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RE-EVALUATION OF MORPHOLOGICAL CHARACTERS QUESTIONS CURRENT VIEWS OF PINNIPED ORIGINS

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Koretsky, I. A., Barnes, L. G., Rahmat, S. J. — The origin of pinnipeds has been a contentious issue, with opposite sides debating monophyly or diphyly. This review uses evidence from the fossil record, combined with comparative morphology, molecular and cytogenetic investigations to evaluate the evolutionary history and phylogenetic relationships of living and fossil otarioid and phocoid pinnipeds. Molecular investigations support a monophyletic origin of pinnipeds, but disregard vital morphological data. Likewise, morphological studies support diphyly, but overlook molecular analyses. This review will demonstrate that a monophyletic origin of pinnipeds should not be completely accepted, as is the current ideology, and a diphyletic origin remains viable due to morphological and paleobiological analyses. Critical examination of certain characters, used by supporters of pinniped monophyly, reveals different polarities, variability, or simply convergence. The paleontological record and our morphological analysis of important characters supports a diphyletic origin of pinnipeds, with otarioids likely arising in the North Pacific from large, bear-like animals and phocids arising in the North Atlantic from smaller, otter-like ancestors. Although members of both groups are known by Late Oligocene time, each developed and invaded the aquatic environment separately from their much earlier, common arctoid ancestor. Therefore, we treat the superfamily Otarioidea as being monophyletic, including the families Enaliarctidae, Otariidae (fur seals/sea lions), Desmatophocidae, and Odobenidae (walrus and extinct relatives), and the superfamily Phocoidea as monophyletic, including only the family Phocidae, with four subfamilies (Devinophocinae, Phocinae, Monachinae, and Cystophorinae).

Key words: Pinnipeds, evolution, adaptation, phylogeny, morphology.

Introduction

The evolutionary history and phylogenetic relationships of the otarioid Pinnipeds (the living fur seals, sea lions, walrus and their extinct relatives) and phocoid Pinnipeds (the living and fossil true seals) were surveyed using evidence from the fossil record combined with reviewing comparative morphological, molecular and cytogenetic investigations.

As recently as 1960 (e. g. McLaren, 1960 a, 1960 b), the meager fossil record of pinnipeds created only speculative discussions about the evolutionary origin of the group. Since then, the fossil record has increased dramatically, generating more evidence to help clarify the origin and dispersal of pinnipeds. The past 60 years have seen a resurgence of interest in all aspects of pinniped phylogenetic relationships (Chapskii, 1955, 1961, 1974; Mitchell, 1966–1968, 1975; Sarich, 1969 a, 1969 b; Repenning, 1975, 1976, 1990; McLaren, 1975; Tedford, 1976; Repenning and Tedford, 1977; Tedford et al., 1994; Barnes, 1972, 1979, 1987 a, 1988–1990, 2008; Barnes and Mitchell, 1975; de Muizon, 1982, 1992; Koretsky, 1986–1988, 2001; Koretsky and Ray, 1994, 2008; Koretsky and Barnes, 2003, 2008; Koretsky and Peters, 2008; Pavlinov and Rossolimo, 1987; Wyss 1987, 1988 b; Flynn et al., 1988; Wozencraft, 1989; Berta et al., 1989; Berta and Wyss, 1990, 1994; Berta and Sumich, 1999; Perry et al., 1995; Bininda-Emonds and Russell, 1996; Cozzuol, 2001; Higdson et al., 2007; Koretsky and Rahmat, 2013, 2015; Koretsky and Domning, 2014), directly arising from the prodigious increase in the numbers of fossil pinniped specimens available in museum collections (see Ray, 1977; Barnes et al., 1985) and ending the need for an introductory apology in publications (e. g., Kellogg, 1922) for the previously limited fossil record.

True seals (Family Phocidae) did not appear in the North Pacific until Late Pliocene time (Barnes and Mitchell, 1975) and have separate evolutionary histories from Otariidae since the Late Oligocene time

(Koretsky, 2001). The Koretsky and Barnes (2006) study on the evolutionary history and paleobiogeography of pinnipeds revealed that morphological evidence supports the development of Otariidae in the North Pacific (Deméré et al., 2003) and Phocidae in the North Atlantic, with their early geographic divisions due to separate origins. Currently, the paleontological record shows that Phocids, otariids, and odobenids (= walruses) have equally early origins in the Late Oligocene.

Some researchers believe that the origin of Phocidae was in the North Pacific (Wyss, 1994) and that primitive seals were large-sized animals (Wyss, 1994; Berta and Sumich, 1999). However, the fossil record of Phocidae in the North Pacific consists of only a few genera, is relatively late and provides no evidence about the earlier evolution of the Family. Several investigators have also contradicted Wyss about the size of basal phocids (Koretsky, 1987, 2001; Finarelli and Flynn, 2008; Churchill et al., 2014, a, b). The recent finding of a fossil seal mandible from the North African coast (Koretsky and Domning, 2014) and the size of the primitive “Oligocene seal” (Koretsky and Sanders, 2002) from the North Atlantic region of the United States, the two oldest seals known to date, demonstrate that early phocids were likely small-sized animals. Churchill et al. (2014 a, b) also found that walruses and otariids arose from smaller-sized ancestors and increased in body size over time.

Following Wyss (1987), several characters have been used in support of a monophyletic origin of pinnipeds by numerous authors. However, this review will demonstrate that some of these characters: 1) can be interpreted with different polarity; 2) are highly variable, nonexistent, and insignificant for taxonomic purposes; 3) are irrelevant to the monophyly/diphyly issue; or 4) are simply convergent.

Before discussing higher taxonomic levels of the phylogenetic tree, it is necessary to clearly understand lower taxonomic levels, or alpha-taxonomy. Like any tree, if the roots are weak, the crown becomes fragile and unstable as well. As previously suggested by Mitchell (1975), preliminary work has been performed on the specific level of each taxon, investigating morphology, sexual and age dimorphisms, morphometric analysis, the validity of each species and their relationships within the genus and among the subfamilies (see Koretsky, 2001; Koretsky and Holec, 2002; Koretsky and Grigorescu, 2002; Koretsky, 2006; Barnes et al., 2006; Barnes, 2008).

In order to re-open the discussion of the origin of pinnipeds, a limited, yet demonstrative phylogenetic analysis of twelve morphologically important characters were included to raise questions about the widely accepted monophyletic origin theory. We incorporate, where possible, the well-known geochronologically oldest or structurally basal representative of each of the four groups of carnivores (such as *Enaliarctos* for Otarioidea, *Devinophoca* for Phocidae, *Amphicyon* for Ursidae and *Potamotherium* for Mustelidae) as the ingroup, with *Canis* serving as the outgroup.

While molecular data (Anbinder, 1980; Arnasson, 1977; Wolsan, 1993; Sato et al., 2006) supports a monophyletic origin of pinnipeds, numerous morphological studies (Koretsky and Holec, 2002; Koretsky and Sanders, 2002; Koretsky and Barnes, 2006; Koretsky and Rahmat, 2013–2015) support a diphyletic origin, with otarioids likely arising from large bear-like animals and phocids arising from smaller otter-like ancestors. This review will demonstrate that the theory of a monophyletic origin of pinnipeds should not be completely accepted, as is the current ideology, but that a diphyletic origin remains viable due to morphological, paleobiological and paleogeographic analyses. Certain shortcomings in monophyletic hypotheses will be revealed and morphological evidence supporting a diphyletic origin of seals will be detailed to re-evaluate the discussion of this contentious subject and increase awareness of the controversial taxonomic relationships in Phocidae.

History of nomenclature and classification of pinnipeds

Illiger (1811) originally proposed the name Pinnipedia for the predominantly marine, “fin-footed” carnivorans (see Simpson, 1945): the extant true or hair seals (family Phocidae), the fur seals and sea lions (family Otariidae, subfamily Otariinae), and the walruses (family Odobenidae, subfamily Odobeninae). Since that time, the name Pinnipedia has been used as an order of the class Mammalia (e. g., Scheffer, 1958 : 47), as a suborder of the order Carnivora (e. g., Simpson, 1945 : 121), or merely as a vernacular term to refer collectively to two or more families of marine arctoid Carnivora (e. g., Mitchell, 1968; Repenning and Tedford, 1977; King, 1983).

The otarioid pinnipeds have had a rather varied taxonomic history (Mitchell, 1968; Repenning and Tedford, 1977; Barnes et al., 1985). In virtually all modern classifications, pinnipeds are considered to be arctoid carnivorans, or close relatives of them, and sea lions and walruses have commonly been considered more closely related to each other than either is to true seals (family Phocidae; e. g., Howell, 1928, 1930 : 32, 34–35; Simpson, 1945 : 233; Scheffer, 1958 : fig. 1; McLaren, 1960 b; King, 1964, 1983; Sarich, 1969 a, b; Mitchell, 1968, 1975; Mitchell and Tedford, 1973; Tedford, 1976; Arnason, 1977; Repenning and Tedford, 1977; Barnes, 1972, 1979, 1987 a, b, 1989; Flynn et al., 2005; Arnason et al., 2006; Nyakutura and Bininda-Emonds, 2012).

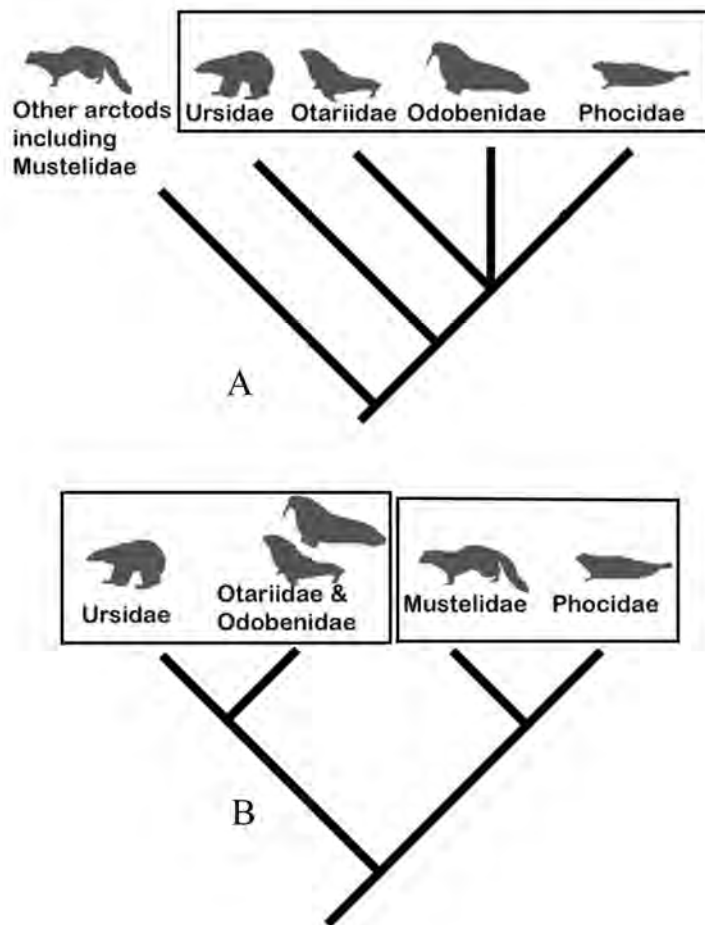


Fig. 1. Two competing hypotheses regarding phylogenetic relationships among pinnipeds: A — theory of pinniped monophyly proposes common ancestry for all pinnipeds from a terrestrial arctoid (Wyss, 1987; Flynn et al., 1988; Berta et al., 1989); B — alternative view of otarioid diphyly proposes independent origin of otarioid and phocid lineages from different terrestrial arctoid ancestors (Barnes, 1989).

