even if the crest were present on the P4 of this single phocid) this character does not convincingly cojoin phocids and mustelids.

The fourth character reported by de Muizon concerns the configuration of the mastoid region. Mustelids (exclusive of melines and leptarctines) and phocids were described as being characterized by the loss of the crest joining the mastoid and paroccipital processes and the formation of a posterolaterally oriented concave shelflike surface in this region. In my view, the shortcoming of this feature is related to the fact that its form in phocids is highly modified and is thus not strictly comparable to the mustelid condition. In most phocids the mastoid region is greatly expanded and pachyostotic. As a result, in these the presumed primitive broad shelf condition of phocids has been obliterated and, again, a character cited as uniting phocids and some mustelids, for all intents and purposes goes unseen in phocids. In the three modern species of *Monachus*, the only phocids that bear a remote resemblance to the mustelid condition of a flattened concave surface of the mastoid, the region is quite differently constructed. In the mustelids where a shelf is present, it is formed almost exclusively of the mastoid with the paroccipital process of the exoccipital making only a minute posterior contribution. In *Monachus*, however, a distinct crest joining the paroccipital and mastoid processes (of which the

entire posterior half is formed by the exoccipital) is present. The anterior half of the crest does not closely approximate the smooth area seen in mustelids nor is the broad posterolaterally directed mastoid shelf of mustelids clearly developed in *Monachus* (or in any phocid for that matter). In all remaining phocids the mastoid (as was described above) is greatly inflated and decidedly not mustelid-like in form; hence, I remain somewhat doubtful about the significance of this comparison.

De Muizon offers several other predominantly postcranial characters (see characters 17–25 in his fig. 1) that are used to ally specifically phocids, *Potamotherium*, and *Semantor* (a poorly known genus that is generally considered to resemble closely *Potamotherium*). These characters will be addressed in a later paper. At this point, however, given the less than satisfactory placement of phocids as highly modified members of a “musteloid” clade, and given the preponderance of evidence supporting pinniped monophyly, I consider these characters of questionable significance.

My objections aside, if the above characters are taken at face value, it appears that the evidence supporting de Muizon's argument for a phocid-lutrine linkage is not nearly as strong as that supporting the close relationship of phocids and odobenids advocated here. It should also be stressed that if a phocid-walrus pairing is accepted, present evidence would not accommodate the uniting of phocids plus odobenids and mustelids; as currently framed the two hypotheses (phocids + walrus, and phocids + mustelids) appear to be mutually exclusive. Similarly Tedford's (1976) more general case for a phocid-mustelid pairing does not present a strong alternative to the relationship suggested here. Thus, the current case for a mustelid-phocid linkage is not strongly founded and, in my view, the burden of proof lies on those wishing to demonstrate diphyly.

Regarding the question of which carnivore family represents the nearest pinniped ally, I simply wish to point out one feature alluded to in the earlier discussion of ear ossicle morphology: pinnipeds share with ursids the lack of a muscular process on the malleus. Obviously this is extremely meager

evidence and I offer it simply as an interesting character. The question of the relationship of pinnipeds to other carnivores is much in need of review and all that can presently be said with any degree of assurance is that pinnipeds are arctoids. Even so, the lack of this process nicely corroborates Weber's (1904, p. 551) prudent observation that: “Ein zusammenhang der Pinnepedia mit den Ursidae is wohl die gesichertste Annahme.”

FOSSIL EVIDENCE

The claim could be made that the inclusion of fossil data would weaken the phylogenetic conclusions offered here. It appears, however, that information from fossils corroborates rather than refutes the central theme of my argument, namely that phocids and odobenids are closely allied.

In the case of the lack of a supraorbital process, for example, it can be argued the desmatophocines (sensu Repenning and Tedford, 1977) and at least some enaliarctines (both alleged primitive otarioids) also lacked distinct supraorbital processes and that, therefore, primitively this process was also lacking in otariids. This may be so, but if one examines shared derived attributes there appears little that would preclude the allocation of many of these suspected primitive otarioids to a group more closely allied to phocids. I suspect that desmatophocids and at least some enaliarctines are actually members of the phocid-odobenid grouping or are indeed (depending on how one chooses to define it) members of the phocid lineage itself. A review of several cranial features substantiates this view.

