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EVOLUTION OF PREY CAPTURE STRATEGIES AND DIET IN THE PINNIPEDIMORPHA (MAMMALIA, CARNIVORA)

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ABSTRACT : Pinnipeds represent a lineage of terrestrial carnivores that have secondarily adapted to a marine existence and must capture and process prey under water. We examined known diets and skull morphologies associated with different prey capture strategies in extant and fossil pinnipedimorphs using a phylogenetic context to reveal their evolutionary feeding history and diversity. Unlike their arctoid ancestors, no extant pinnipedimorph masticates food. Prey capture is accomplished by four methods, characterized by numerous craniodental features (in parentheses): 1) pierce feeding (homodonty; M_1 anterior to dentary midlength; enlarged orbit); 2) suction feeding (elongate and vaulted palate; robust pterygoid hamuli; mandibular fusion); 3) filter feeding (high-crowned, intricately cusped postcanine teeth; upper and lower teeth interdigitating; post-dental ridges); and 4) grip and tear feeding (straight, sharply pointed postcanine cusps; enlarged incisors). Pierce feeding is typical of most pinnipedimorphs, while filter feeding is limited to extant crabeater seals and grip and tear feeding to living leopard seals. A tendency toward suction feeding occurs in at least four independent lineages (otariine sea lions, bearded seal, and dusignathine and odobenine walruses), although it is best developed in odobenines. Only a weak correlation between functional anatomy and diet was observed for extant taxa. For example, suction feeding is utilized by walruses to capture and consume benthic mollusks, but skulls with convergent evolution of suction associated characters are also well designed for capturing larger fish and squid (*e.g. Otaria byronia*).

Keywords: Pinnipedia, Phocidae, Otariidae, Odobenidae, Evolution, Adaptation, Feeding, Diet, Morphology, Skull

Evolution des Strategies de Capture de la Proie et Regime alimentaire chez les Pinnipedimorpha (Mammalia, Carnivora)

Résumé : Les Pinnipèdes constituent une lignée de Carnivores terrestres adaptés secondairement à une existence marine ; ils doivent capturer et manipuler leurs proies sous l'eau. Nous avons étudié les régimes alimentaires et les morphologies crâniennes associés aux différentes stratégies de capture de la proie chez les pinnipédimorphes actuels et fossiles. Les résultats sont intégrés dans un cadre phylogénétique afin de retracer l'histoire et la diversité évolutive des modes d'alimentation. A la différence de leurs ancêtres arctoïdes, aucun pinnipédimorphe connu ne mastique sa nourriture. La capture de la proie est effectuée selon quatre modes caractérisés par de nombreux traits du crâne et des dents (caractères entre parenthèses) : 1) l'alimentation par percement (homodontie; M_1 est situé à l'avant de la mi-longueur de la denture; orbite agrandie); 2) l'alimentation par succion (palais allongé et voûté; hamuli du ptérygoïde robuste; fusion mandibulaire); 3) l'alimentation filtrante (dents postérieures aux canines avec une couronne haute et des cuspides complexes; dents supérieures et inférieures inter digitées; crêtes situées à l'arrière des séries dentaires de la mandibule et des maxillaires); et 4) l'alimentation par «saisie et déchiquetage» (cuspides des post-canines droites et très pointues; incisives agrandies). L'alimentation par percement caractérise la plupart des pinnipédimorphes, alors que l'alimentation filtrante paraît être limitée aux phoques actuels se nourrissant de crabes et l'alimentation par «saisie et déchiquetage» paraît être limitée aux phoques léopards. Une tendance vers l'alimentation par succion s'observe dans quatre lignées indépendantes au moins (les lions de mer, le phoque barbu ainsi que les morses dusignathines et odobénines), mais elle est la plus développée chez les morses odobénines. La relation entre l'anatomie fonctionnelle et le régime alimentaire observé sur les taxons actuels présente une faible corrélation. Par exemple, l'alimentation par succion est utilisée par les morses pour capturer et consommer des mollusques benthiques et d'autres invertébrés, mais des crânes présentant une évolution convergente des caractères liés à l'alimentation pas succion sont également bien adaptés à la capture de poissons et de calmars de plus grande taille (par exemple l'otarie du sud, *Otaria byronia*).

Mots clés : Pinnipedia, Phocidae, Otariidae, Odobenidae, Evolution, Adaptation, Régime alimentaire, Morphologie, Crâne

INTRODUCTION

There have been many hypotheses developed to explain causal factors leading to the invasion of land by primitive tetrapods during the Late Devonian. The most popular of these theories include reduced predation and competitive pressures on land and an increased availability of food and other resources relative to the marine environment (Holman, 1970; Vermeij & Dudley, 2000). Regardless of the cause(s), the shift from an aquatic environment to a terrestrial one has led to a great diversification of terrestrial vertebrates, as well as to the development of many remarkable methods for coping with such challenges as gas exchange, water loss, locomotion, and feeding in a non-fluid environment. Despite these evolutionary «accomplishments,» however, secondary re-adaptation to a wholly aquatic lifestyle has occurred in many independent lineages of amniote vertebrates and has resulted in remodeling of terrestrially adapted morphologies and physiologies to cope with an aquatic environment (Vermeij & Dudley, 2000). Among living reptiles, chelonians (turtles and tortoises), hydrophiids (sea snakes), crocodilians, and the marine iguana have secondarily - and independently - returned to a marine existence. The extinct plesiosaurs, ichthyosaurs, placodonts, and mosasaurs are well-known secondarily marine reptiles from the Mesozoic. The birds also have numerous secondarily aquatic members, including southern sphenisciforms (penguins), several northern alcids (auks), and fossil taxa such as the Cretaceous *Hesperornis*. Among mammals, the wholly aquatic cetaceans (whales), sirenians (manatees and dugongs), sea otter and the amphibious pinnipeds (seals, sea lions, and walruses) represent four lineages that have readapted to life in the water. Fossil evidence also suggests that at least one edentate (a marine sloth; de Muizon & McDonald, 1995) and ursid (bear; Tedford *et al.*, 1994), and the desmostylians (Inuzuka *et al.*, 1994) were secondarily aquatic. Similar to the invasion of land from the water, moving from a terrestrial to an aquatic environment requires the evolution of methods for coping with increased heat loss, salinity, gas exchange, locomotion, and feeding, among others. Attempts to determine the causal mechanisms behind secondary re-invasions of the water are typically speculative, but utilization of nearshore marine food resources with subsequent aquatic adaptation and diversification appears to be a common postulate (see for example Domning's (1978) study of sirenians and O'Leary & Uhen's (1999) examination of cetaceans). Vermeij & Dudley (2000) further note that for such an invasion to take place, the invading taxon must be able to effectively compete for resources in the new environment. Thus, knowledge of the feeding methods and capabilities of fossil marine tetrapods is requisite to understanding possible factors that may have allowed them to secondarily invade marine habitats. Here, we examine the functional morphology of feeding in living and extinct pinnipeds and attempt to document evolutionary transitions and diversity in feeding behaviours and diet within the group. Our analysis is conducted within a phylogenetic framework, thus allowing us to elucidate the probable timing of changes in feeding strategies between lineages.

Extant pinnipeds are carnivoran mammals that include three major lineages, the Phocidae («true» seals), Odobenidae (walruses), and Otariidae (fur seals and sea lions). It has been argued that pinnipeds are paraphyletic, with phocids having close ties with the Mustelidae (otters and kin) and otariids plus odobenids having a common ancestry with ursids (*e.g.* Wozencraft, 1989). However, overwhelming evidence from both morphological (*e.g.* Berta & Wyss, 1994; Bininda-Emonds & Russell, 1996; Vrana *et al.*, 1994) and molecular (*e.g.* Flynn & Nedbal, 1998; Ledje & Árnason, 1996*a*, *b*) sources clearly indicates that the group is monophyletic, although their precise origin within arctoid carnivores remains controversial. A second, more recent debate over pinniped relationships concerns the position of the Odobenidae to the other two extant lineages. Odobenids have been traditionally grouped with the Otariidae as the Otarioidea, a hypothesis that has received support from both morphological (*e.g.* Bininda-Emonds & Russell, 1996; Wozencraft, 1989) and molecular (*e.g.* Ledje & Árnason, 1996*a*, *b*) evidence. Others have found odobenids and phocids to be more closely related (together constituting the Phocomorpha), a result evidenced by both morphological (*e.g.* Berta and Wyss, 1994) and (in part) molecular (Vrana *et al.*, 1994) data.

Two major extinct clades are known in addition to extant lineages. *Enaliarctos* is the most basal known taxon, and has been recovered from deposits of late Oligocene to Miocene age in western North America and Japan (Berta, 1991*a*; Kohno, 1992). A second basal taxon, *Pteronarctos*, is known from western North American Miocene deposits (Berta, 1991*b*). *Enaliarctos* and *Pteronarctos*, together with the Pinnipedia constitute the Pinnipedimorpha (*sensu* Berta & Wyss, 1994). The extinct group formed by *Allodesmus*, *Desmatophoca*, and *Pinnarctidion* is the sister group to the Phocidae, and with the phocids comprise the Phocoidea. Table 1 summarizes chronological and locality data for these and other fossil taxa included in this analysis.