This perceived close evolutionary relationship prompted Mitchell (1968, 1975), Barnes (1979, 1987 b, 1988–1990), and Hall and Kelson (1981) to classify sea lions, fur seals, walruses and their diverse and numerous extinct relatives into one expanded family, Otariidae, that contained several subfamilies. In such classifications, walruses are recognized as the subfamily Odobeninae of the Otariidae, rather than as a separate Family. Repenning and Tedford (1977) recognized these same basic taxonomic relationships, although at a different hierarchical level, when they classified Odobenidae, Otariidae, and the extinct families Enaliarctidae and Desmatophocidae in an expanded superfamily Otarioidea. Hay (1930) implied a similar arrangement when he named Desmatophocidae, as did Kellogg (1931) when he named Allodesmidae, and Simpson (1945 : 233) when he suggested that Desmatophocidae and Allodesmidae might make two natural otariid subfamilies. These fossil representatives gave the perspective to show that the living fur seals, sea lions and walruses are only the extant remnants of a much larger earlier otarioid evolutionary radiation.

The living members of the Otariidae family *sensu stricto* include fur seals and sea lions, and have been divided either into two subfamilies, the Otariinae and the Arctocephalinae (e. g., Scheffer, 1958), or joined into one subfamily, the Otariinae (e. g., Mitchell, 1968; Repenning and Tedford, 1977).

Trouessart (1897, 1904, 1905) proposed a clear system of classification of Pinnipedia, in particular of Phocidae, when he included these Antarctic phocids in the subfamily

Monachinae: *Lobodon* Gray, 1844; *Ommatophoca* Gray, 1844; *Hydrurga* Gistel, 1848; and *Leptonychotes* Gill, 1872.

However, in Simpson's (1945) classification, the Antarctic phocids were separated. For example, *Lobodon* and the other genera mentioned above were included in a subfamily Lobodontinae. Except for the introduction of the subfamily Lobodontinae, the classification system proposed by Simpson (1945) is essentially a simplified, and not always validated, variant of the older system of Trouessart, and does not completely satisfy modern requirements.

Regrettably, there still is no clear concept of the subfamilial structure of true seals, allowing controversy to persist. For example, some investigators perceive phocids as comprising only one subfamily, Phocinae (Wyss, 1988 a; McKenna and Bell, 1997), while others separate them into two subfamilies (Phocinae and Cystophorinae or Phocinae and Monachinae, see King, 1983, 1989; Burns and Fay, 1970; de Muizon, 1982; Wyss, 1994; Perry et al., 1995; Bininda-Emonds and Russell, 1996; Ärnason et al., 2006; Higdon et al., 2007), three subfamilies: Phocinae, Monachinae and Cystophorinae (Ognev, 1935; Grassé, 1955; Scheffer, 1958; King, 1964; Chapskii, 1974; Pavlinov and Rossolimo, 1987; Koretsky and Holec, 2002), or even four subfamilies: Phocinae, Lobodontinae, Monachinae, and Cystophorinae (e. g., Allen, 1880; Simpson, 1945 : 122–123). In contrast, other researchers (Sokolov, 1979; Wozencraft, 1989) do not separate true seals into subfamilies at all. Finally, in some classifications, the family Phocidae includes walruses and the extinct Desmatophocidae (Adam and Berta, 2001).

Since Chapskii's (1955, 1961, 1967, 1971, 1974, 1975) publications, the taxonomy of Phocidae has undergone considerable change (Muizon, 1981 a–c; Amson and Muizon, 2014). Chapskii provided a comprehensive analysis of phocine suprageneric systematics, presenting a clear description of diagnostic cranial traits separating true seals into tribes and subtribes, including Phocini, Monachini, and Lobodontini. Chapskii (1974) proved King's (1966) transfer of the genus *Cystophora* from Cystophorinae into Phocinae and placement of the genus *Mirounga* in the subfamily Monachinae untenable. His concept was further validated by Robinette and Stains (1970) and Polly (2008) in their comparative study of the calcaneum of seals, where they emphasized that separating *Cystophora* and *Mirounga* taxonomically (at the subfamilial level) is inadmissible. Anbinder's (1980 : 76) molecular analysis supported this view by showing that chromosome analyses “do not permit the separation of genera *Cystophora* and *Mirounga*, and this contrasts with the concept of their separate taxonomic status and of inclusion of *Cystophora* in Phocinae”. Recently, the first record of fossil material of the subfamily Cystophorinae was described (Koretsky and Rahmat, 2013). The Middle Miocene fossil material from the Paratethyan realm revealed two new species, *Pachyphoca chapskii* and *P. ukrainica*, that belong to the subfamily Cystophorinae and their phylogenetic analysis also demonstrated that *Mirounga* and *Cystophora* are sister taxa.

Continuing an old tradition, Wyss (1987) revived the issue of a monophyletic origin of the “Pinnipeds”. Almost 200 years ago, Cuvier (1825) questionably merged into a single genus, the: Common Seal (*Phoca vitulina*); Leopard Seal (*Hydrurga leptonyx*); and Mediterranean Monk Seal (*Monachus monachus*). Repeating Cuvier's mistake, Nilsson (1841) proposed even further merging in an artificial system of classification that combined into a single family, the Grey Seal (*Halichoerus grypus*) with the walrus and the fur seal. Later, Gray (1869, 1874), and even more recent authors, followed the same classification trend. By using improper criteria and not examining morphological features with phylogenetic importance, repeated classification mistakes stunted the understanding of the subfamilial taxonomy of phocids (Chapskii, 1974; Bechly, 2000).

In addition, pinniped monophyly is even not supported by some karyotypic and molecular data (Anbinder, 1980; Ärnason et al., 2006; Wolsan and Sato, 2010), or by the Bininda-Emonds and Russell (1996) cladistic analysis of phocids, based on skeletal

morphology. According to the karyosystematic analysis of Anbinder (1980 : 108), all pinnipeds are monophyletic, a conclusion that even his own data (1980 : 109, fig. 32) does not seem to support. In this study, Anbinder (1980) states that all pinnipeds differ from each other by having very specific karyotypes, just as in other carnivores such as Canoidea and Feloidea. Of course, at some level, all carnivorans are monophyletic, because at an early geological age they were all derived from a primitive form of Fissipedia.

“Pinniped” Relationships to Some Carnivorans

Some early researchers postulated a non-carnivoran origin of pinnipeds, with Wortman (1894 : 159–160; 1906 : 90–91) proposing that they evolved from oxyaenid creodonts. Most researchers, however, have concluded that pinnipeds evolved from arctoid fissiped carnivorans (Matthew, 1909, citing dental and osteological characters; Weber, 1904, soft anatomical features; Fish, 1903, brains; Ling, 1965, sweat glands; Sarich 1969 a, b, albumins; Ärnason, 1977, karyotypes; Tedford, 1976, dentition and cranial anatomy; Hunt and Barnes, 1994, basicranial circulation; Ärnason et al., 2006, mitochondrial DNA; Sato et al., 2006, nuclear DNA; and Wolsan and Sato, 2010, nuclear DNA) by the Late Oligocene or earlier.

Thus, there has been continuing controversy (e. g., Kellogg, 1922; Howell, 1930 : 33–35; Mitchell, 1967; Berta et al., 1989; Repenning, 1990; Higdon et al., 2007) over whether pinnipeds evolved from a single terrestrial ancestor (monophyletic origin) or from two independent terrestrial ancestors (diphyletic origin; fig. 1). This debate is, in some cases, irrespective of any arguments about the validity of using an order Pinnipedia. The “classic” theory of a diphyletic origin of pinnipeds proposes that true seals (Phocoidea or Phocidae) have a North Atlantic origin and are most closely related to musteloids, whereas sea lions and walruses (superfamily Otarioidea by Repenning and Tedford, 1977; Barnes, 2008, and in herein) have a North Pacific origin and are most closely related to ursids (Mivart, 1885; McLaren, 1960 b; Mitchell, 1967; Tedford, 1976; Muizon, 1982; Hunt and Barnes, 1994; Koretsky and Barnes, 2006, 2008). Both major pinniped groups are recognized as being derived from among the terrestrial arctoid carnivorans, not from among the groups containing cats, viverrids or dogs (Tedford, 1976; Ärnason, 1977; Sato et al., 2006; Rybczynski et al., 2009).

The monophyletic origin hypothesis contends that all pinnipeds are derived from a single terrestrial arctoid (Simpson, 1945 : 233; Davies, 1958; Scheffer, 1958; Ärnason, 1977; King, 1983; Wiig, 1983; Flynn et al., 2005; Finarelli, 2008), with either ursids being the likely sister group (Wyss, 1987; Flynn et al., 1988; Berta et al., 1989; Higdon et al., 2007), or Musteloidea as a sister group to Pinnipedia (Sato et al., 2006). Proponents of a monophyletic origin usually recognize a suborder or other higher taxon called the Pinnipedia or Pinnipedimorpha.

Wyss (1987) reviewed osteological evidence of walrus relationships and concluded that pinnipeds are monophyletic. In his cladogram, phocids were grouped in an unresolved trichotomy with the primitive enaliarctine, *Pinnarctidion*, and the highly evolved *Allodesmus*. *Odobenus*, Otariidae and *Enaliarctos* were viewed as successively more distantly related sister taxa, with the latter two considered to be “...the unresolved sister groups of the remaining pinnipeds... (Wyss 1987 : 24)”. This theory proposes that phocids had their closest relationships with the most derived animals that have traditionally been classified as Otariidae (or Otarioidea): Allodesminae and the walruses.