In addition to the lack of a supraorbital process, desmatophocids are distinguished (Repenning and Tedford, 1977) by nasals penetrating the frontals (fig. 5B), a posteriorly broad palate, and a mortised jugal-squamosal contact (fig. 5B), features common to phocids as well. Furthermore, features of the best known desmatophocid, *Allodesmus*, include: enlarged ear ossicles (“the incus and malleus are about five times more massive than are those of any otariid,” Mitchell, 1966, p. 6), a broad basioccipital widening posteriorly, a short contact between the dorsal process of the premaxillae and the nasals, and a wide sep-

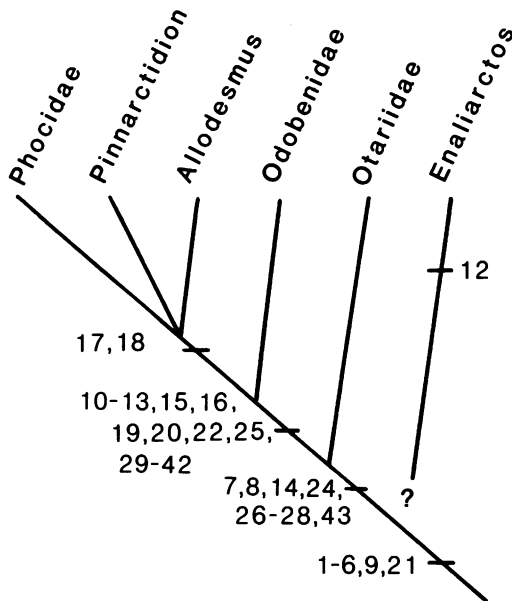


Fig. 7. Cladogram depicting the phylogenetic relationship of pinnipeds advocated here (characters appear in table 2).

aration between the canals for the vestibulocochlear and facial nerves (Mitchell, 1966; Barnes, 1972; Repenning and Tedford, 1977). (In fact: "One specimen of *Allodesmus*, UCMP 83363, has an almost phocidlike separation of the facial canal from the vestibulocochlear fossa," Repenning and Tedford, 1977, p. 11.) As discussed above, this latter set of features is judged here to comprise phocid-odobenid synapomorphies.

The type species of the Enaliarctinae (Mitchell and Tedford, 1973) *Enaliarctos mealsi*, and *Pinnarctidion bishopi* (Barnes, 1979) are the only enaliarctines described from relatively complete cranial material. Both taxa lack a distinct supraorbital bar; *Pinnarctidion*, at least, displays several features suggestive of phocid-odobenid affinities. These include inflation of the auditory bulla, a very wide subarcuate fossa (fossa cerebellaris), and a division between the openings of the canals for the vestibulocochlear and facial nerves. It is also of note that the paroccipital and mastoid processes of *Enaliarctos* are relatively widely separated (from fig. 5 of Mitchell and Tedford, 1973) and "they are connected by a strong but narrow

ridge of bone bearing a shallow depression ventrally" (ibid., p. 228). In *Pinnarctidion* the two processes appear to be even more greatly separated (although they are connected by a crest) and the shelf joining them is much more broadly developed (Barnes, 1979). *Pinnarctidion* also displays the mortised jugal-squamosal articulation on the zygomatic arch typical of all phocids (see Barnes, 1979, figs. 6, 7). As in phocids, but unlike otariids and odobenids, the palate of *Allodesmus*, and to a lesser degree, that of *Pinnarctidion*, widens posteriorly. Given the wide distribution of a posteriorly broad palate among carnivores, this feature is most likely a primitive feature for the order, but if the phylogenetic scheme advocated here is correct (fig. 7) then the parallel condition seen in ursids, otariids, and odobenids would dictate that the broad condition of some pinnipeds is secondarily derived.

Enaliarctos is known from nearly complete skeletal material and is currently being described (Berta, in prep.). Given our current scant knowledge of *Enaliarctos* morphology I have marked its placement in figure 7 as the sister group of the remaining pinnipeds with a query. This arrangement is suggested by the retention of the fossa for the tensor tympani and the primitive condition of the lacrimal (Berta, personal commun.). If *Enaliarctos* is, in fact, more firmly established to represent the sister group to the remaining pinnipeds, this poses an ambiguity in the character "lack of supra-orbital process"; either its absence characterizes pinnipeds and a reversal occurs in otariids, or it has been lost independently in *Enaliarctos* and "phocoids." Clearly, more complete knowledge of *Enaliarctos* and its allied forms will shed much light on our understanding of higher-level pinniped relationships particularly in establishing character polarity among other aquatic arctoids.