That modern pinnipeds are well adapted for an aquatic life is clearly evidenced by their possession of limbs specialized for swimming, development of thick blubber or fur for thermoregulation, ability to withstand prolonged apnea while diving through behavioural modifications (*e.g.* bradycardia), and dependence on the ocean for most of their needs. However, they lead an amphibious lifestyle in that

Taxon	**Age and Locality**
Basal Pinnipedimorphs	
Enaliarctos	Late Oligocene – Early Miocene; eastern and western north Pacific
Pteronacrtos	Early Miocene; eastern north Pacific
Otariidae	
Thalassoleon	Late Miocene – Early Pliocene; eastern and western north Pacific
Phocoidea	
Acrophoca	Late Miocene – Early Pliocene; eastern south Pacific
Allodesmus	Middle Miocene – Late Miocene; eastern and western north Pacific
Desmatophoca	Early Miocene – Middle Miocene; eastern north Pacific
Homiphoca	Early Pliocene; eastern and western south Atlantic
Pinnarctidion	Early Miocene; eastern north Pacific
Piscophoca	Early Pliocene; eastern north Pacific
Odobenidae	
Aivukus	Late Miocene; eastern north Pacific
Alachtherium	Early Pliocene – Early Pleistocene; eastern north Atlantic
Dusignathus	Late Miocene – Late Pliocene; eastern north Pacific
Gomphotaria	Late Miocene; eastern north Pacific
Imagotaria	Late Miocene; eastern north Pacific
Neotherium	Middle Miocene; eastern north Pacific
Pontolis	Late Miocene; eastern north Pacific
Protodobenus	Early Pliocene; eastern north Pacific
Valenictus	Late Miocene – Late Pliocene; eastern north Pacific

Table 1. Summary of known ranges and ages of fossil taxa included in this study.

they are still strongly tied to land (or ice), where birthing, nursing, and moulting occur. The earliest known pinnipedimorphs were likewise well-adapted to life in the water, as *Enaliarctos* has a skeletal morphology that is well suited for swimming (Berta & Ray, 1990). This, and the discovery of distinctly phocid femora from older Late Oligocene deposits of the eastern United States (Koretsky & Sanders, *in press*) strongly suggest that pinnipedimorphs originated well before 29 Mya (million years ago). Regardless, a marine-based diet has been hypothesized for all known taxa including *Enaliarctos* (Berta & Ray, 1990), and there has been no suggestion that any pinnipedimorph regularly fed or feeds on terrestrial food resources. Prey capture, handling, and swallowing occurs in the water for all modern species.

The diet of living species is readily determined through direct observation, stomach content analysis, scat analysis, and a variety of other methods (see Bowen & Siniff, 1999). Extant pinnipeds utilize many marine food resources, which can be grouped into the five broad categories of: 1) fish, 2) cephalopod mollusks (squid and octopi), 3) bivalve mollusks (clams and kin), 4) small decapod crustaceans (planktonic euphausid krill and benthic shrimp), and 5) large warm-blooded prey (including penguins and other seals). Pinnipeds show considerable overlap in their utilization of these resources, and for some species seasonal, sexual, ontogenetic, and geographic variations in diet have been recorded (*e.g.* Dellinger & Trillmich, 1999; Fay, 1982; Tollit *et al.*, 1998). However, some general trends in diet can be identified, as revealed in fig. 1 (based primarily on King, 1983 and Riedman, 1990 and supplemented by: Daneri, 1996; Fay, 1982; Fisher & Stewart, 1997; George-Nascimento *et al.*, 1985; Koen Alonso *et al.*, 1999; Lowry *et al.*, 1980, 1988; Øritsland, 1977; Pinedo & Barros, 1983; Rice, 1973; and Siniff & Stone, 1983). Most pinnipeds are piscivorous or teuthophagous (squid eating). Notable exceptions include the Antarctic fur seal (*Arctocephalus gazella*), leopard seal (*Hydrurga leptonyx*), and crabeater seal (*Lobodon carcinophagus*), which feed extensively (or exclusively, in the case of *L. carcinophagus*) on Antarctic krill (*Euphausia superba*) and the bearded seal (*Erignathus barbatus*) which feeds on small benthic crustaceans and bivalve mollusks in the Arctic. The walrus (*Odobenus rosmarus*) is a specialist that feeds almost exclusively on benthic bivalves. Although many otariids, elephant seals, and the walrus will occasionally kill and eat (often conspecific) pinnipeds or penguins (*e.g.* Bradshaw *et al.*, 1998; Gentry & Johnson, 1981; Harcourt, 1993; Hofmeyr & Bester, 1993; Lowry & Fay, 1984), only the leopard seal is known to depend on warm-blooded prey as a regular food source (Hiruki *et al.*, 1999; Siniff & Stone, 1983). The willingness with which leopard seals approach and confront large warm-blooded prey is clearly illustrated in accounts of close encounters of this species with humans (DeLaca *et al.*, 1975).

Determining the diet of fossil vertebrates is far more problematic than it is for extant taxa. However, a number of methods allow for such predictions. Firstly, observation on *in situ* fossilized stomach contents of a complete or nearly complete skeleton provides the most direct and accurate method for predicting diet. Although this method has been used in some cases (*e.g.* see Currie *et al.*, 1995 for hadrosaurs), the conditions needed to preserve gut contents in association with a skeleton are rarely met. A second method commonly used to assess diet is to catalogue potential prey that occur in the same geologic horizon and locality as the predator. This method is undesirable, however, as carcasses of predator or prey may be transported prior to fossilization and no direct correspondence between the two can be assumed. Isotope analysis is a third method for diet assessment, and has proven very useful in determining whether basal whales fed in freshwater or marine habitats (*e.g.* Roe *et al.*, 1998). However, the isotope method fails to indicate specific prey taken by a predator and is therefore of limited utility in assessing the precise diet of fossil taxa. A fourth method involves the analyses of microwear patterns on teeth, and has proven useful in determining the diets of other fossil carnivores (*e.g.* Van Valkenburgh *et al.*, 1990). Application of this technique to pinnipeds, however, fails to reveal probable diet as pinnipeds do not masticate their food, and no correlation exists between striation morphology and (known) diet in modern taxa (Berta & Adam, unpublished data; but see Gordon (1984), who was able to predict tongue movements in the walrus from tooth striations).

The final and most commonly used method for inferring the diet of fossil taxa uses techniques of functional morphology and analogy with living forms.

By examining the morphology associated with a particular method of capturing and handling prey in living species, inferences of feeding behaviour and diet can often be drawn for fossil taxa with similar morphologies (*e.g.* Van Valkenburgh 1989). Application of comparative methods within a phylogenetic framework also allows for more rigorous evaluation of specific hypotheses of unpreserved traits (*e.g.* behaviour) derived from preserved morphology (Lauder 1995; Witmer 1995).

Aquatic tetrapods, including pinnipeds, are largely limited to using the head for both prey capture and handling, as the forelimbs are typically modified for swimming (Taylor, 1987). Thus, the skull, teeth, and mandibles provide the most reliable indicators of feeding and diet in aquatic forms, and are the regions of the body on which we have concentrated our efforts. We identified the major feeding behaviours of living pinnipeds and craniodental features and diets associated with these bahaviours. We then scored better known fossil taxa for functional characters in an attempt to deduce the feeding behaviour and diet of extinct forms. However, as revealed below, there does not appear to be a strong correlation between morphologies consistent with different feeding behaviours and diet in pinnipeds, as different methods of capture may be employed to obtain many prey types.

METHODS AND MATERIALS

We surveyed the literature to identify prey capture methods employed by modern pinnipeds, and established functional characters of the skull, mandibles, and teeth associated with each feeding type. The condition of these characters was then assessed for all modern pinnipeds in addition to numerous fossil taxa for which adequate material was available. Museums from which specimens were examined are listed in tabl. 2. For brevity, descriptions of the feeding methods and their associated characters are presented in the results section below, along with character distributions among taxa examined. In addition to pinnipeds, representative examples of the terrestrial canoid carnivore groups Canidae, Procyonidae, Mustelidae, and Ursidae were also included for comparison. Insofar as was possible, we sampled two specimens each of males and females, and used only adult specimens [as judged from suture closure and development of secondary sexual characteristics (*e.g.* pronounced sagittal crests)] as listed in tabl. 3. Although most characters consisted of simple binary codings, others were derived from standard measurements of the skull and dentary as detailed in fig. 2. In cases where original fossils or casts could not be observed, we relied on published descriptions and photographs (Barnes & Raschke, 1991; Deméré, 1994*a*, *b*; de Muizon, 1981; de Muizon & Hendey, 1980; Horikawa, 1994; Kohno *et al.*, 1994; Repenning & Tedford, 1977).

In order to infer evolutionary patterns and diversity of feeding strategies, we employed a phylogenetic framework. Unfortunately, no phylogeny produced to date includes complete samples of fossil and extant pinnipedimorph species (although we are presently developing such an analysis). In *lieu* of this, we constructed a composite phylogeny of the pinnipedimorphs (fig. 1) based on the framework of Berta & Wyss' (1994) morphological analysis, which includes better known fossil taxa. Onto this framework we grafted more complete consensus phylogenies of the extant Otariidae and phocid subfamilies Monachinae and Phocinae, as presented by Bininda-Emonds *et al.* (1999). For the Odobenidae, we used Deméré's (1994*a*) phylogenetic analysis, but included one additional taxon, *Protodobenus*, which we place *incertae sedis* as the sister taxon to *Odobenus* plus *Valenictus*. This result is consistent with preliminary analyses of our own data set (Adam & Berta, in preparation).

Table 2. Summary of museum names and abbreviations.