The view of pinniped relationships by Wyss (1987) is diametrically opposite to even the traditional monophyletic proposals, in which the shared common ancestry of Phocidae and Otariidae was very ancient (Late Oligocene) and involved primitive carnivorans (e. g., Davies, 1958; Scheffer, 1958; King, 1964, 1983), rather than animals that are usually considered to represent relatively highly derived stem groups.

Wyss (1988 a, b), Berta et al. (1989), and Wyss and Flynn (1993) interpreted skeletal features of various fossil and living pinnipeds as supporting pinniped monophyly. Also, Wyss and Flynn (1993) resurrected Pinnipedia as a formal taxon (excluding *Enaliarctos*) at a new, yet unspecified, hierarchical level, to be part of a new and still higher taxon, the Pinnipedimorpha, (that included *Enaliarctos*). Berta and Wyss (1994) presented phocids as members of a clade that includes walruses, allodesmines, and desmatophocines, groups that traditionally had been regarded as close to otariids (Repenning and Tedford, 1977; Yonezawa et al., 2009; Churchill et al., 2014 a) or, in fact, as being otariids (Mitchell, 1968).

In contrast, Mitchell (1967), McLaren (1960 b), Tedford (1976), Barnes (1987 b), Wozencraft (1989), and Repenning (1990) argue that Pinnipedia, whether used as a suborder or as an order, is an artificial taxon. Wozencraft (1989), in a phylogenetic analysis of Recent Carnivora, came to the same conclusion as Tedford (1976) and Muizon (1982), in recognizing a close relationship between mustelids and phocids, although he differed from these authors in his interpretation detailing the interrelationships of these groups. In addition, Wozencraft (1989) adhered to the traditional practice of uniting ursids and otarioids as a monophyletic group. Barnes and Hirota (1994 : 355) showed that the seven characters that Berta and Wyss (1994 : 41–42) interpreted as uniting Allodesminae (and other Otarioidea) with Phocidae were spurious, improperly defined, or not of phylogenetic significance.

McLaren (1960 b), Tedford (1976) and Repenning and Tedford (1977) reviewed the evidence for relationships of both otariid and phocid seals within the context of the order Carnivora. They summarized evidence in favor of a hypothesis that otariids had an origin from terrestrial fissiped carnivores separate from that of phocids. Tedford (1976) classified both phocids and otariids in the carnivore infraorder Arctoidea. Accepting pinniped diphyly, he classified the Otariidae (and the subfamily Odobeninae) in the parvorder Ursida with bears, and the Phocidae in the parvorder Mustelida, with mustelids in the superfamily Musteloidea. Later Wiig (1983) rejected Tedford's hypothesis (1976) on methodological grounds concerning a sister-group relationship of the otariids with the ursids, and separately, the phocids with the mustelids.

Tedford (1976) also placed sea lions and walruses into a single group, the superfamily Otarioidea, with variously related fossil relatives. It has been accepted by several authors (Repenning and Tedford, 1977; Barnes, 2008) that this group is monophyletic.

Classically, a monophyletic group can be defined as arising from another group of equal or lesser rank. Therefore, if an order Pinnipedia evolved from the order Carnivora, then Pinnipedia is conceptually a monophyletic group. The same conclusion would be reached if one were to recognize a suborder Pinnipedia as having arisen from a suborder Fissipedia. However, since pinnipeds are commonly viewed as having arisen from, or actually to be arctoid carnivorans, they are now treated as groups in Arctoidea, reducing the use of the formal group Pinnipedia (McKenna and Bell, 1997, use "Phocoidea" [= Pinnipedia]). Most researchers addressing the concepts of monophyly versus diphyly in pinnipeds debate whether or not all pinnipeds arose from a single aquatic arctoid species, making this the main topic of importance (fig. 1).

Here, we interpret pinnipeds to be diphyletic in origin, at least as far back as Late Oligocene, with each pinniped group developing and invading the aquatic environment separately from their much earlier, common arctoid ancestor. This hypothesis is supported by the finding of a phocid from Late Oligocene deposits (Koretsky and Sanders, 2002) that is close in age to the terrestrial or semiaquatic carnivore that maybe the ancestor of Phocidae. Therefore, we treat the family Otariidae (*sensu lato* of some others), or superfamily Otarioidea (of Repenning and Tedford, 1977), as being monophyletic, and as including the families Enaliarctidae, Otariidae (fur seals and sea lions), Desmatophocidae (including Allodesminae), and Odobenidae (Odobeninae plus Imagotariinae and Dusignathinae). We also regard as monophyletic the family Phocidae, in which we include four subfamilies:

the extant Phocinae, Monachinae and Cystophorinae and the extinct Devinophocinae. The proposed hypotheses for pinniped relationships reflect differences in the interpretations of polarity of characters, their level of analysis and the extent to which convergence affects the assessment of relationships (Howell, 1930; Barnes, 1972, 1989; Mitchell, 1975; Berta et al., 1989; Repenning, 1990; Berta and Wyss, 1990; Koretsky, 2001; Koretsky and Rahmat, 2013).

Cranial characters and taxonomy

Classical comparative vertebrate morphology has greatly influenced the systematic studies of pinnipeds. At present, the primary common ground for making comparisons between fossil and modern pinnipeds is comparative osteology. Data for comparative paleobiochemical methods have not yet been obtained from fossil pinnipeds.

Differences in cranial morphology between phocids and otariids were the basis of Mivart's (1885) original argument in support of a diphyletic origin. Since that time, the conservative basicranial region of the skull has become accepted as important in the classification of carnivorans, with this region appearing bear-like in Otariidae and otter-like in Phocidae (McLaren, 1960 b).

Cranial material, mandibles, and dentition are the most useful resources for comparative osteology and are the basis for nomenclature of fossil pinnipeds. Cranial and mandibular characters are, therefore, used most effectively in identification of taxa and in cladistic analyses. However, due to the extreme fragility of cranial phocid remains, postcranial material is commonly used for classification purposes (Koretsky and Rahmat, 2013).

Auditory region and evolution of pinnipeds

The "pinniped" ear shows evidence of the adaptation of carnivores to the marine environment, especially to deep-water feeding (Repenning and Ray, 1977; Hemillä et al., 2006). Wyss (1987) compared the ear region of walruses with those of other pinnipeds, but considered a diversity of their morphological characters and concluded that all fossil and living pinnipeds are a monophyletic group. Other researchers (McLaren, 1960 b; Repenning, 1972 a, b, 1976; Ray, 1976; Repenning and Ray, 1977; Koretsky and Holec, 2002; Hemillä et al., 2006) examined the same characters as Wyss and came to a different conclusion. Repenning (1972 b) stated that the structure of the middle and inner ear in phocids is different from that of otariids and odobenids because they evolved from different ancestors. To cite just one example, the transverse orientation of the basal whorl of the phocid cochlea differs from the posterolateral orientation seen in otariids and odobenids.

Previously, Repenning (1976) suggested, based on the structure and the ratio of the area of the tympanic membrane to the area of the oval window, that earlier enaliarctines were adapted to deep diving. Later, Odobenids adapted to shallow-water bottom feeding and lost some adaptations for deep diving, different than earlier imagotariines and enliarctids. Therefore, as deep divers, most living and fossil phocids have enlarged the entire cochlea and the basal whorl, as an adaptive mechanism for greater sensitivity in hearing and in sensing the direction of sound in water (Repenning and Ray, 1977 : 675).

Skulls of the earliest adequately-known phocid *Devinophoca* (Koretsky and Holec, 2002) and the primitive phocid *Leptophoca* (Koretsky, 2001, 2006) give unique information on ear structure. The presence of a single-chambered bulla with a large entotympanic and much smaller ectotympanic in *Devinophoca* (Koretsky and Holec, 2002; Koretsky and Rahmat, 2015) and *Leptophoca* (Koretsky, 2001) is more similar to primitive Mustelidae than to Ursidae, according to Repenning (1972 b) and Tedford (1976). While the auditory bulla of lutrines and phocids has a groove between the mastoid and tympanic, this groove is absent in the bulla of otariids, a condition similar to ursids (McLaren, 1960 b; Ivanoff,

2001). Detailed discussion about inflation of the auditory bulla can be found in Barnes and Hirota (1994), who showed that this condition is non-existent in otariids.

Internal acoustic meatus

Repenning (1977) and Repenning and Tedford (1977) inaccurately concluded that a round internal acoustic meatus was primitive for all otarioids because it is round in both modern Otariinae and in terrestrial arctoid carnivorans. However, at the time of their study the shape of the internal acoustic meatus had not been described for any of the Enaliarctinae, now recognized as being the most basal otarioid. Enaliarctines have a bilobed internal acoustic meatus (rather than round), which is the primitive character state for Otarioidea (in contrast to the small, slim fissure in primitive Phocidae). Along its ventral path to the oval window, the basal whorl of the cochlea extends transverse to the orientation of the skull in all phocids, rather than posterolaterally as in otariids and odobenids (Koretsky and Holec, 2002). Barnes (1979) showed that the internal acoustic meatus is bilobed in the enaliarctine otarioid *Pinnarctidion*, and it is bilobed in a specimen that Berta (1991) has referred to as *Enaliarctos mitchelli* (see Berta, 1991 : fig. 4). However, rather inexplicably, Berta (1991) and Berta and Wyss (1994) accepted the incorrect assumption by Repenning and Tedford (1977) that the internal acoustic meatus was round in primitive otarioids, resulting in an uncritical character coding and reversing the polarity of this character in their cladistic analysis.

Two derived character states evolved from the enaliarctine condition of a bilobed internal acoustic meatus. The first is a wider internal acoustic meatus, with two joined pathways as canals for the vestibulocochlear and facial nerves. This condition is present in Allodesminae, Imagotariinae, Dusignathinae and Odobeninae, and, as concluded by Repenning and Tedford (1977), indicates phylogenetic affinities within this clade. The other derived character state is a narrower and more rounded opening of the internal acoustic meatus, in which the paths of the vestibulocochlear and facial nerves are close together. This condition appears to have evolved convergently in Otariinae and in Desmatophocinae. It is the less common character state when considering all species of extinct and extant otariids and is one of several characters that separate Desmatophocinae from Allodesminae.