Considering one additional point, the construction of the auditory bullae of *Allodesmus* and *Pinnarctidion* agrees with what I have regarded above (point 9) as the primitive phocid condition, and does not contradict my allocation of these genera to a group including odobenids plus phocids. The bulla of these forms is characterized by a posterior placement of the caudal opening of the carotid

canal and, apparently, by an only slightly inflated entotympanic. This is in agreement with my suggestion that the expansions of the entotympanic in phocids and some mustelids are independent derivations. A complete distribution of the characters discussed above is presented in table 2.

Finally, in establishing the affinities of these fossil forms (as was the case for characters related to pinniped monophyly), I wish to warn against the a priori consideration of any character as necessarily convergent. I would urge that presumed "otarioids" displaying phocid attributes (i.e., mortised jugal-squamosal contact, nasals penetrating frontals, narrow premaxilla-nasal contact, enlarged ear ossicles) be compared seriously against phocids. These resemblances can only accountably be dismissed as convergent if the allocation of these taxa to an "otarioid" grouping can be defended with an alternative set of shared derived characters.

CONTRADICTIONARY EVIDENCE

So as not to provide a lopsided account, I present below several features which are potentially incongruent with the phylogenetic alliances advocated here. In my opinion, of course, these characters do not offer as strong a case for otarioid monophyly as do those discussed above supporting a walrus-phocid sister-group relationship.

1. *Flipper morphology* (King, 1983; personal observ.). The phocid foreflipper may be rather box shaped (phocines) or elongate (most monachines), with the elongation being achieved by an increase in size of the first digit and a diminution of the fifth. In its elongated form, the claws of the foreflipper are usually reduced. In otariids the foreflipper is greatly elongate, the claws are reduced, and long cartilaginous rods distal to each digit support an extension of the flipper border. The walrus foreflipper is short and very nearly square, the claws are reduced, and short cartilaginous extensions are present. As mentioned in a preceding section, digits I and V form the two longest of the pinniped hind flipper. Claws are present on all digits but may be greatly reduced. In otariids the two outer claws are greatly reduced; the middle three are long and used for grooming. As in

the foreflipper, cartilaginous extensions are present. The claws of the *Odobenus* hind foot are reduced (the outer two slightly more so) and short cartilaginous extensions are present. It would appear then, that cartilaginous extension of the digits might represent a otariid-odobenid synapomorphy. Importantly, the distal end of the ungual phalanges of *Alloidesmus* are blunt and rugose for the attachment of cartilaginous extensions (Mitchell, 1966, p. 15). The unguals of the tarsus of *Monachus* are relatively blunt and extremely rugose but they are not marked distally by an articulation surface for a cartilaginous rod. King (1969) reported the occurrence of cartilaginous extensions in the phocid *Ommatophoca* and suggested their probable existence in *Hydrurga* as well. Thus it seems conceivable that the primitive pinniped flipper was approximated by that of the walrus (short cartilaginous extensions present), that in otariids with their emphasis on forelimb propulsion these extensions have become greatly elongate, and that in phocids with their emphasis on hind limb propulsion the extensions have become secondarily lost. The discovery of "enaliarctine" ungual phalanges would prove most useful for settling the choice between these two alternatives. Also related to this matter is Howell's (1929) observation that in *Zalophus* the terminal digital cartilages of the pes appear to undergo reduction during ontogeny, being relatively more poorly developed in adults. This observation is included in Howell's more general, admittedly conjectural, concluding remarks in the context of his notion that phocids may have undergone some form of "retrogressive evolution." I believe that this idea holds some degree of merit and is certainly worthy of reexamination.

2. *Closure of subarcuate fossa*. The subarcuate fossa is a posteriorly situated pit on the dorsal surface of the petrosal that houses the parafllocculus of the cerebellum. The fossa is rather broad and deep in ursids, phocids, *Potamotherium*, juvenile lutrines, and juvenile otariids. In contrast, this excavation is largely filled in by bone in adult otariids, odobenids, adult lutrines, mustelids, and procyonids. Thus, although the closure of the subarcuate fossa in otariids and odobenids is unique among pinnipeds, this feature is widespread