Abbreviation	Museum Name
AMNH	American Museum of Natural History (New York, New York)
LACM	Los Angeles County Museum of Natural History (Los Angeles, California)
NMNH	National Museum of Natural History (Washington, D.C.)
NSMT	National Science Museum (Tokyo, Japan)
SDNHM	San Diego Natural History Museum (San Diego, California)
SDSU	San Diego State University Museum of Zoology (San Diego, California)
UCMZ	University of Calgary Museum of Zoology (Calgary, Canada)

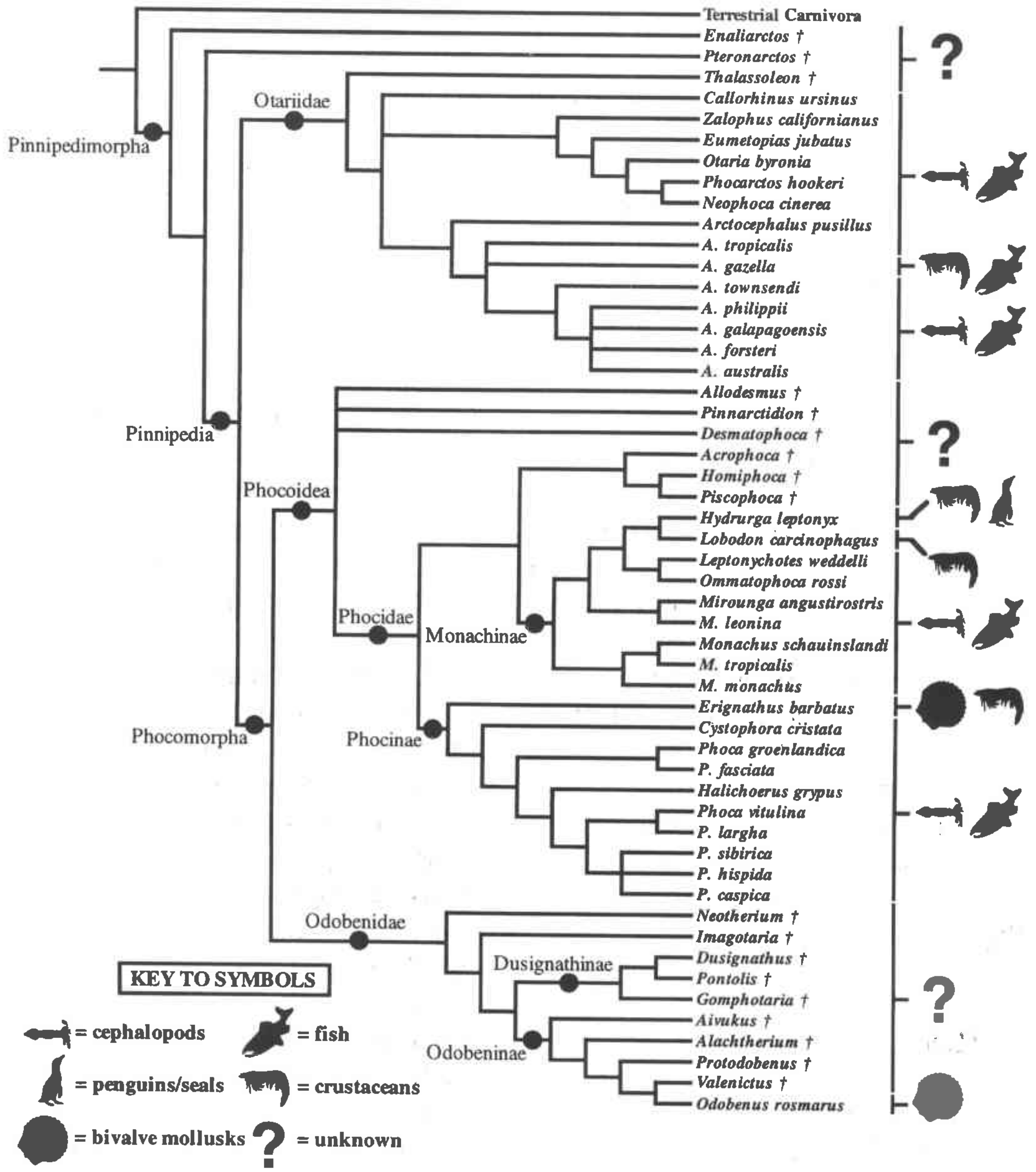


Figure 1. Composite phylogeny derived from Berta & Wyss (1994), Bininda-Emonds *et al.* (1999), and Deméré (1994*a*). Primary diets of extant taxa are indicated to the right by symbols representing fish, cephalopods, bivalve mollusks, crustaceans, and penguins/seals (see key). † denotes fossil taxa.

Due to the hybrid nature of our phylogeny, branch and tree strength indices (*e.g.* bootstrap and jackknife values and tree consistency indices) could not be calculated. With respect to the two major controversies over pinniped internal relationships (*i.e.* point of origin within arctoid carnivores and relationships of walruses to phocids or otariids), however, all of the observed morphological changes associated with different feeding behaviours occur at either more or less inclusive levels of the phylogenetic hypothesis used here. As a result, our observations are not affected by the contrasting opinions held for either basal pinniped affinities or odobenid-phocid-otariid relationships.

Group	Species	Specimens examined
Terrestrial carnivores	*Canis latrans*	NMNH 250483, 250484, 551009, 551042
	Procyon lotor	NMNH 360771, 360782, 360783, 507418
	Lutra canadensis	NMNH 127606, 131449, 136746, 136747
	Ursus maritimus	NMNH 512105, 512108, 512111, 512112
Basal pinnipedimorphs	*Enaliarctos emlongi* †	NMNH 250345, 314290, 314540
	Pteronarctos goedertae †	LACM 5058/123083*; NMNH 167648, 206274, 250282, 250320, 335432
Otariidae	*Arctocephalus australis*	NMNH 484934, 484936, 484937, 501119, 504900
	A. forsteri	NMNH 396062, 396921, 504891, 550479, 550480
	A. galapagoensis	NMNH 259790, 259832
	A. gazella	NMNH 392266*a*, 392266*b*
	A. philippi	SDMNH 21550
	A. pusillus	LACM 52231; NMNH 34902, 484928
	A. townsendi	NMNH 83618, 395886
	A. tropicalis	NMNH 550090, 550091
	Callorhinus ursinus	NMNH 286145, 286149, 286152, 286269, 286270
	Eumetopias jubatus	NMNH 13217, 14507, 21073, 21302, 21309, 270970, 276031, 276040; SDNHM 23174
	Neophoca cinerea	NMNH 484832, 504729, 571463; UCMZ 1994.001
	Otaria byronia	NMNH 23240, 484912, 501114, 550227; SDNHM 23344
	Phocarctos hookeri	NMNH 344983, 344985, 395143, 484526, 848531
	Zalophus californianus	NMNH 16296; SDSU 1010, S-597, uncatalogued
	Thalassoleon mexicanus †	NMNH 215020*
Phocoidea	*Cystophora cristata*	NMNH 188909, 188911, 188914, 188915, 188927, 188931
	Erignathus barbatus	NMNH 230954, 290657, 500249, 500250, 500251, 550411
	Halichoerus grypus	NMNH 19837, 35291, 504211, 504297
	Hydrurga leptonyx	NMNH 270326, 275208, 275245, 396931, 571676
	Leptonychotes weddelli	NMNH 269528, 269529, 269530, 395810, 504875, 550074
	Lobodon carcinophagus	NMNH 269531, 296532, 275204, 550080, 550083
	Mirounga angustirostris	NMNH 38234, 20927, 21895, 260867
	M. leonina	NMNH 15336, 20927, 241199, 484893
	Monachus monachus	AMNH 73607, 73608; NMNH 23250, 219059
	M. schauinslandi	NMNH 243839, 243840, 243849, 334574, 334577, 395999
	M. tropicalis	NMNH 100361, 102523, 102533, 102534
	Ommatophoca rossi	NMNH 270321, 275206, 302975, 339989
	Phoca caspica	NMNH 341615, 341616, 341617
	P. fasciata	NMNH 22915, 311771, 399449, 504959, 571867
	P. groenlandica	NMNH 99436, 188766, 188769, 188766, 188773, 188775
	P. hispida	NMNH 16136, 225766, 225767, 225781, 225794, 305090
	P. largha	NSMT 29056, 29066, 29067, 29069
	P. sibirica	NMNH 175689, 175690, 550028, 550030, 550034
	P. vitulina	NMNH 504085, 504110, 504298, 550044, 550047
	Acrophoca longirostris †	NMNH 360407*, 421632
	Allodesmus kernensis †	LACM 127939*
	Desmatophoca brachycephala †	NMNH 120199*
	Pinnarctidion rayi †	NMNH 250321
	Piscophoca pacifica †	NMNH 360406*
Odobenidae	*Odobenus rosmarus*	NMNH 21331, 22014, 22104
	Aivukus cedroensis †	NMNH 215019*
	Dusignathus seftoni †	SDNHM 38342
	Imagotaria downsi †	NMNH 13487, 175349*
	Pontolis magnus †	NMNH 3792
	Protodobenus japonicus †	NMNH 140726*
	Valenictus chulavistensis †	SDNHM 36786, 38228, 63026, 63237

Table 3. List of specimens examined in this study. Museum abbreviations are defined in Table 2. † denotes fossil taxa, * indicates cast specimens.