Alisphenoid canal

The alisphenoid canal transmits the internal maxillary artery and is generally a tube in the pterygoid strut between the palate and basicranium. Flynn et al. (1988) showed that canids, ursids, the lesser panda, otariids and odobenids retain the alisphenoid canal, while procyonids, mustelids and phocids have lost this structure. Although the alisphenoid canal is absent in Phocidae and Mustelidae, a shared derived character, primitive *Leptophoca* and *Devinophoca* have the presence of a shallow groove (Koretsky and Rahmat, 2015 : fig. 2). A completely formed alisphenoid canal is present in Otarioidea, Ursidae, Canidae, and most Procyonidae (Chapskii, 1955; McLaren, 1960 b; Heptner et al., 1976; Barnes and Hirota, 1994). While an impression of the internal maxillary artery is visible on the bone in one specimen of one species of *Allodesmus*, the canal is fully formed in other Allodesminae, such as *Brachyalloidesmus packardi* (Barnes 1972).

Enaliarctos (from Late Oligocene–Early Miocene, ~ 24–22 Ma), thought to be the most primitive otariid pinniped by some (Mitchell and Tedford, 1973; Berta, 1991), has a fully developed alisphenoid canal. Similarly, *Puijila darwini* (from the Early Miocene, ~ 21 to 24 Ma) is a semi-aquatic carnivoran from the Arctic Circle that also presents an alisphenoid canal and small postglenoid foramen. Rybczynski et al. (2009) suggested that *Puijila* belongs to some group of “otter-like protopinnipeds” or aquatic carnivores.

Recently, the importance of the alisphenoid canal as a morphological character has been demonstrated (Deméré et al., 2003; Amson and Muizon, 2014). The absence of

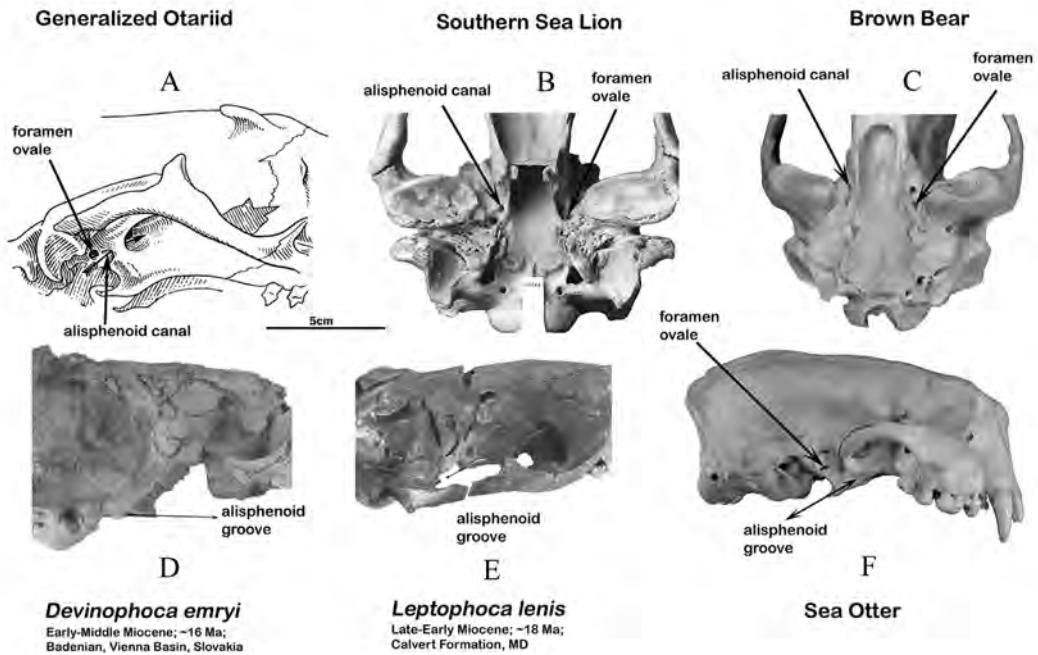


Fig. 2. Carnivoran skulls showing location of the alisphenoid canal, indicated by arrows, and alisphenoid groove, indicated by double-headed arrows (modified from Koretsky and Rahmat, 2013) in: A — a representative of generalized otariids; B — Southern seal lion (*Otaria byronia*); C — brown bear (*Ursus arctos*); D — devinophocine seal *Devinophoca emryi* (USNM 553684); E — phocine seal *Leptophoca lenis* (CMM-V 2021); F — sea otter (*Enhydra lutris*).

an alisphenoid canal in the primitive seals *Devinophoca emryi* and *D. claytoni* supports Tedford's (1976) view that lack of this character either: 1) relates phocids to early members of mustelids and not to ursids (fig. 2, c, f); or 2) supports a paraphyletic origin of Pinnipedia (Koretsky and Rahmat, 2015).

Despite the importance and clear condition of this character, supporters of a monophyletic origin of "pinnipeds" (Wyss, 1987; Berta and Sumich, 1999) did not consider the polarity of the alisphenoid canal as decisive evidence for diphyly. However, in a more recent paper, the absence of the alisphenoid canal was mentioned (Deméré et al., 2003). Even Wiig (1983), another supporter of monophyly, who heavily criticized Tedford's 1976 paper, acknowledged the importance of this character. The complete lack of consideration of such an important character by proponents of monophyly clearly shows the need for further discussion of the origin of pinnipeds. Although the presence/absence of one significant character does not confirm whether Phocids arose monophyletically or diphyletically, such critical characters need to be considered in order to question the commonly assumed theory of monophyly and increase discussions on the possibility of diphyly.

Enlargement of maxilla

Both Wyss (1987) and Berta and Sumich (1999) support their monophyletic origin theory by stating that the contribution of an enlarged maxilla to the orbital region is a common character in all "pinnipeds". However, the enlargement of the maxilla has been shown to be a multistate character (compare the matrices by Berta and Wyss, 1994 : 37 and Koretsky, 2001 : 74–75).

The maximal maxillary enlargement as a pronounced convexity is typical for phocines, according to Burns and Fay (1970). This differs from the maxillae of monachines (wide and concave) and cystophorines (narrow and concave; Chapskii, 1974). The preorbital parts of the maxilla in Devinophocinae are wide and concave, similar in shape to that of Monachinae (Koretsky and Holec, 2002; Koretsky and Rahmat, 2013 : fig. 2). Ursids and

lutrines do not show enlargement of the maxilla, and in this way are like other terrestrial mammals.

Moreover, according to some authors, the phocid condition is not a phylogenetically useful character, but has been attributed to a lateral expansion of the maxilloturbinals, considered to be an adaptation to efficiency in warming of inspired air (Muizon and Hendeby, 1980; Bininda-Emonds and Russell, 1996).

Overall, seals who adapted to colder waters could present with either a convex or concave shaped maxilla as a likely adaptive morphological character (providing increased flow rate, not air storage). Moreover, the maxillary shape is an adaptive character for diving and should not be included when discussing phylogenetic relationships at higher taxonomic levels (see Bechly, 2000). Koretsky and Rahmat (2015) demonstrated the following general distribution pattern of phocid taxa: 1) phocines have a circumpolar distribution in the Arctic regions and in the temperate zones of the Northern Hemisphere; 2) cystophorines (excluding *Mirounga*) are distributed similarly to phocines; 3) monachines are distributed in the subtropical belt; and 4) lobodontines and *Mirounga* have a circumpolar distribution in the Southern Hemisphere (King, 1964; Heptner et al., 1976).

Zygomatic arch

Berta (1991) and Wyss (1987) described the zygomatic arch of walruses, Phocidae, and the extinct desmatophocid otarioid *Allodesmus* as “mortised” and theorized in their cladistic analyses that this is a unique, derived character that joins the three groups into a higher category, the Phocoidea. Their description of the zygomatic arch as “mortised” is based on Mitchell’s (1966) earlier characterization of the zygomatic arch of *Allodesmus kelloggi*. However, morphologically, the zygomatic arch of *Allodesmus* is unlike that of *Odobenus*, and in neither group is the zygomatic arch similar to that of Phocidae.

The primitive otarioid zygomatic arch, as found in Enaliarctidae, Otariidae, Desmatophocinae, Imagotariinae, and Dusignathinae, is comparable to the terrestrial arctoid fissipeds. For example, the zygomatic process of the squamosal is elongated anteriorly and tapered, overriding the posteriorly elongated and tapered posterior end of the jugal (fig. 3, A). The jugal has a small, tapered, vertically-directed postorbital process that lies somewhat anterior to, and does not contact, the anterior termination of the zygomatic process of the squamosal.

In Allodesminae, the zygomatic arch is highly modified from this primitive condition. The entire zygomatic process of the squamosal is deepened dorsoventrally and has a vertically oriented and straight anterior border. The postorbital process of the jugal is elongated, extended vertically and closely applied to the vertical anterior border of the zygomatic process of the squamosal (like *Desmostylus*). There is no separation between the squamosal and the postorbital process of the jugal as in fissiped arctoids and in primitive Otarioidea.



Fig. 3. Right zygomatic arch (jugal-squamosal joint) in: A — Otariids, showing overlapping; B — Phocids, showing interlocking (modified from King, 1983); C — Odobenids, showing lobate postorbital process.

In Phocidae, the entire middle portion of the zygomatic arch is elevated, the elongated zygomatic process of the squamosal is inclined anteriorly and its anterior extremity is expanded and lobate, not straight (fig. 3, B). The postorbital process of the jugal projects posterodorsally over the end of the squamosal, and has a tapered apex (Chapskii, 1955 : fig. 5; 1971 : fig. 1; 1974 : fig. 16).

In Odobeninae, the zygomatic process of the squamosal is short, pointed, and thick, not expanded dorsoventrally as in Allodesminae, nor lobate anteriorly as in Phocidae. The jugal retains a primitive relationship with the squamosal (as in fissiped arctoid carnivorans, Enaliarctidae and other primitive Otarioidea) and does not contact the squamosal as it does in Allodesminae and Phocidae. The entire zygomatic arch of the jugal in walrus is deep dorsoventrally (Horikawa, 1995; Kohno et al., 1995) and has a dorsally directed and lobate postorbital process (fig. 3, C).

In each of the three groups (Allodesminae, Odobeninae and Phocidae), the zygomatic arch is modified from the primitive structure found in arctoid fissiped carnivorans, but in a unique way. Thus, these three distinctive zygomatic arch modifications suggest that Phocidae, Allodesminae and Odobeninae should not be joined into one clade and questions the use of this character to support a monophyletic origin.