TABLE 2

Distribution of Morphologic Features Discussed in Text

Symbols: 0, primitive; +, derived; 2, intermediately derived; ?, unknown; 9, known but undescribed.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Ursidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0
Otariidae	+	+	+	+	+	+	+	+	+	0	0	0	0	+	0	0	0	0	0	0	+	0
<i>Enaliarctos</i>	+	+	+	9	9	+	0	+	?	0	0	+	?	9	?	?	0	0	?	9	9	0
<i>Odobenus</i>	+	+	+	+	+	+	+	+	+	+	2	+	+	+	?	2	0	0	+	+	+	+
<i>Allodesmus</i>	+	+	+	+	+	+	+	?	?	+	2	+	+	9	+	2	+	+	?	9	?	+
<i>Pinnarctidion</i>	+	+	9	9	9	+	+	?	9	+	2	+	?	9	?	2	2	+	?	9	?	?
Phocidae	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

1. isolation of petrosal from surrounding bones
2. jugular foramen greatly enlarged
3. round window large with development of round window fossula, larger still among living forms in *Odobenus* and Phocidae
4. internal auditory meatus wide and shallow
5. basal whorl of scala tympani enlarged
6. large petrosal apex
7. lack of pit for origin of tensor tympani
8. lacrimal fuses early, greatly reduced or absent, does not contact jugal or palatine
9. cochlear aqueduct large
10. epitympanic recess large
11. inflated auditory bulla
12. large supraorbital process absent
13. basioccipital broad, widened posteriorly
14. distensible cavernous tissue lining middle ear cavity and external auditory meatus
15. premaxilla-nasal contact reduced
16. division between canals for vestibulocochlear and facial nerves
17. posterior widening of palate
18. mortised jugal-squamosal contact
19. pinnae absent
20. merging of canal for cochlear aqueduct with round window
21. loss of muscular process on malleus
22. ear ossicles enlarged

among arctoids and is therefore of doubtful systematic importance here. Moreover, the appearance of a large subarcuate fossa in both the Mio-Pliocene otariid *Thalassoleon* and the Miocene odobenid *Imagotaria* (Repenning and Tedford, 1977) casts further doubt on the significance of this apparent contradiction.

3. *Reduction of tentorial ossification.* Carnivores are characterized by an intracranial osseus lamina (ossified tentorium) which serves to divide the cerebrum from the cerebellum. Typically (including otariids and odobenids) the ossified region is strongly developed and broadly contacts the petrosal along its dorsolateral edge. In phocids the tentorial ossification is only weakly developed and does not reach the petrosal. In some

mustelids the lamina is greatly reduced (e.g., *Mephitis*, *Conepatus*) but is broad or moderately broad in most (e.g., *Taxidea*, *Lutra*). Thus, this character shows a high degree of variability within Arctoidea and I would not regard it as strong evidence of a phocid-mustelid relationship.

CONCLUSION

As the most efficient summary of the data presented above, I offer the following cladogram of the major pinniped subdivisions (fig. 7). In this branching scheme Otariidae and *Enaliarctos* are regarded as the unresolved sister groups of the remaining pinnipeds, an assemblage which includes *Allodesmus*, *Pinnarctidion*, and true phocids. This arrange-

TABLE 2—(Continued)

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Ursidae	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Otariidae	+	+	0	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+
<i>Enaliarctos</i>	9	9	9	9	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	9	?
<i>Odobenus</i>	+	+	+	+	+	+	+	+	+	2	+	+	+	+	+	+	+	+	+	+	+
<i>Allodesmus</i>	9	9	9	9	?	+	?	?	?	2	?	?	2	0	+	?	?	?	?	9	+
<i>Pinnarctidion</i>	?	?	?	?	?	+	?	?	?	?	?	?	?	?	?	?	?	?	?	+	?
Phocidae	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

23. reduction of processus gracilis and anterior lamina of malleus
 24. tendency toward anterior concavity on malleolar head
 25. articulation surface on malleolar head figure 8 in shape
 26. malleolar manubrium shortened
 27. maxilla makes significant contribution to orbital wall and forms anterior orbital rim
 28. unossified region in ventral orbital wall (orbital vacuity)
 29. reduced deciduous dentition
 30. inguinal testes
 31. inflated hepatic sinus, well developed caval sphincter, large intervertebral sinus, duplicate posterior vena cava, gluteal route for hind limb veins
 32. specializations of vertebral column (see text)
 33. hind limb propulsion, hind flippers rotate during powerstroke, on land limbs do not support body weight, development of posterior process on astragalar head, shortening of calcaneal tuber
 34. aquatic copulation
 35. large baculum
 36. cartilaginous extension of manubrium
 37. sparse pelage (* postulated for *Allodesmus*, see Mitchell, 1966, p. 22)
 38. lack of grooming
 39. proximal position of sweat duct orifice
 40. nonmedullated primary hairs
 41. thick layers of subcutaneous fat
 42. large oval window
 43. emphasis of digit I on manus and digits I and V on pes

ment greatly diminishes the currently recognized morphological gap between true phocids and any of the groups that could be regarded as their closest allies.