Taxon	**Pierce Feeding**					**Suction Feeding**						**Filter Feeding**				**Grip & Tear Feeding**	
	P1	**P2**	**P3**	**P4**	**P5**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**F1**	**F2**	**F3**	**F4**	**G1**	**G2**
Canidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustelidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Procyonidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ursidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Basal Pinnipedimorphs																	
Enaliarctos †	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pteronarctos †	1	1	0	1	1	0	0	0	0	?	0	0	0	0	0	0	0
Otariidae																	
Arctocephalus australis	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. forsteri	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. galapagoensis	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. gazella	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. towndsendi	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. tropicalis	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. philippii	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
A. pusillus	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Callorhinus ursinus	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Eumetopias jubatus	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0
Neophoca cinerea	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0
Otaria byronia	1	1	1	1	1	2	1	1	0	1	0	0	0	0	0	0	0
Phocarctos hookeri	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0
Zalophus californianus	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Thalassoleon †	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Phocoidea																	
Cystophora cristata	1	1	1	1	1	0	0	0	1	2	0	0	0	0	0	0	0
Erignathus barbatus	1	1	1	1	1	3	0	1	0	1	0	0	0	0	0	0	0
Halichoerus grypus	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Hydrurga leptonyx	1	1	1	1	1	0	0	0	1	1	0	0	1	1	0	1	1
Lobodon carcinophagus	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0	0
Mirounga angustirostris	1	1	1	1	1	0	0	0	1	2	0	0	0	0	0	0	0
M. leonina	1	1	1	1	1	0	0	0	1	2	0	0	0	0	0	0	0
Monachus monachus	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
M. schauinslandi	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
M. tropicalis	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Ommatophoca rossii	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Phoca caspica	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
P. fasciata	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
P. groenlandica	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
P. hispida	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
P. largha	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
P. sibirica	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
P. vitulina	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Acrophoca †	1	1	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0
Allodesmus †	1	1	1	1	1	0	1	?	0	1	0	0	0	0	0	0	0
Desmatophoca †	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Homiphoca †	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Pinnarctidion †	1	?	1	1	1	0	0	0	0	?	?	0	0	0	0	0	0
Piscophoca †	1	1	1	1	1	0	?	?	1	1	0	0	0	0	0	0	0
Odobenidae																	
Odobenus rosmarus	1	0	1	0	1	2	1	1	2	3	1	0	0	0	0	0	0
Aivukus †	1	?	1	1	1	1	0	?	1	?	0	0	0	0	0	0	0
Alachtherium †	1	1	1	0	1	2	1	1	1	1	0	0	0	0	0	0	0
Dusignathus †	1	1	1	1	1	1	0	?	1	2	1	0	0	0	0	0	0
Gomphotaria †	1	1	1	1	1	1	1	0	2	3	0	0	0	0	0	0	0
Imagotaria †	1	1	1	1	1	1	0	0	0/1	1	0	0	0	0	0	0	0
Neotherium †	1	1	1	?	1	0	0	0	0	?	0	0	0	0	0	0	0
Pontolis †	1	1	1	?	1	1	0	0	0	2	0	0	0	0	0	0	0
Protodobenus †	1	1	1	0	1	1	1	?	0	1	0	0	0	0	0	0	0
Valenictus †	?	?	?	0	1	2	1	1	3	3	1	0	0	0	0	0	0

Table 4. Summary matrix of codings for characters associated with different pinnipedimorph feeding strategies. Numerical codings (0-3) represent character states described in the text. Unknown character states are indicated by a question mark (?). † denotes fossil taxa.

RESULTS

Feeding Strategies

Methods by which aquatic vertebrates capture and handle prey have been reviewed in Taylor (1987), and most recently by Werth (2000*a*) for marine mammals. From these works and our literature survey, we identified four general feeding behaviours used by pinnipedimorphs to secure and process prey. These are: I) pierce, II) suction, III) filter, and IV) grip and tear feeding. Descriptions of these strategies and the morphologies associated with each are given below. We assigned an alpha-numeric code to each functional character associated with a particular feeding type, with P, S, F, and G representing each of the four feeding strategies described above, respectively. Table 4 summarizes our observations and codings for these characters.

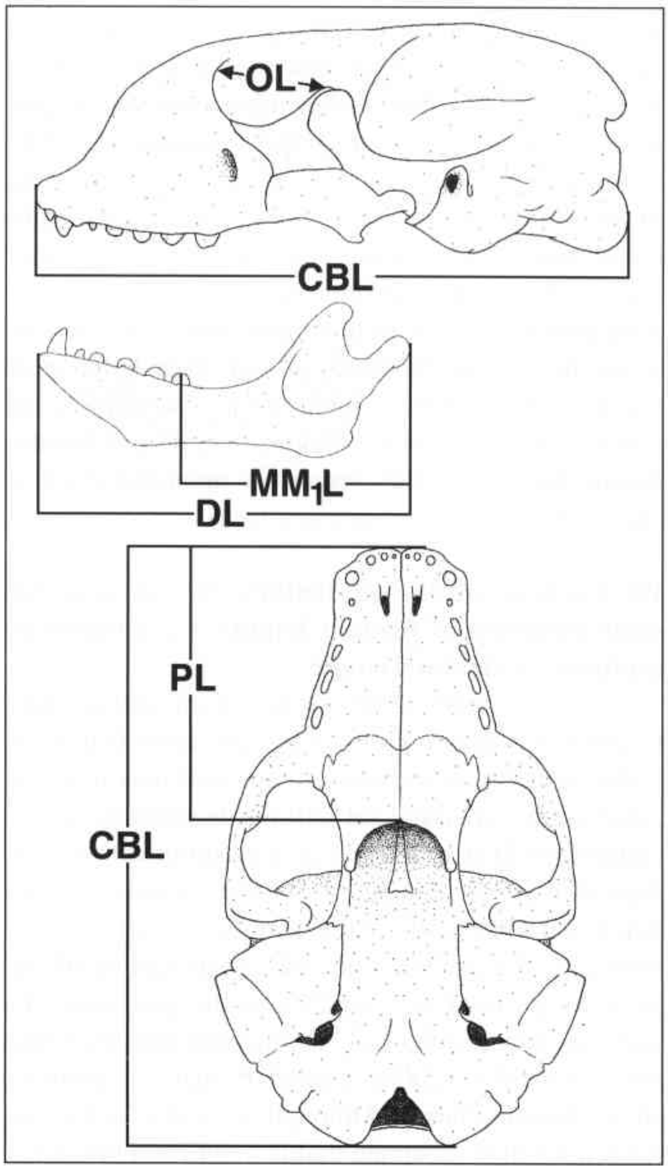
I. Pierce Feeding. Mastication involves the mechanical breakdown of bite-size items of food into smaller pieces that can be more readily swallowed coupled with the beginning of chemical digestion by salivary juices. Modern pinnipeds do not orally process their prey, but instead typically (as with most other marine tetrapods) hunt prey that they can swallow whole (Taylor, 1987; Werth, 2000*a*). The ability to masticate is therefore primitive for arctoid carnivores, as exemplified by the Canidae, Mustelidae, Procyonidae, and Ursidae. In contrast, most aquatic tetrapods utilize a piercing bite, where prey are captured in the mouth and held in place by (usually) small, sharp teeth. Below we identify three characters (P1-P3) that are typically found within the Carnivora and which can be used to differentiate between the primitive masticatory feeding strategy (state 0 for characters P1-P3) and the derived piercing strategy (state 1 for characters P1-P3). Furthermore, the pursuit of prey under water requires adaptation of the special senses to allow for prey detection. Characters associated with these changes are also presented below (P4-P5) as indicative of the terrestrial-aquatic transition. We assume that the derived condition of these latter characters is indicative of under water hunting and swallowing of whole prey, and by corollary non-masticatory pierce feeding. These characters are :

P1. Postcanine teeth with distinct occlusal wear facets. (0 = yes, 1 = no)

Within the Carnivora, the carnassial dentition (fourth upper premolar, P^4, and lower first molar, M_1) is typically modified to form a cutting (*e.g.* most felids and mustelids) or crushing (*e.g.* ursids) surface, or a combination of these (*e.g.* canids). When in occlusion, opposing teeth meet each other and form distinct shearing or grinding surfaces. In a non-masticatory, pierce feeding strategy, opposing teeth do not meet at occlusion and no distinct occlusal wear facets are present. We scored the presence (state 0) or absence (state 1) of occlusal wear facets on postcanine teeth for this character. Precise occlusion of the postcanine teeth occurs only in terrestrial carnivorans. As noted by Berta (1981*a*, *b*), however, both *Enaliarctos* and *Pteronarctos* have a well developed paracone and metacone on P^4, in addition to distinct wear facets on the carnassial set. The remaining postcanine teeth, however, do not bear distinct occlusal wear facets. We thus scored these basal pinnipedimorphs with derived state 1, but recognize that they more likely represent an intermediate stage in the loss of precise postcanine masticatory efficiency. Of additional note is that in extant otariid taxa, occlusion of the posterior teeth is so imprecise that posterior lower postcanines lie labial to the uppers when the jaws are in occlusion. To the best of our knowledge, this condition has not been noted before for otariids and is not found in any other mammalian group. The odobenine *Valenictus* was scored as unknown for this character as it lacks postcanine teeth.

P2. Location of M_1 on dentary. (0 = at approximate midpoint of dentary length, 1 = anterior to midpoint of dentary length)

Greaves (1983, 2000) proposed a model wherein he predicted that in carnivorans, the most beneficial trade-off between maximum gape and maximal bite force at the carnassial set will occur when the lower carnassial (M_1) is located at a position that is less than 60% of the distance from the mandibular condyle to the anterior tip of the dentary. According to his model, to increase bite force the carnassials should be positioned closer (*i.e.* <60%) to the jaw joint. To increase gape while still maintaining maximal bite force, Greaves (2000) predicted that a carnivore should become larger. Although not addressed by his model, it can be assumed that if freed from bite force constraints, a carnivoran could also increase effective carnassial gape by positioning these teeth farther anterior along the dentary length without a need to increase overall size. A loss of masticatory ability at the carnassial dentition, therefore, would be indicated by an anterior migration of M_1. Our observed ratio of MM_1L/DL (fig. 2) revealed that among examined terrestrial carnivores, all species had M_1 positioned approximately at or posterior to the midpoint of the greatest length of the dentary (state 0). In contrast, all pinnipedimorphs with the exception of the walrus had the M_1 positioned well anterior to the midpoint of the dentary length (state 1; fig. 3). *Pinnarctidion*, *Aivukus*, and *Valenictus* were coded as unknown due to the absence of M_1 or absence of well preserved mandibles.