Dental nomenclature

All species of Recent Otariinae and Phocidae have relatively highly modified cheek teeth, with molars and premolars that are very similar (homodonty). Their relatively simple morphology has evolved to be comparable to the anterior premolars of ancestral fossil otariids, as an adaptation to a piscivorous diet in various lineages of pinnipeds. Although it is commonly recognized that most seals have both premolars and molars, these homodont cheek teeth are not usually differentiated by pinniped researchers, and they are simply referred to collectively as “postcanines”. The discovery of very primitive Otariidae and Phocidae with dentitions similar to their terrestrial carnivoran ancestors’ increases clarity in tooth classification to determine which teeth positions are molars and which are premolars (Mitchell and Tedford, 1973; Barnes, 1979, 1992; Koretsky and Holec, 2002; Koretsky and Domning, 2014; Koretsky and Rahmat, 2015). Therefore, we refer to seal tooth positions more precisely as molars and premolars in this survey on evolution and taxonomy.

Derived features in the heterodont dentitions and archaic structure of the postcranial elements of the earliest otariids (Barnes, 1979) and some phocids (Koretsky and Holec, 2002; Koretsky and Ray, 2008) support the relationship of “pinnipeds” to terrestrial arctoids, as was mentioned by Flynn et al. (1988). However, the otariids’ shelf-like, anteromedially-placed protocone of P4, and the transversely narrow form of M1, with a longitudinally-elongated protocone, are ursid synapomorphies that are not found in Phocidae. In addition, the shape and position of the carnassial notch on P4 in primitive phocids (i. e., *Devinophoca*; Koretsky and Holec, 2002: fig. 8) are the same as in primitive Mustelida (sic, see Wolsan, 1993). Also, in primitive mustelids and primitive phocids, the protocone of P4 is conical and not formed by a cingulum as in ursids (Wolsan, 1993). Regarding other teeth, Wolsan (1993) found that having the anterior and posterior cingula of M1 continuous around the lingual base of the protocone is a character derived in Mustelida, unknown in ursids and plesiomorphic in phocids. In *Potamotherium*, which might be a sister taxon to phocids (Flynn et al., 1988), the M1 is mustelid-like by being transversely elongated without a metacone and having a paracone larger than the metacone (as in primitive phocids also).

The recently described *Afrophoca libyca*, the oldest known seal to date from the Old World, showed no accessory cusps on premolars, opposite to what is seen in *Potamotherium*, *Lutra* and *Puijila darwini* (Koretsky and Domning, 2014). *Puijila* also has a shelf-like protocone on P4 (similar to otariids) and multicusped postcanine teeth.

Overall, dental morphology reveals that phocids and mustelids are closely related, while otariids are similar to ursids, further supporting our hypothesis that a diphyletic

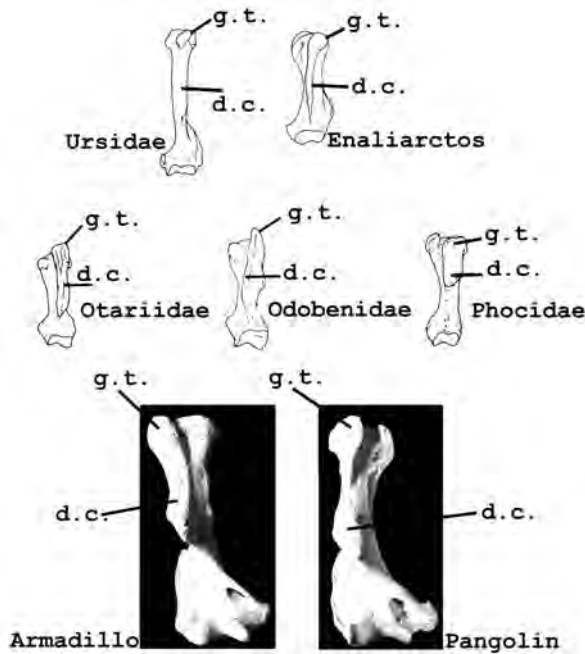


Fig. 4. Schematic drawing of left humerus of representative ursid, otariid, odeobenid and phocid and generalized terrestrial arctoid (*Armadillo* and *Pangolin*) in cranial aspects. Abbreviations: g. t. — greater tuberosity; d. c. — deltopectoral crest (modified from Berta et al., 1999).

origin of pinnipeds cannot be overlooked.

Entepicondylar foramen and other characters of the humerus and femur

The presence of the entepicondylar foramen (fig. 4) is plesiomorphic for Carnivora, found in *Procyon*, *Martes*, *Enhydra*, and *Lutra*, and generally absent in Ursidae (but present in arctotheres and other arctoids) and in Otarioidea. This foramen is also present in primitive members of virtually all mammalian orders and in mammal-like reptiles. Thus, the presence of an entepicondylar foramen is a primitive condition. While the presence or absence of the entepicondylar foramen has often been used in phocid systematics (King, 1966; McLaren, 1975; Muizon, 1981 a, 1982; Wyss, 1987, 1988 b; Bininda-Emonds and Russell, 1996; Valenzuela-Toro et al., 2016), this character also requires some clarification.

The foramen is always absent in the tribe Monachini, always present in Cystophorinae, and mostly present, but variable (and in some individuals, even present on one side and absent on the other) in Phocinae (Koretsky and Barnes, 2008). We consider the phocine and cystophorine conditions as being primitive and the monachine condition (absence of the foramen) to be derived. This is contradictory to the conclusion of Wyss (1994) and results in opposite scoring of the polarity of this character, which does not support monophyly.

Other “uniquely derived characters” of “pinnipeds” mentioned by Wyss (1988 a : 427) are: “strong” deltoid crest, marked shortening of the humerus, and well-developed greater and lesser trochanters of the femur. These characters require careful examination, as they are present in

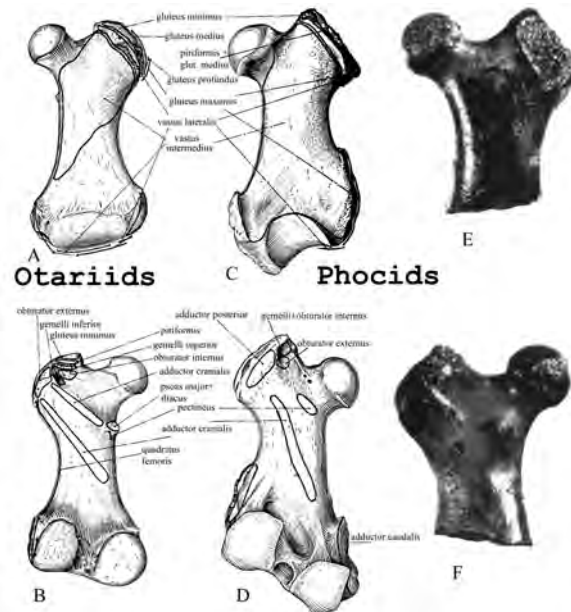


Fig. 5. Left femora of otariids and phocids, showing areas of muscle attachments (modified from Howell, 1930) in anterior aspects (A, C, E) and posterior aspects (B, D, F). Oligocene seal from South Carolina (E, F; see Koretsky and Sanders, 2002).

other taxa as well. An enlarged deltoid crest is present not just in phocids and otariids (as an aquatic adaptation), but also in fissorial mammals such as pangolins and armadillos (fig. 4). Shortening of the humerus is also seen in cetaceans and sirenians. Derived characters clearly indicated as convergent were eliminated from the phylogenetic analysis, since the most important procedure is not parsimony-analysis, but character-analysis (Bechly, 2000).

A short and anteroposteriorly flattened femur (fig. 5) is also found in penguins. All pinnipeds have a well-developed greater trochanter of the femur. However, the lesser trochanter is absent in most phocids. Male *Cystophora cristata* have a lesser trochanter, while females do not. Additionally, the fossil cystophorines *Pachyphoca ukrainica* and *P. chapskii* have a well-defined lesser trochanter (Koretsky and Rahmat, 2013 : fig. 6). The presence of a lesser trochanter in only a few cystophorine seals makes Wyss' assertion (1988 b) that all pinnipeds possess this character incorrect and therefore cannot be used to support monophyly.

Reverse position of iliac crest

The overall shape of the "pinniped" pelvis is very distinct from other carnivores, and has been used to offer additional support for the monophyly of the group (King, 1966; Wyss, 1988 a; Muizon, 1981 c; 1982). However, this unique shape is not surprising when considering the aquatic adaptations of these animals.

There are fundamental differences between otariid and phocid pelvises (Howell, 1928) and there is no general Pinniped pelvis (fig. 6). The phocid ilium is bent laterally almost at 90° (King, 1956, 1966; Bininda-Emonds and Russell, 1996), vastly different to the almost flat otariid pelvis.

The sharp lateral bend of the ilium, and the consequently deep gluteal fossa, are the result of the attachment of the *iliocostalis* muscle and relocation of the *gluteus minimus*, *gluteus medius* and *piriformis* muscles (Howell, 1928; Piérard, 1971; Howard, 1975; Muizon, 1981 c; Koretsky and Rahmat, 2013 : fig. 6). This lateral position increases the leverage of these muscles in adducting, extending, and internally rotating the femur during swimming. These muscles attach to the greater trochanter of the femur and upon contraction cause the femur to rotate. This becomes more important for the lateral propulsion movements in phocids, versus the vertical thrust movements of otariids.

While the gluteal fossa is absent in otariids (Wyss, 1988 a), it exists in *Canis* and *Ursus* as a shallow depression. Bininda-Emonds and Russell (1996) suggested that the loss of this fossa is an apomorphy occurring independently in all otariids and in some phocids.

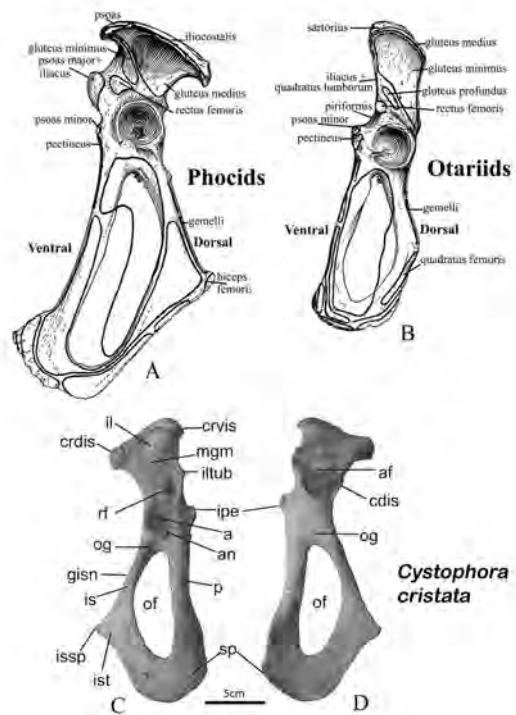


Fig. 6. Left innominate bone of phocids and otariids, showing areas of muscle attachment (modified from Howell, 1930). Innominate bones of the modern *Cystophora cristata* (USNM 550411, ♂, R.) in C, lateral (= ventral) and D, medial (= dorsal) views.