I have not overlooked the biogeographic ramifications of this branching scheme (the North Pacific is generally considered to be the "otarioid" center of origin while phocids are thought to be an Atlantic group). At this preliminary juncture, however, other than to point out that the data presented here suggest a somewhat different division (with primitive "phocoids"—odobenids, *Allodesmus*, and *Pinnarctidion*—being Pacific and phocids representing an Atlantic offshoot with an ancestry somewhere within "allodesmines + dematophocines") I do not wish to elaborate further.

Although there is currently an overabundance of competing arrangements, I have refrained from proposing a formal classification of pinnipeds both because of the preliminary nature of this study and because I see no point in debating the appropriate ranks of various monophyletic groupings. All essential classificatory information can efficiently be conveyed with a cladogram.

I fully expect critics to argue that many of the specializations cited here in support of a phocid-odobenid relationship are merely convergences related to aquatic life, or to put it another way, simply adaptations related to being more aquatic than otariids. Anticipating such claims I offer in my defense the distribution of these features. As I have pointed out, many of the derived characters described

here are unique among marine mammals. Even those that are not (but consistently link the same two pinniped families) are not automatically invalidated as synapomorphies by their appearance in cetaceans or sirenians. If such characters were, in fact, so prone to convergence as to be of dubious phylogenetic significance, one would expect their occurrence in all three pinniped families (rather than just two). For example, I would place little confidence in the character "fusiform body shape" to define Pinnipedia (as it occurs in all aquatic mammals) but I see no rationale for disregarding such characters as "loss of pinnae" or "greatly enlarged malleolar head," or "inflated incus" as valid phocid-walrus synapomorphies. No functional or ecoadaptive scenario alters the fact that all other carnivores and otariids retain pinnae and small ossicles while phocids and the walrus do not. I oppose the notion that the appearance of such features is necessarily convergent.

Although this is by no means an exhaustive treatment, I have offered a suite of characters that need to be addressed in future considerations of pinniped relationships. If nothing else, this analysis highlights the inadequacy of the evidence currently used to support the traditional otariid/odobenid pairing and the widely accepted notion of the diphyly of pinnipeds; for proponents of those views who remain unconvinced by my arguments, it is hoped that this will encourage them to more amply support theirs. As I have shown, rather than supporting the relationship of the walrus and otariids, many characters suggest the close alliance of phocids and odobenids. Judging from the evidence presented here, one would predict that data from morphologically broader and phylogenetically more diverse surveys of pinniped anatomy would bolster the case for the grouping of odobenids and phocids rather than yielding support for the customary pairing of odobenids and otariids. In either event, this investigation points to the urgent need for a detailed review (including careful attention to character polarity determination) of anatomical features pertinent to our understanding of the relationships of the major groups of Recent and fossil pinnipeds. Through such studies, insights into the broader notions of carnivore phylogeny will also be gained. I also wish to emphasize

that the mutual relationships of given taxonomic units are not refuted by demonstrations of differences between them. In the example presented here, it is quite clear that phocids are extremely divergent morphologically and that phocids and odobenids are phenetically quite dissimilar; this, however, does not preclude their close relationship. In closing I wish to note the prescient summing discussion of *Odobenus* by Fay et al. (1967, p. 777): in its morphology and behavior (as in its karyotype) "the walrus resembles the phocids in some ways and the otariids in others and is in some respects intermediate between the two. Taxonomists have generally disregarded or deemphasized the intermediate and phocoid characters in order to stress their view that the walrus is little more than a specialized otariid [references]. We feel that our cytogenetic evidence does not support that view but is suggestive of a more nearly intermediate position between the Phocidae and Otariidae." In my opinion, systematists have been misled in their conventional grouping of otariids and odobenids by being overly impressed by the shared primitive retentions in several anatomical regions of these two groups while overlooking the apomorphies common to phocids and *Odobenus*. It is shared derived characters, however, that offer the only valid clues to phylogenetic affinities.

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APPENDIX

List of specimens examined. During the course of this investigation most of the pinniped collection of the Department of Mammalogy at the AMNH was at least cursorily examined. However, particular attention was paid to the specimens listed here (including nonpinnipeds). Abbreviations: AMNH, American Museum of Natural History; MNHN, Muséum National d'Histoire Naturelle; VP, Vertebrate Paleontology.