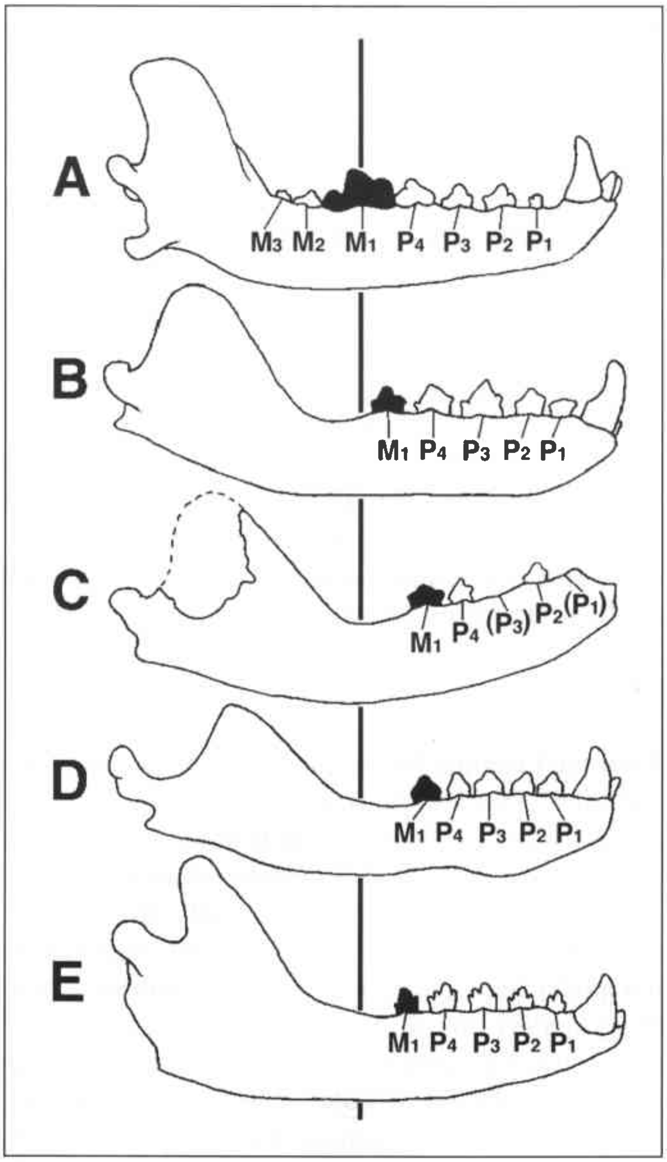


Figure 3. Lateral view of right dentaries of (A) a coyote (*Canis latrans*), (B) *Enaliarctos mealsi*, (C) *Pteronarctos goedertae*, (D) California sea lion (*Zalophus californianus*), and (E) harbour seal (*Phoca vitulina*), scaled to the same size. The dark vertical line represents the midpoint of the dentary length (DL), and premolars (P_{1-4}) and molars (M_{1-3}) are labeled (P_1 and P_3 not preserved in (B)). Note that M_1 (darkened) is positioned anterior to the midpoint in all pinnipedimorphs (B-E) (character P2).

←

Figure 2. Pictorial summary of standard measurements taken from skulls and mandibles. Pictured is the skull and lower jaw of a bearded seal, *Erignathus barbatus*. From top to bottom: skull, left lateral view; left dentary, lateral view; skull, ventral view. CBL=condylobasal length; DL=dentary length; MM_1L=distance of M_1 from mandibular condyle; OL=orbit length (measured as the greatest distance between the tip of the postorbital process and the anterodorsal rim of the orbit); PL=palate length.

P3. Condition of postcanine teeth. (0 = premolars and molars differentiated, 1 = postcanine teeth homodont)

The correspondence between homodonty and pierce feeding has been well established, with homodonty characterizing most secondarily marine vertebrates (Taylor, 1987; Werth, 2000*a*). In the primitive condition (state 0), molars and premolars are well differentiated and each tooth contributes differently to the masticatory breakdown of a bolus. Among taxa exhibiting homodonty, the premolars and molars are similarly shaped and simply used to seize and cripple prey prior to being swallowed whole (state 1). The terrestrial carnivores examined here, plus *Enaliarctos* and *Pteronarctos*, are characterized by state 0, whereas all later pinnipeds have homodont dentition (unknown in *Valenictus*).

P4. Orbit size. (0 = unenlarged, 1 = enlarged)

Under water, the amount of light available for a predator to visually detect evasive prey drops dramatically. In response to low light levels, a number of marine predators (*e.g.* ichthyosaurs) have enlarged the eyes relative to their terrestrial counterparts (Motani *et al.*, 1999). Larger eyes enable these predators to collect more of the available light by photoreceptive cells of the retina. Motani *et al.* (1999) note, however, that eye size also increases with greater dependence of the visual system in detecting prey. Terrestrial carnivorans depend largely on vision in detecting their prey and typically have binocular vision with overlapping left and right fields of view. Pinnipeds also detect prey using visual cues, although overlapping fields of view tend to be situated more dorsally than in terrestrial carnivorans (Hobson, 1966). Given that both terrestrial carnivores and pinnipeds use visual cues and binocularity to detect prey, any difference in eye size is likely to reflect an adaptation to lower light levels under water. Among our sample, terrestrial carnivores have maximum orbit sizes (OL, fig. 2) that range from 13-18% of condylobasal length (CBL, fig. 2) (state 0) whereas in pinnipedimorphs this ratio ranges from 21-33% (state 1), with exception of the group of odobenine walruses *Alachtherium*, *Valenictus*, *Protodobenus*, and *Odobenus* (fig. 4). Similar differences were observed for absolute orbit size, and we believe that potential effects of eye size scaling negatively with body size (Motani *et al.*, 1999) are negligible for the clade examined here. Insufficient material precluded assessment of orbit size in *Neotherium* and *Pontolis*.

P5. Infraorbital foramen. (0 = unenlarged, 1 = enlarged)

Berta & Wyss (1994) found that an enlarged infraorbital canal is synapomorphic for the Pinnipedimorpha. However, the trend towards a large infraorbital canal is widespread among aquatic mammals (Dehnhardt *et al.*, 1999). Although not well understood, it is believed that the mystacial vibrissae, which are innervated by the maxillary branch of the trigeminal nerve passing through the infraorbtal canal, act in monitoring the fluid environment of aquatic mammals (Ashton & Oxnard 1958; Dehnhardt *et al.*, 1999). Tactile sensitivity studies of the vibrissae of captive pinnipeds indicate that they are exceptionally sensitive (*e.g.* Kastelein & van Gaalen, 1988; Kastelein *et al.*, 1990), and it has been suggested that pinniped vibrissae play an important role in detecting prey movements immediately prior to capture (Renouf, 1980). The ability of harbour seals (*Phoca vitulina*) to detect water eddies left by moving objects with their vibrissae has only recently been demonstrated (Dehnhardt *et al.*, 2001). Pending a more thorough understanding of vibrissae and how they are used during prey capture in an aquatic medium, we here interpret a large infraorbital canal to reflect an enlarged maxillary branch of the trigeminal nerve innervating the vibrissal pads. Increased vibrissal innervation is, in turn, indicative of taxa that have completed the transition from land to water and which likely pursued evasive prey under water. Enlarged canals are indicated by both an increase in size and by the anterior opening of the canal on the zygomatic arch (state 1). Unenlarged infraorbital foramina are smaller, with their anterior opening located on the rostrum, and are indicative of prey pursuit and capture on land (state 0). Among our sample taxa, all pinnipedimorphs plus the mustelid *Lutra* are characterized by enlarged infraorbital foramina.

II. Suction feeding. In a fluid environment, the simple act of opening of the jaws creates low pressure inside of the oral cavity relative to the environment, and water moves into the mouth due to the pressure differential. The ability to generate suction has been observed for several pinnipeds, such as the crabeater seal (*Lobodon carcinophagus*; Klages & Cockcroft, 1990). Suction forces generated by most taxa appear to be rather small and functional only at short distances, however, and it is questionable whether or not they are sufficient to capture large mobile prey such as fish and squid. Crabeater seals may be able to use their limited suction to capture multiple small planktonic krill on which they feed, although in the wild they appear to take single prey with simple biting motions (Kooyman, 1981). Although long suspected (Fay, 1982; Gordon, 1984), the direct use of suction to capture and consume prey by a pinniped has only been recently demonstrated for the walrus by Kastelein and colleagues (Kastelein & Mosterd 1989; Kastelein *et al.*, 1994). The walrus is able to produce an impressive -118.8 kPa of oral pressure under water and -87.9 kPa in air (Kastelein *et al.*, 1994). Suction feeding has also been demonstrated in ziphiid (Heyning & Mead, 1996) and globicephalid (Werth, 2000*a*, *b*) odontocete cetaceans and the mysticete gray whale (*Eschrichtius robustus*) (Werth, 2000*a*). There are numerous skeletal characters associated with producing large suction forces with the mouth (below), and analogous modifications of the skull are seen in many suction feeding taxa. For example, suction feeding has been predicted for the Pliocene cetacean *Odobenocetops*, which displays remarkable convergence in skull morphology with the modern walrus (de Muizon, 1993*a*, *b*; de Muizon *et al.*, 1999).