Abbreviations: a — acetabulum; af — auricular fossa; an — acetabular notch; cdis — caudal dorsal iliac spine; crdis — cranial dorsal iliac spine; crvis — cranial ventral iliac spine; gisn — greater ischial sciatic notch; il — ilium; iltub — iliac tuberosity; ipe — iliopectineal eminence; is — ischium; issp — ischial spine; ist — ischial tuberosity; mgm — m. gluteus medius; of — obturator foramen; og — obturator groove; p — pubis; rf — m. rectus femoris attachment; sp — symphysis pubis.

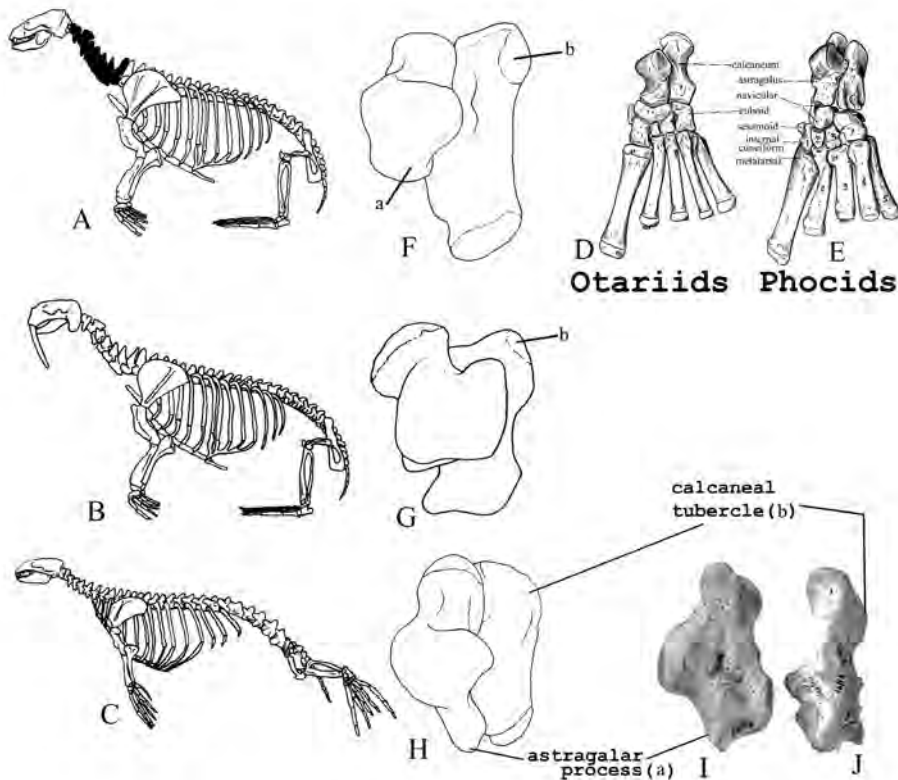


Fig. 7. Left lateral view of generalized skeleton of representative pinnipeds: A — otariids; B — odobenids; C — phocids. Dorsal view of left tarsus and metatarsus in D — otariids and E — phocids. Dorsal view of right astragali and calcanea (modified from Howell, 1929; Berta et al., 1999) of: F — otariid; G — odobenids; H — phocid; a — astragalar process and b — calcaneal tubercle. I — left astragalus of *Erignathus barbatus* (adult female, USNM 16116) in latero-palmar view; J — left calcaneum of *Erignathus barbatus* (adult female, USNM 16116) in dorsal view.

In addition, the otarioid *rectus femoris* process (attachment for the muscle that flexes the hip joint and extends the knee) is a large prominence that is situated cranio-ventrally to the acetabulum, while in phocids it is present as a small rugosity. A single *psaos-pectineus* process in otarioids is represented in phocids by a small *psaos minor* process located more caudally, while the *pectineus* arises from no eminence at all, but from the border of the pubis (fig. 6, C, D).

Apparently, depth of the gluteal fossa and varying degree of ilium eversion is not related to phylogeny on a higher taxonomic level. Supporting our hypothesis are the different swimming methods in otariids (fig. 7, A) and phocids (fig. 7, C), with vertical thrusts of the body and forelimbs in otariids and transverse thrusts of the axial skeleton and hindlimbs in phocids and sea otters (Howell, 1930; Tarasoff, 1972; Bryden and Felts, 1974; English, 1976; Gordon, 1983; Godfrey, 1984; Feldkamp, 1987; Fish, 1993, 1994 a, b). Walruses, however, may either use their forelimbs like otariids, or their hind limbs like phocids (fig. 7, B, G). Observations of the swimming motion of walruses indicate that the hindlimb is most often the source of propulsion, while the forelimbs are used for maneuvering as well as for propulsion (Gordon, 1983).

Thus, aquatic propulsion in otariids is produced by bilateral thrusts of the forelimbs, with the hindlimbs and axial skeleton playing a less active role. Forelimb movements during thrust production include a large range of adduction as well as retraction. Otariids are also capable of moving their hindlimbs in vertical and horizontal planes and use them for body support and movement on land (Gambarjan and Karapetjan, 1961).

Along with the limitation in flexion and extension of the hindlimbs in seals, there has been an increase in the size of the muscles used to move the foot. Gambarjan and Karapetjan (1961) found that the relative weights of powerful extensor muscles (the *extensor digitorum longus*, *gastrocnemius* and *peroneus longus*) increase in order from *Lutra* to *Enhydra* to phocids.

Their results indicate a change in emphasis from thrusting the whole limb (*Lutra*) to moving the hind foot only (seals). A similar weight pattern is seen in foot flexion. Thus, there appears to be an increase in size of both the flexors and extensors of the hindlimb in conjunction with increasing aquatic adaptation in these mammals (Tarasoff, 1972).

Overall, eversion of the ilium cannot be used for phylogenetic analysis of “pinnipeds” because it represents a likely convergent evolution (Mitchell, 1975; Wozencraft, 1989; Koretsky and Rahmat, 2013) and is only useful at a lower taxonomic level (subfamilial). Thus, differences in both the morphology of the otarioid and phocoid pelvis and the functional anatomy of the fore- and hindlimbs raises serious questions about the validity of these characters to support a monophyletic origin.

Astragalus and calcaneum

Wyss (1988 b) claimed that the astragalus of walruses is intermediate between that of Otariinae and Phocidae. However, the astragalus and calcaneum of walruses is similar to those of Otariinae (see Robinette and Stains, 1970), and generally to all fossil Otarioidea (fig. 7, F, G). The morphology of the calcaneum and astragalus of Otarioidea is very similar to typical arctoid carnivorans, notably ursids. Otarioidea retain a primitive arctoid ankle joint, presumably because they have the ability to walk on land on all four limbs. The ankle

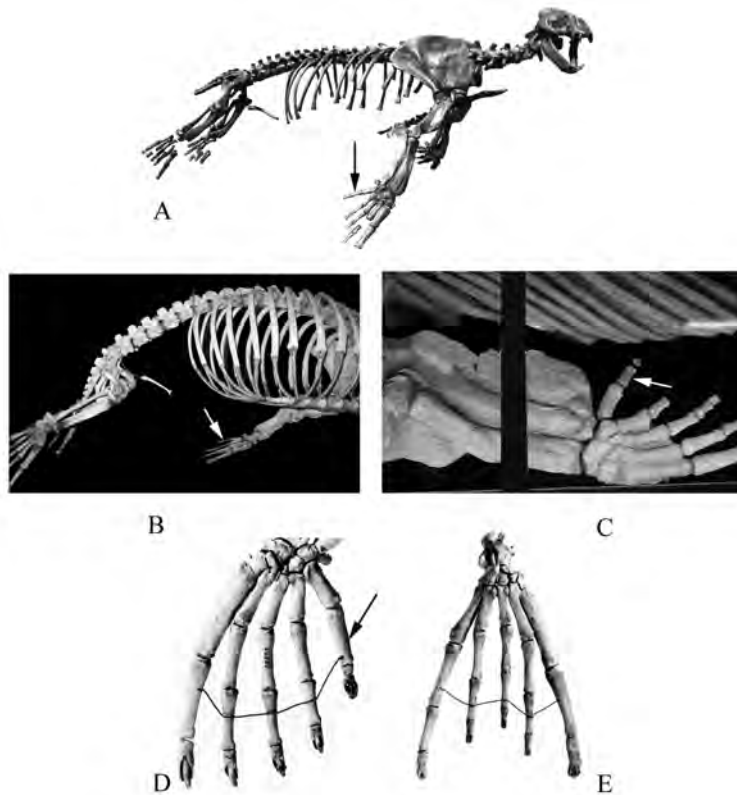


Fig. 8. A — *Allodesmus kelloggi*, LACM 4320, holotype, mounted skeleton, Natural History Museum of Los Angeles County; B — *Zalophus*, Clark Park, CA; C — *Allodesmus kelloggi*, forelimb, Buena Vista Museum of Natural History, Bakersfield, CA. Forelimb (D) and hindlimb (E — reversed, left, adult male) of *Monachus tropicalis* (USNM 22543). Arrow indicates middle phalanx in the V digit of the hindlimb.

joint, including the astragalus and calcaneum, is highly modified in Phocidae (Berta et al., 2015), and correlates with their permanently extended foot.

Because the foot cannot be flexed, phocids cannot walk on land in a plantigrade fashion the way that sea lions and walrus can. The phocid calcaneum (fig. 7, H–J) is likely derived for true seals and differs morphologically from any other carnivoran, including otters. Robinette and Stains (1970) and Polly (2008) also found that the calcanea of phocids differ from those of otariids and odobenids, supporting an ursid origin for odobenids and otariids. Their studies found an inconclusive origin (from either mustelids or ursids) for phocids.

The morphological differences of the calcaneum strongly support a diphyletic origin of pinnipeds and casts further doubt into the monophyletic hypothesis. Opponents of a diphyletic origin may argue that odobenids and otariids have the same calcaneal structure because their movement on the ground is identical. However, their identical movement on the ground could be due to their derivation from the same stock (in this case, ursids), supporting diphyletic and not monophyly.