Odobenus rosmarus

- AMNH 203342, skull (juvenile)
207763, skull
182091, skull, skeleton (juvenile)
42121, skull, incus
183134, skull, malleus, incus
164218, skull
73304, skull, malleus
2995, skull

Monachus tropicalis

- AMNH 35354, skull
77741, skull, skeleton

M. monachus

- MNHN (uncataloged), incus, malleus

Phoca (?)

- AMNH 100379, skull, incus, malleus
202195, skull, skeleton

P. vitulina

- MNHN (uncataloged), incus, malleus

P. (=Pagophilus) groenlandica

- MNHN (uncataloged), incus, malleus, stapes

P. (=Pusa) hispida

- MNHN (uncataloged), incus, malleus, stapes

- Cystophora cristata*
 MNHN (uncataloged), incus, malleus, stapes
 AMNH 108, skull
- Homiphoca capensis*
 MNHN (uncataloged), incus, malleus, stapes
- Halichoerus grypus*
 MNHN (uncataloged), incus, malleus, stapes
- Lobodon carcinophagus*
 AMNH 202194, skull, incus, malleus
 MNHN (uncataloged), incus, malleus, stapes
- Leptonychotes weddelli*
 MNHN (uncataloged), squamosal, ecto-tympenic (juvenile)
 (uncataloged), incus, malleus, stapes
 AMNH 232563, skull
- Hydrurga leptonyx*
 MNHN (uncataloged), incus, malleus, stapes
 AMNH 36200, skull, skeleton
- Erignathus barbatus*
 AMNH 98, skull, incus, malleus, stapes
 MNHN (uncataloged), incus, malleus
- Mirounga angustirostris*
 AMNH 77930, skull, skeleton
- Callorhinus ursinus*
 AMNH 42263, skull, incus, malleus, stapes
- Arctocephalus* sp.
 AMNH 202490, skull, skeleton
 202540, skull, skeleton
- Zalophus californicanus*
 AMNH 5514/6854, skull, incus, malleus, stapes (juvenile)
 AMNH 201339, skull, malleus
- Eumetopias jubatus*
 AMNH 42263, malleus, stapes
 21536, skull
- Otaria byronia flavescens*
 AMNH 205919, skull
- Lutra canadensis*
 AMNH 15978, skull
 202999, skull
- L.* sp.
 AMNH 201214, skull
 MNHN A1924, skull (juvenile)
 A1898, incus, malleus
- Pteronura brasiliensis*
 MNHN A1916, incus, malleus
- Enhydra lutris*
 MNHN A1919, incus, malleus
- E. lutris lutris*
 AMNH 215275, skull, skeleton (juvenile)
- Aonyx* sp.
 MNHN A1899, incus, malleus
- Potamotherium* sp.
 AMNH(VP) 22520, posterior skull
 MNHN 56690, ear region
- Galictis* sp.
 MNHN A1929, incus, malleus, stapes
- Mephitis* sp.
 AMNH 201674, skull
 27 (VP teaching collection #), skull, incus, malleus, stapes
- Martes* sp.
 MNHN A1940, incus, malleus
- Taxidea taxus*
 AMNH 5495, skull
 MNHN A1955, incus, malleus
- Spilogale*
 AMNH 202979, skull
- Conepatus* sp.
 AMNH 14632, skull
- Felis pardalis* (?)
 AMNH 14703, skull, incus, malleus, stapes
- Felis catus*
 AMNH 15 (VP teaching collection #), skull
- Canis* sp.
 AMNH 200277, skull, incus, malleus
 88, skull
- Ursus* sp.
 AMNH 202886, skull
- U. americanus*
 AMNH 28474, skull (juvenile)
- U. maritimus*
 AMNH 19259, skull, malleus

U. thibetanus

AMNH 201981, skull, skeleton, incus,
malleus

Potos sp.

AMNH 201175, skull, incus, malleus

Procyon sp.

AMNH (VP teaching collection, uncata-
loged), skull, incus, malleus
AMNH 202971, skull

Ailurus fulgens

AMNH 202365, skull

Elephas maximus

AMNH 44, skull

Mesoplodon grayi

AMNHCA 200117, ear region

Trichechus inunguis

AMNH 200528, skull, incus, malleus,
stapes

T. manatus

AMNH 30, skull

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