Descriptions of the mechanics and functional morphology of suction feeding in the walrus are given in Gordon (1984) and Kastelein *et al.* (1991, 1994, 1997), and are summarized as follows: once a walrus has exhumed its bivalve prey using a jet of water followed by vibrissal inspection (Kastelein & Mosterd, 1989), the whole bivalve is positioned between the gum and upper lip. The tongue is pressed against the hard palate and the lips pressed tightly against each other. The walrus then retracts its tongue, generating negative intraoral pressure. The foot, body, and siphon are torn from the shells and swallowed. The shell, plus any soft remains, are not ingested and simply dropped. These observations are consistent with the general absence of shells in the stomachs of wild walrus (Fay, 1982).

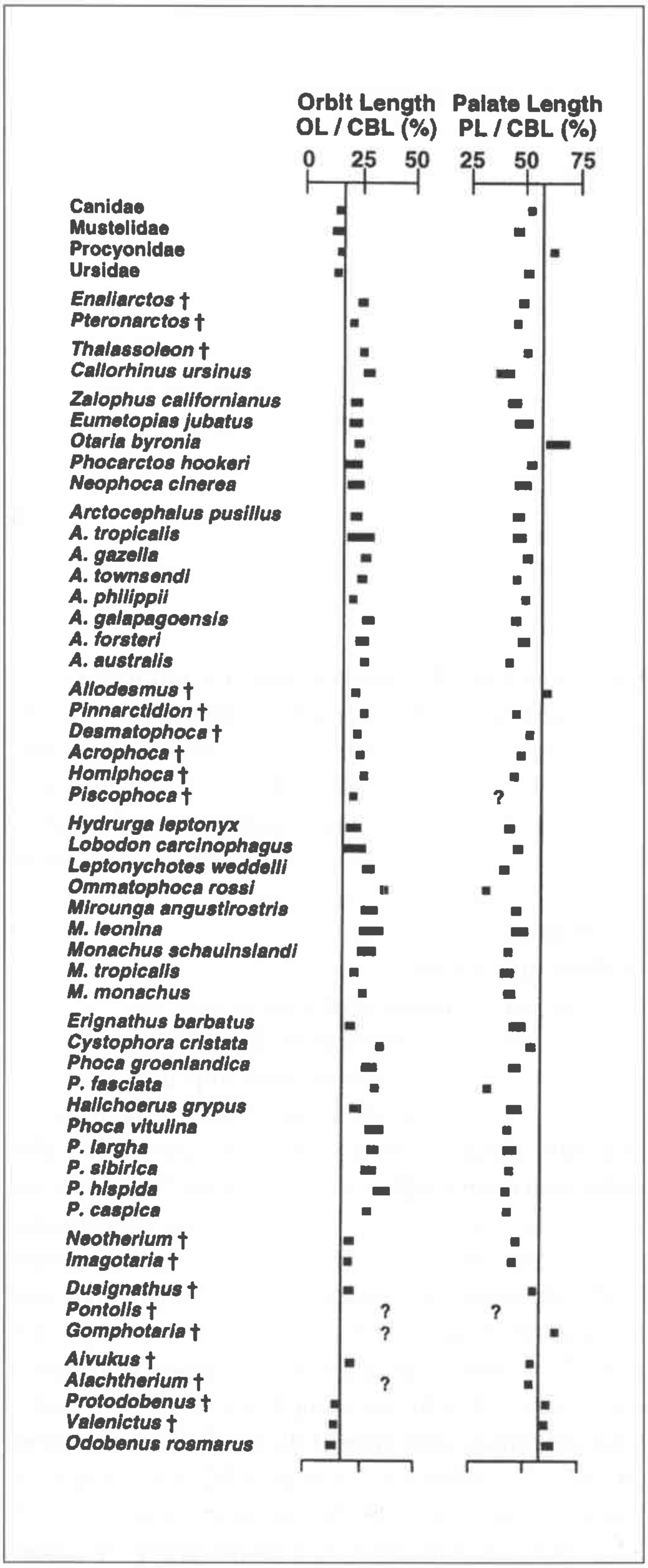


Figure 4. Chart showing the range of values obtained for orbit size (OL/CBL; character P4) and palate length (PL/CBL; character S2). Unknown values are indicated by question marks (?). Vertical solid lines depict threshold values used to define character states (see text).

Although early authors assumed that the tusks of walruses played a role in the excavation of benthic mollusks (see references in Fay, 1982), observations on live animals indicate that the tusks are not used in prey capture (Fay, 1982; Kastelein & Mosterd, 1989; Kastelein & Gerrits, 1990). Rather, the enlarged canine tusks of *Odobenus* and (presumably) other fossil walruses are used during intraspecific battles to establish dominance hierarchies (Miller, 1975) and on occasion to gain purchase on slippery ice (Fay, 1982). We therefore exclude any characters pertaining to the use of tusks in feeding. Characters (S1-S6) functionally associated with suction feeding are :

S1. Vaulting of hard palate. (0 = palate relatively flat, 1 = palate transversely arched, 2 = palate transversely and longitudinally arched, 3 = palate flat but with raised maxillary alveolar processes)

In most terrestrial carnivores and pinnipedimorphs, the hard palate is flat (state 0). The walrus, in contrast, has a palate that is concave dorsally in both transverse and longitudinal planes (state 2). Presumably, this «vaulting» provides greater intraoral space and presents the tongue with an extended space in which it can be protracted prior to being retracted to produce suction (Kastelein and Gerrits, 1990). This additional space would allow for greater suction force to be generated relative to a flat palate. A similar vaulting in both transverse and longitudinal planes is observed in the odobenines *Alachtherium* and *Valenictus*, as well as the southern sea lion, *Otaria*. As recognized by Deméré (1994*a*), in some odobenines (*Aivukus*, *Dusignathus*, *Gomphotaria*, *Imagotaria*, *Pontolis*, and *Protodobenus*) and otariids (*Eumetopias*, *Neophoca*, and *Phocarctos*) the palate is transversely, but not longitudinally, concave (state 1). We propose that this represents an intermediate condition in the evolution of suction feeding, although a lack of information on the suction abilities of these taxa precludes confirmation of this. We also recognize a third condition as represented in the bearded seal (*Erignathus barbatus*), in which although the palate is relatively flat, the maxillary alveolar processes are enlarged and give the ventral rostral surface a concave appearance in transverse section (state 3). The ridge formed by these alveolar processes may act in a similar fashion to the concave moulding of the palate in taxa characterized by state 1.

S2. Lengthening of hard palate.
(0 = absent, 1 = present)

As noted above, large intraoral pressure changes are generated in suction feeders. Kastelein & Gerrits (1990) postulated that in order to cope with these pressures, the hard palate of the walrus is extended posteriorly. Posterior expansion of the hard palate necessarily replaces part of the soft palate, a structure that is likely insufficiently constructed for coping with large intraoral pressure changes. In most taxa examined here, palatal length (PL, fig. 2) is less than 65% of CBL. Numerous taxa, however, stand out in having a palatal length greater than 65% CBL (state 1) (fig. 4) : 1) *Alachtherium*, *Odobenus rosmarus*, *Protodobenus*, and *Valenictus* among odobenines, 2) the dusignathine *Gomphotaria*, 3) *Allodesmus* among phocoids, and 4) *Otaria* among otariids. State 1 also characterizes *Procyon lotor*. This omnivorous species, however, is not predicted to have suction fed, as it does not capture food underwater with the mouth. The posterior palatal extension seen in its skull may indicate palatal strengthening to accommodate torsional forces acting on the rostrum resulting from mastication of hard food items.

S3. Condition of pterygoid hamuli.
(0 = weakly developed, 1 = robust and knob-like)

In association with the large intraoral pressure changes generated during suction, the pterygoid hamuli of the walrus skull have also become enlarged (Deméré, 1994*a*; Kastelein & Gerrits, 1990; fig. 5). Normally, these structures are thin and blade-like (state 0), but in the odobenids *Alachtherium*, *Odobenus*, and *Valenictus* plus the southern sea lion (*Otaria byronia*) and bearded seal, the hamuli are enlarged and knob-like. Kastelein *et al.* (1991) consider this enlargement to be correlated with strong development of the *m. velum palatini* in the walrus, which is the primary supporting muscle of the (reduced) soft palate. Enlargement of this muscle (and the hamuli) is assumed to be related to reinforcing the soft palate for large intraoral pressure changes during suction feeding. The shape of the hamuli is unknown in the odobenids *Protodobenus* (*contra* Horikawa, 1994), *Aivukus*, and *Dusignathus*, as well as the phocoids *Allodesmus* and *Piscophoca*.