Flipper structure

The structure of the Odobenidae manus (except for some minor details) is very similar to Otariidae (King, 1964; Mitchell, 1968; Repenning and Tedford, 1977). Wyss (1988 a) regards this as being a primitive phocid feature of flipper morphology and a secondary modification that supports monophyly (fig. 8).

As clearly explained by Wozencraft (1989), the polarity that Wyss (1987) used for the auditory region is “quite atypical” (p. 505). The polarity of flipper structure assigned by Wyss (1988 a) is also not representative and may signify parallel or convergent evolution (Mitchell, 1966, pls. 15, 17, 25; Wozencraft, 1989 : 504–505), a possibility even Wyss mentioned in his study.

Berta and Wyss (1994) and Wyss (1988 a) cited the existence of a short middle phalanx in the fifth digit of the manus as being a unique derived character shared by all pinnipeds. This observation is misleading (see fig. 8, A–C), and the polarity of the character cannot be determined because the middle phalanx of the fifth digit is not known in most fossil pinnipeds, including the oldest otarioid, *Enaliarctos mealsi*. Also, in the well preserved holotype skeleton of the allodesmine desmatophocid, *Allodesmus kelloggi* (fig. 8, A, C), the digit in question is not shortened (Mitchell, 1966, pls. 15, 17, 25; Barnes, 2008 : fig. 31.1C). Berta et al. (1989) and Wyss (1988 a, 1989) state that *E. mealsi* has a short middle phalanx on digit V. However, this bone is not preserved in the only known skeleton of the species

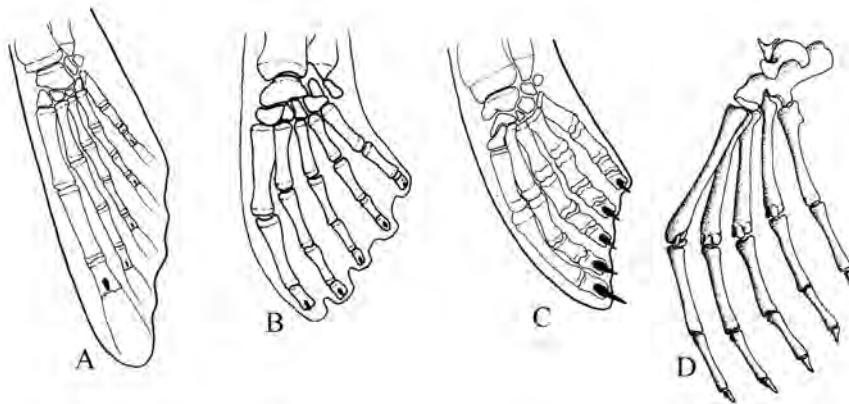


Fig. 9. Claws and cartilaginous extensions on the flipper of pinnipeds (modified from Howell, 1930 and Taylor, 1989) of: A — otariids (small claws and large cartilaginous extensions); B — odobenids (cartilaginous extensions of the phalanx and the nails are reduced to small nodules); C — phocids (large claw, even without a small nodules of the cartilaginous extensions); D — lutrines (with well-developed claws).

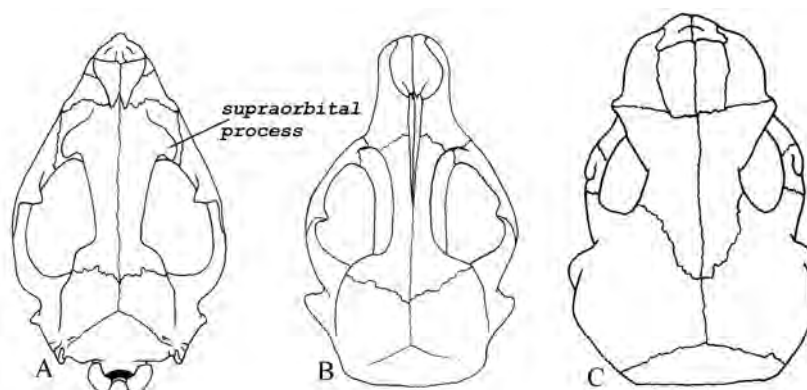


Fig. 10. Dorsal views of skulls of modern representative of pinnipeds (modified from Howell, 1929; King, 1983 b) of: A — otariids (supraorbital process of the frontal bone is large and shelf-like); B — phocids (supraorbital process is absent); C — odobenids (supraorbital process is absent also).

(Berta and Ray, 1990). Therefore, no fossil evidence exists for the polarity of this character and their analysis cannot be validated.

In general, the terminal phalanx in phocids is claw-shaped (fig. 9, C). Meanwhile, the flat terminal phalanges of otariids have very slight indications of a small claw and instead of “nails,” their abrupt terminations distally have cartilaginous extensions (fig. 9, A, B).

The detailed morphology and discussion of “pinniped” flipper structure was presented by Bininda-Emonds and Russell (1996), who reached a conclusion opposite to Wyss (1994), demonstrating additional support to a likely diphyletic origin.

Sexual dimorphism

Generally, phocine seals do not form harems and males do not fight for females. Instead, they form reproductive pairs. Phocids lack any sort of supraorbital process, correlating with reproductive behavior that does not include combat (Chapskii, 1952; Linderfors et al., 2002). This is consistent with the hypothesis that the otariine supraorbital process is present to protect the eyes of fighting males (fig. 10). In Phocidae, the eyes are very large and dorsally directed, creating feeding advantages. While the Cystophorine elephant seals (*Mirounga* spp.) differ from other seals by being combative and forming harems, they still lack the eye-protecting supraorbital processes found in otariines. The male-to-male combat in elephant seals involves slashing with canine teeth, with blows usually directed to the thick hide of the chest and neck and rarely to the top of the head.

We interpret the large supraorbital processes of Otariinae species as a unique derived character that has appeared since the Late Miocene (circa 10 to 11 million years ago) in this lineage only, likely to protect the eyes from bites to the top of the head during combativeness among males. Evolutionary enlargement of this structure would correlate with the advent of polygyny and may be an indicator of the evolution of polygyny in modern members of Otariinae only. Thus, the lack of supraorbital processes in seals, both in combative and non-combative species, reveals further evidence to question a monophyletic origin of pinnipeds.

Taxa and characters used in cladistic analysis

In constructing a phylogenetic tree comparing eared seals, walruses, and true seals, we used only characters that separate basal Phocidae from basal Otarioidea. Thus, we focused only on 12 characters that can be examined in both groups at the same time. Each of the following characters is monomorphic for each of these higher taxa.

This analysis includes four groups of carnivores as an in-group (*Enaliarctos* — as a

Table 1. Matrix of character-state data for the phylogenetic analysis of basal “pinnipeds”

Species	1	2	3	4	5	6	7	8	9	10	11	12
<i>Canis lupus</i>	0	1	0	1	0	0	0	0	1	0	0	0
<i>Amphicyon intermedius</i>	0	1	1	1	0	0	0	0	0	1	0	0
<i>Enaliarctos mealsi</i>	0	1	1	1	0	0	0	0	1	1	0	0
<i>Devinophoca claytoni</i>	1	0	0	0	1	1	1	1	?	?	?	?
<i>Devinophoca emryi</i>	1	0	0	0	1	?	1	1	1	0	0	?
<i>Potamotherium vallettoni</i>	1	0	0	0	1	1	1	1	0	0	1	1
<i>Puijila darwini</i>	1	0	1	?	0	0	1	?	?	0	0	1

basal, most primitive and geologically oldest otarioid; *Devinophoca* — as the most primitive representative of Phocidae; *Amphicyon* — structurally a basal ursid; and *Potamotherium* and *Puijila* — as the best documented early mustelid), with *Canis* as the out-group.

The matrix of character-state data, showing 12 unordered and unweighted cranial and postcranial characters, is given in table 1.

Characters and character-states are listed below. “0” designates the most primitive state among the taxa studied; “1” is a derived state; “?” indicates unknown or missing data.

1. Alisphenoid canal: (0) present; (1) absent.
2. Internal carotid artery: (0) curved in bulla; (1) straight through bulla.
3. Tympanic bulla: (0) hyperinflated; (1) not hyperinflated.
4. Ursid loop of internal carotid artery: (0) absent; (1) present.
5. Pterygoid sheet laterally splayed: (0) no; (1) yes.
6. Pterygoid hamulus lost: (0) no; (1) yes.
7. Mastoid-paroccipital forming crest: (0) no; (1) yes.
8. Internal acoustic meatus divided into definite foramina: (0) yes; (1) no.
9. Entepicondylar foramen of humerus: (0) present; (1) absent.
10. Transverse crest of radial trochlea of humerus: (0) absent; (1) present.
11. Ilium: (0) not everted; (1) everted.
12. Tarsus: (0) as in ursids; (1) highly modified.

Results of cladistic analysis

Basic dichotomies exist between basal Phocidae and basal Otarioidea, with no overlaps in the following character matrix (table 1). Each group has its own unique set of derived characters, shown as nodes in figure 11 (and consequently its own unique set of primitive character states).

A. Derived characters of Phocidae (shared with Mustelids): 1) loss of alisphenoid canal; 2) hyperinflated tympanic bulla; 3) laterally splayed pterygoid sheet; 4) loss of pterygoid hamulus; 5) mastoid-paroccipital crest; 6) entepicondylar foramen on humerus; 7) lateral eversion of the ilium; and 8) modified tarsus.

B. Derived characters of Otarioidea include: 1) ursid loop of the internal carotid artery in a basioccipital sinus (present in Enaliarctinae and basal Imagotariinae and Desmatophocinae; lost in derived Imagotariinae, Desmatophocidae and Otariinae); and 2) loss of entepicondylar foramen in the humerus.

The mh*; routine in Winclada based on Hennig86 (Farris, 1988) produced one maximally parsimonious tree, 24 maximum and 15 minimum steps-long with a consistency index of 0.80 and a retention index of 0.80.

Phylogenetic affinity can be demonstrated only by shared derived characters (synapomorphies) and characters common to different taxa (homoplasies) provide no information in this respect.

Diphily of pinnipeds implies independent origin of otarioid (Pacific origin) and phocid (Atlantic origin) lineages from different terrestrial arctoid groups and supports a strictly monophyletic clade consisting of walruses, sea lions, and their supposed

fossil relatives, but excluding phocids (Barnes, 1989, Ärnason et al., 2006; Koretsky and Barnes, 2006).