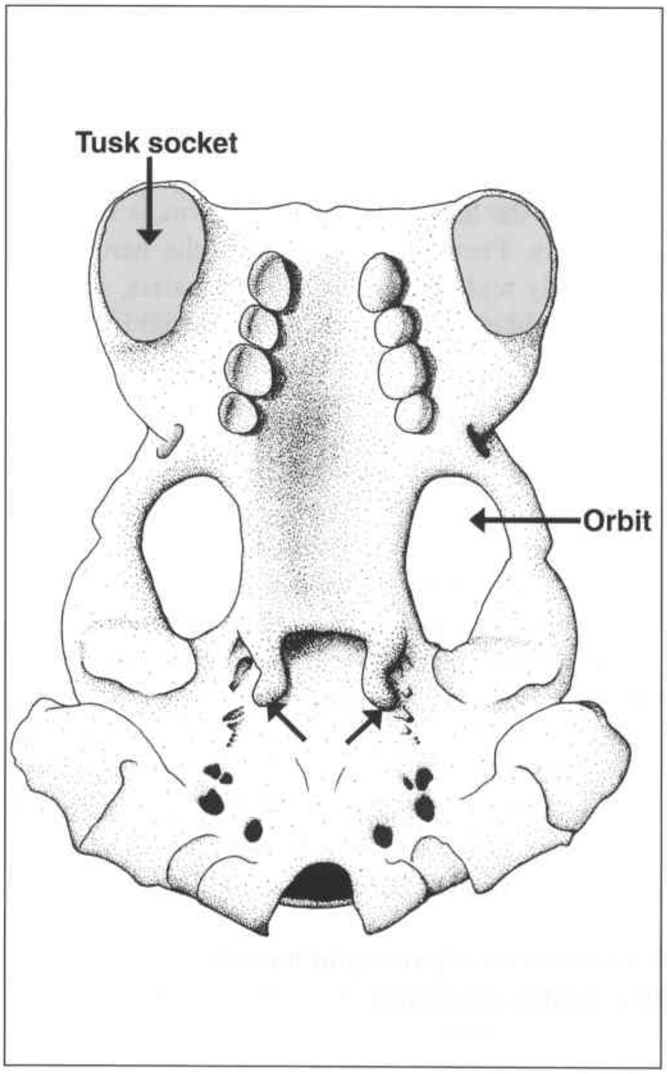


Figure 5. Ventral view of the skull of a modern suction-feeding walrus (*Odobenus rosmarus*) showing robust pterygoid hamuli (arrows; character S3).

S4. Number of upper incisors (per quadrant). (0 = three, 1 = two, 2 = one, 3 = none)

Kastelein & Mosterd (1989) report that walruses extract their bivalve prey from the shells by placing it between the upper lip and gum prior to lingual retraction. As the tongue is retracted, the soft parts of the mollusk are drawn into the mouth (which is typically in occlusion during suction). A loss of incisor teeth in the jaws is likely an adaptive feature to allow the free passage of these soft items into the mouth from the area of the upper gum and labium, where the shell is secured. As discussed below, incisor loss does not contribute to the generation of suction *per se*, and this character must be associated with other characteristics if it is to be interpreted as being indicative of suction feeding. Although the retention of an ancestral number of incisors (state 0) is characteristic of terrestrial carnivores, basal pinnipedimorphs, and otariids, incisor loss is a common feature among phocomorphs. The loss of a single upper incisor (state 1) is found in monachine phocids and the phocine *Cystophora cristata* (hooded seal), as well as in the fossil phocids *Acrophoca*, *Homiphoca*, and *Piscophoca*. State 1 also characterizes the odobenid genera *Aivukus*, *Alachtherium*, *Dusignathus*, and *Imagotaria* [multistate with state 0, after Deméré (1994*a*)]. The loss of two upper incisors (state 2) is found only in the dusignathine walrus *Gomphotaria* and the modern walrus. A complete loss of upper incisors (state 3) is found in the odobenine *Valenictus*.

S5. Number of lower incisors (per quadrant). (0 = three, 1 = two, 2 = one, 3 = none)

As with the preceding character, a loss of incisors in the lower jaw is associated with the free passage of food from the area of the gum and lip to the mouth during suction, and not with the generation of suction. Retention of all three incisors (state 0) is found in terrestrial carnivorans and the basal pinnipedimorph *Enaliarctos*. The loss of a single incisor (state 1) characterizes living and extinct otariids and phocoids, with the exception of the elephant (*Mirounga*) and hooded (*Cystophora cristata*) seals which have lost two lower incisors (state 2). Among the odobenids examined here, *Alachtherium*, *Imagotaria*, and *Protodobenus* have lost a single lower incisor, *Dusignathus* and *Pontolis* have lost two, and *Gomphotaria*, *Odobenus*, and *Valenictus* have lost all lower incisors (state 3). The number of lower incisors is unknown for *Enaliarctos* and *Pteronarctos*, as well as for *Pinnarctidion* and the fossil odobenids *Aivukus* and *Neotherium* (Deméré, 1994*a*).

S6. Condition of mandibular symphysis. (0 = dentaries not ankylosed, 1 = dentaries ankylosed)

Scapino (1981) developed a method for classifying the rigidity of the mandibular symphyses in carnivores, and attempted to correlate symphyseal structure with torsional forces acting upon the lower jaw during feeding. Although not addressed in his paper, the enlarged lingual muscles originating from lower jaws of the walrus (Gordon, 1984; Kastelein *et al.*, 1997) would likely cause considerable torsional forces to be experienced by the mandibles during suction feeding. Assuming a similar response to torsion in terrestrial carnivores and pinnipeds, we coded two states according to whether the mandibular symphysis was completely ankylosed (state 1) or not (state 0). In the unfused state, the mandibular symphyses are relatively flexible and, in our opinion, might become deformed by forces generated by the lingual musculature during tongue retraction. With time, such deformation would likely result in considerable wear on occluding teeth and render them inefficient at food capture and perhaps make them prone to developing pathologies. A more solid foundation would be provided if lingual musculature attached to fused dentaries, a condition that would allow little or no mandibular deformation accompanying tongue retraction during suction feeding. A fused mandibular symphysis is therefore associated with suction feeding, as is an overall increase in the robustness of the mandibles (Kastelein & Gerrits, 1990). Among our sampled pinnipedimorphs, only the odobenines *Odobenus* and *Valenictus* and the dusignathine *Dusignathus* have a fused mandibular symphysis. Among outgroup taxa, only the polar bear (*Ursus maritimus*) has fused mandibles. This latter taxon feeds on seals, and may require additional reinforcement of the lower jaw to cope with potentially large, struggling prey.

III. Filter feeding. The ability to filter feed by any marine mammal is remarkable, as the flow of water through the mouth is bidirectional, meaning that water entering the oral cavity through the mouth must also be expelled out through the mouth. Filter feeding is best known in baleen whales, which usually take in large mouthfuls of water and prey, and expel water via protraction of the tongue as prey items are trapped on the inner surface of the baleen. In the balaenids (right (*Eubalaena* sp.) and bowhead (*Balaena mysticetus*) whales), a unidirectional flow of water is accomplished by maintaining an open gape and swimming slowly through the water (Werth, 2000*a*). Among pinnipeds, the ability to filter feed has only been demonstrated in captive crabeater seals (Klages & Cockcroft, 1990). Previously, King (1961) had predicted that crabeater seals were able to filter feed based on numerous aspects of their jaws and skull, as described below. Mitchell (1989) noted similar morphological features in the toothed mysticete *Llanocetus denticrenatus*, and predicted that it may have been an efficient filter feeder.

F1. Postcanine tooth cuspation. (0 = cusps absent or not lattice-like, 1 = cusps lattice-like)

Among mammals, the postcanine dentition of the crabeater seal is unique in that each tooth bears 3-5 long, distinct and posteriorly bent cusps (fig. 6A). The teeth appear to be quite delicate, and in lateral view each tooth is lattice-like, the form of which would effectively allow the passage of water but not of prey any larger than a couple of millimeters in length (King, 1961; state 1). In other pinnipeds, although distinct cusps are often present (*e.g.* among phocines), none bears the long sieve-like processes of *Lobodon*.

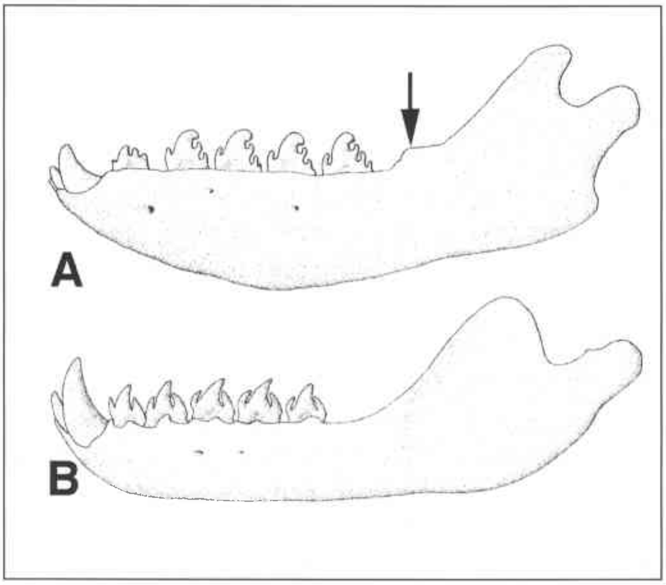


Figure 6. Left lateral view of the dentary of (A) a crabeater seal (*Lobodon carcinophagus*) showing the unique cusp pattern (character F3) and post-dental ridge (arrow; character F4) associated with filter feeding, and (B) a leopard seal (*Hydrurga leptonyx*) showing the enlarged incisors (compare with A; character G1) and sharply pointed cusps of the postcanine dentition (character G2) associated with grip and tear feeding.

F2. Postcanine tooth interdigitation.
(0 = not or only slightly interdigitating,
1 = strongly interdigitating)

In addition to the lattice-like appearance of individual teeth in crabeater seals (character F1), King (1961) also notes that when the mouth is closed, upper and lower teeth interdigitate in such a way that only very small gaps penetrate between the cheek teeth (state 1). Thus, both individual teeth (character F1) and their occlusal interaction preclude the escape of small prey from within the oral cavity while water is being expelled. Precise interdigitation of upper and lower postcanine teeth is also observed in the leopard seal (*Hydrurga leptonyx*) as well as the fossil phocid *Acrophoca*. In contrast, among other pinnipedimorphs the teeth either occlude or, if they interdigitate, large gaps exist between the teeth through which small prey would likely escape (state 0).