Molecular analyses

While morphological evidence supports a diphyletic origin of pinnipeds, the molecular analyses supporting monophyly must also be reviewed. Obviously, molecular studies use only characters from living taxa, thereby ignoring character states for fossil members of living clades and completely ignoring important morphological data from extinct lineages (Finarelli and Flynn, 2006). When extant-only data is used, numerous molecular analyses favor a large sized common ancestor for Caniformia and Arctoidea. However, fossil morphological data supports small bodied ancestors. The Finarelli and Flynn (2006) molecular study found that the common ancestor for Caniformia and Arctoidea were likely small-bodied and not large-bodied as previously thought. Excluding morphological characters from fossil taxa in molecular studies is a significant deficiency that cannot be overlooked. Incorporating fossil and extant character data is vital to generate ancestral reconstructions and accurately determine the dispersal of characters in the entire evolutionary history of a clade.

Molecular studies support pinniped monophyly, but have demonstrated that within pinnipeds, Odobenidae is more closely allied with otariids than with phocids and that there is a basal split between Phocidae and an *Odobenus*-*Otariidae* clade (Flynn et al., 2005; Arnason et al., 2006; Fulton and Strobeck, 2006). Nyakatura and Bininda-Emonds (2012) determined that different molecular analyses on the phylogenetic relationships within Phocidae result in numerous variations, indicating a lack of resolution. Even so, these studies do find that *Odobenus* is the sister taxon to *Otariidae*, agreeing with the majority of morphological and molecular evidence.

The Fyler et al. (2005) molecular sequence study supports pinniped monophyly, but found that the presence of fossil *Monachinae* (*Pristiphoca* and *Pliophoca*) in Europe, and their exclusion in other localities with abundant phocid remains, supports de Muizon's (1982) theory of evolution of this clade in the Tethys Sea and Koretsky and Barnes' (2006) east to west dispersal hypothesis. The Ärnason et al. (2006) molecular study suggested that pinnipeds originated on the North American continent with early otarioid and otariid divergences taking place in the North Pacific and those of phocids in the coastal areas of North Atlantic for later dispersal to colder environments in the Arctic Basin and in Antarctic waters. While monophyletic supporters agree about a North American origin of phocids, the fossil record does not support this claim. Fossil paleontological evidence shows a North Atlantic origin of phocids in the Paratethyan/Mediterranean regions and an east to west distribution (Koretsky and Holec, 2002; Koretsky and Barnes, 2006; Koretsky et al., 2012; Koretsky and Rahmat, 2013, 2015; Koretsky and Domning, 2014; Koretsky et al., 2015).

Overall, pinniped monophyly has consistently been supported by studies that use genetic and molecular data (Flynn and Nedbal, 1998; Bininda-Emonds, 2003; Fulton and Strobeck, 2006). However, fossil material is not included in these studies, raising serious concerns about their validity when describing the evolutionary history of taxa. Missing entries in a phylogenetic data matrix is problematic (Kearney and Clark, 2003) as excluding incomplete characters, excluding incomplete taxa or combining incomplete taxa into composite taxa can alter affinities and correlations (Wolsan and Sato, 2010).

Molecular analyses do provide important data, but results are often varied and not in agreement. While some molecular studies have found that Pinnipedia is closely related to Ursidae (Flynn et al., 2005), others demonstrated strong affinity between Pinnipedia and Musteloidea (Sato et al., 2006). Due to these varying results, molecular data sets have led to an unresolved relationship between Ursidae, Pinnipedia and Musteloidea (Ärnason

et al., 2006). This lack of agreement and inability to come to a common conclusion based solely on molecular data should raise questions about only accepting a monophyletic origin of Pinnipedia. While morphological evidence strongly supports a diphyletic origin, there is still some disagreement in character importance and affinity. Thus, the combinations of molecular and morphological phylogenetic analyses are needed to determine whether pinnipeds arose monophyletically or diphyletically.

Conclusions

The differences between the proposed hypotheses for pinniped relationships reflect discrepancies in the interpretations of character polarity, their level of analysis, and the extent to which convergence affects their assessment (Howell, 1930; Barnes, 1972, 1989; Mitchell, 1975; Berta et al., 1989; Repenning, 1990; Berta and Wyss, 1990; Koretsky, 2001). The paleozoogeography of “pinnipeds” suggests that Otarioidea developed in the North Pacific and based on current knowledge, as supported by paleontological evidence and our phylogenetic analysis (fig. 11), we believe that the origin of phocids was in the North Atlantic in the Paratethyan region (Ärnason et al., 2006; Muizon, 1981 b; Koretsky and Barnes, 2006 : fig. 1; Koretsky and Rahmat, 2013, 2015), with their early geographical division due to separate origins.

Numerous fossil evidence support dual origination and the presence of a small-sized ancestor in both groups (Wolf and Gunther, 1985; Finarelli and Flynn, 2006; Churchill et al., 2015). Moreover, the earliest identifiable phocines on the Atlantic coast of the US (*Monotherium?* from the Early Miocene of Virginia and *Leptophoca* from the Middle Miocene of Maryland) and Early Pliocene phocids on the American east coast, indicate close affinities with the seals of the eastern Atlantic and Paratethys (Van Beneden, 1877; McLaren, 1975; Koretsky, 2001; Koretsky and Ray, 2008; Koretsky et al., 2012; Koretsky et al., 2015).

As discussed above, the extant subfamilies Phocinae, Monachinae, Cystophorinae and the extinct subfamily Devinophocinae should be considered as separate phylogenetic branches of the Family Phocidae, which separated from ancient Carnivora probably in the Early Oligocene or before, then became widely distributed in the Middle Miocene, and practically ceased to exist in the Paratethys in the Early

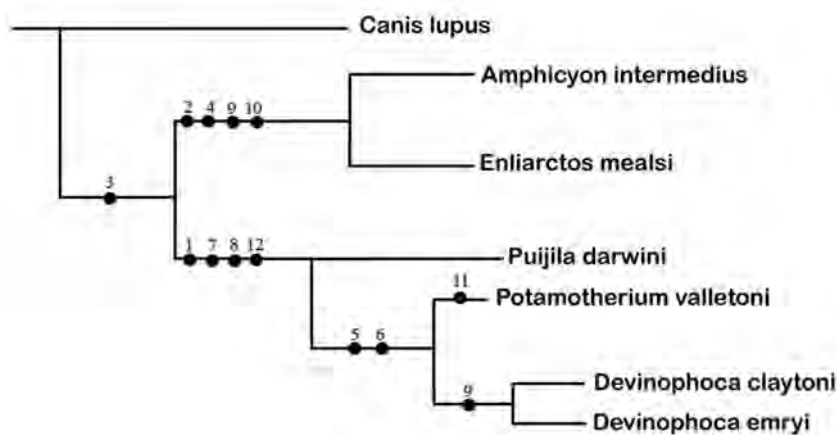


Fig. 11. Wagner consensus tree of the hypothesized phylogenetic relationships among pinnipeds, generated by Winclada based Hennig86 using 12 characters. Tree length 24 maximum steps or 15 minimum steps; consistency index, 0.80; retention index, 0.80. Character states are given in table 1. Diphyly of the pinnipeds proposes independent origin of otarioid (Pacific origin) and phocid (Atlantic origin) lineages from different terrestrial arctoid groups and supports strictly monophyletic clade of walruses, sea lions, and their fossil relatives, excluding phocids.

Pliocene. Most of these fossil animals were members of extant subfamilies, except for a few species of Devinophocinae.

Morphological assessment of cranial and postcranial bones demonstrates that extant and extinct true seals are no doubt descendants of some Oligocene phocids. Indeed, as we mentioned above, specimens referred to the family Phocidae have already been found in the Late Oligocene of South Carolina, USA (Koretsky and Sanders, 2002). Unfortunately, seal-bearing Oligocene marine deposits have not been found in the Paratethys, where geological events (maybe Alpinian and Karpathian elevation) have concealed or destroyed them. Fortunately, the oldest known seal from the Old World to date, *Afrophoca libyca* (Early Miocene; Koretsky and Domning, 2014), was found in the African coast of the Mediterranean and clearly belongs to the extant subfamily Monachinae.

Members of the family Phocidae do not appear in the North Pacific until late Pliocene time (Barnes and Mitchell, 1975), and their evolutionary history is separate from that of the Otariidae at least since Late Oligocene time (Koretsky, 2001; Koretsky and Barnes, 2006; Barnes, 2008).

However, Berta and Wyss (1994) argue that the genus *Allodesmus* is closer to Phocidae than to Otariidae. They joined *Allodesmus* with *Pinnarctidion* and *Desmatophoca* in an unresolved trichotomy within the superfamily Phocoidea and as a sister taxon of Phocidae. The oldest known phocid ("Late Oligocene seal") is not only significantly older than *Allodesmus*, but does not show any resemblance to *Allodesmus* or other primitive otariids. While many of its species were convergent with various living species of the family Phocidae, the Allodesminae are an otariid group and are not closely related to true seals. Barnes and Hirota (1994) concluded that all seven of Berta and Wyss' (1994) characters placing Allodesminae among Phocoidea are incorrectly attributed, non-existent, or not verifiable.

While all aquatic carnivorans did evolve from a common ancestor at some point, the numerous differences in cranial and postcranial morphology shown in this review suggest that phocids and otariids should be treated as separate clades. Thus, we consider pinnipeds to be diphyletic (see fig. 11), at least as far back in time as when the first arctoid ancestors of each group invaded the aquatic environment, and therefore treat both clades, the Otarioidea, Otariidae (s. l.) and the Phocidae as strictly two discrete groups.

Recent research on the body size of pinnipeds revealed morphometric differences between Phocidae and Otariidae, with each group clustered separately (Churchill et al., 2014 a, b). Similar to the morphological studies by Jones and Goswami (2010) and Jones et al. (2013), there is higher morphological diversity in Phocidae than in Otariidae (Churchill et al., 2014).

We acknowledge that genetic and molecular studies cannot be overlooked either. Since there remains persistent conflicts between phylogenetic interpretations based solely on morphology or on molecular data (Sato et al., 2004), morphological and molecular analyses need to be implemented mutually to resolve this intricate question. Molecular investigations support a monophyletic origin of pinnipeds, but disregard vital morphological data. Likewise, morphological evidence supports diphyletic, but ignores molecular analyses. Therefore, the origin of pinnipeds cannot be confirmed to be monophyletic based solely on molecular and genetic studies, as it presently is by most.

Although new research and continued discussion of the origin of pinnipeds is necessary, the evidence in this review demonstrates that a diphyletic origin of otariids and phocids must be taken seriously. While more in-depth studies are needed to completely confirm a diphyletic origin, the morphological character analysis presented herein and varying results from molecular investigations strongly question a monophyletic origin of pinnipeds.

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