F3. Height of postcanine teeth.
(0 = low crowned, 1 = high crowned)

In order to prevent prey escape, the postcanine teeth of a filter feeding pinniped (*e.g. Lobodon*) must be high crowned such that the apex of the tooth closely approaches the gingivum of the opposing jaw in occlusion. The postcanines of the crabeater and leopard seals are markedly high crowned (state 1) relative to the low crowned teeth of other pinnipedimorphs and terrestrial carnivores (state 0).

F4. Post-toothrow processes.
(0 = absent, 1 = present)

An additional feature of the crabeater seal feeding apparatus is the presence of conspicuous postdental ridges on the maxilla and dentary (King, 1961; fig. 6A; state 1). In occlusion, these ridges interdigitate in a manner similar to that described above for the teeth (character F3), and likely act in preventing prey escape through the edentulous angle of the mouth. Although King (1961) reports that similar, but smaller, ridges develop in other lobodontine seals, we were unable to confirm this from our sampled specimens. The absence of postdental ridges (state 0) is plesiomorphic, and indicates non-filter feeding.

IV. Grip and tear feeding. With few exceptions, marine predators feed on prey that they are able to consume whole. Among modern marine mammals, only the killer whale (*Orcinus orca*) and leopard seal (*Hydrurga leptonyx*) regularly feed on, and are capable of dismembering, large prey (Werth, 2000*a*). In the killer whale, the carcass of a large prey item may be torn apart with coordinated efforts of two or more individuals, pressed against the substrate to hold the carcass while swallowable chunks are torn off, or similarly sized pieces may be removed by biting and shaking movements of the head (Guinet *et al.*, 2000; Werth, 2000*a*). Leopard seals appear to utilize only the last of these techniques. When feeding on another seal or penguin, the leopard seal grasps onto the prey item at the water surface of and, shaking its head from side to side, tears off bite size pieces of fat and skin (Hiruki *et al.*, 1999; Werth, 2000*a*).

G1. Enlarged incisors.
0 = absent, 1 = present and not procumbent.

As might be expected of an animal that dismembers prey by gripping the skin and blubber with the anterior dentition and shaking its head, the incisors of the leopard seal are unusually robust and caniniform (fig. 6B; state 1). In most other pinnipedimorphs, the incisors are small and of a size comparable to terrestrial carnivorans (state 0). One exception is the Weddell seal (*Leptonychotes weddelli*), which has enlarged, procumbent, and caniniform incisors that are used to crack ice that forms over breathing holes (Stirling, 1969). We consider the procumbency of these teeth to render them inefficient as gripping teeth, and therefore group enlarged, but procumbent, incisors with unenlarged incisors (this categorization is made with respect to feeding behaviour only - we recognize that large, procumbent incisors are clearly autapomorphic in *L. weddelli* with respect to phylogenetic character transformation).

G2. Shape of postcanine tooth cusps. 0 = not long and sharp, 1 = long and sharp.

Although the postcanine dentition of the leopard seal is homodont, it is unique among pinnipeds in that each tooth has three distinct and sharp cusps that bear witness to their habit of catching large struggling prey (fig. 6B; state 1). Other pinnipedimorphs (with the exception of the crabeater seal, see character F1), have relatively simple homodont postcanine dentition with no sharp and elongate cusps (state 0).

DISCUSSION

Evolution of feeding strategies

Pinnipeds arose from terrestrial arctoid carnivores previous to the Late Oligocene, and have evolved four methods for capturing their prey under water. Pierce feeding involves grabbing prey and swallowing it whole. The use of strong suctional forces to capture and dismember prey is characteristic of suction feeding. Filter feeding is accomplished by taking a mouthful of prey-laden water, and subsequently straining the water and swallowing the prey. Grip and tear feeding involves grasping a large warm-blooded prey item with the anterior dentition and ripping swallowable pieces from it with shakes of the head.

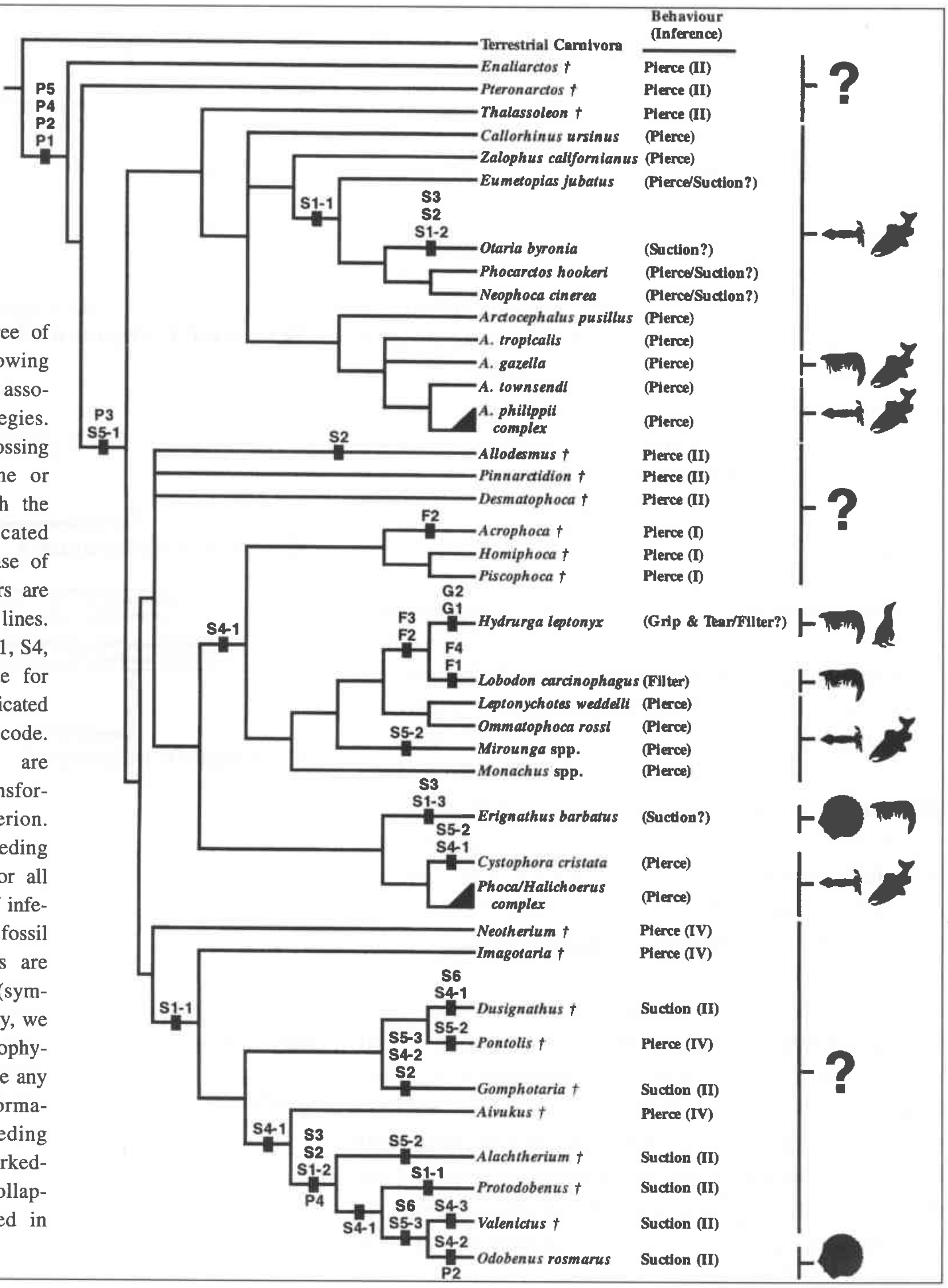


Figure 7.
Condensed phylogenetic tree of the Pinnipedimorpha showing character transformations associated with feeding strategies. Each thick vertical bar crossing an internode indicates one or more transformations, with the specific character indicated above each bar. In the case of reversals, specific characters are indicated below thickened lines. For multistate characters (S1, S4, and S5), the specific state for each transformation is indicated following the character code. Transformation positions are based on the delayed transformation (DELTRAN) criterion. Predicted and known feeding behaviours are indicated for all taxa, in addition to level of inference (in parentheses) for fossil taxa. Principle prey types are also indicated to the right (symbols as in fig. 1). For clarity, we have collapsed larger monophyletic groups that do not have any internal character transformations associated with feeding and which do not differ markedly in diet. A complete (uncollapsed) phylogeny is depicted in fig. 1.

When characters associated with these different feeding strategies are considered in a phylogenetic framework (fig. 7; de Luis & Adam, 1998), a number of trends become evident. However, the interpretation of behaviour and other unpreserved traits from functional osteological characters warrants considerable caution, as has been admonished by numerous authors (*e.g.* Lauder, 1995; Witmer, 1995). Witmer (1995) provides a method for evaluating inferences on the condition of unpreserved traits (*e.g.* behaviour) in fossil taxa from preserved (*e.g.* osteodental) traits within an explicit phylogenetic framework. He defines three levels of inference, as follows. A level I inference (fig. 8A) requires that two extant taxa, which have a similar behavioural trait that is functionally related to a common morphologic trait, bracket a fossil taxon of interest. If the fossil taxon also shares the morphologic trait, it can be decisively assumed that it too possessed the (unpreserved) behavioural trait. Level II inferences (fig. 8B) occur when the two bracketing extant taxa have dissimilar morphologic and behavioural traits. If it can be established that the extant sister taxon to the fossil taxon and the fossil taxon itself shared a certain preserved feature that is functionally related to a behavioural trait in the extant taxon (but not possessed by the more basally positioned extant taxon), then it is equivocal as to whether or not the fossil taxon possessed that behaviour. In level III inferences (fig. 8C), bracketing extant taxa have dissimilar morphological and behavioural traits, and the morphological feature of interest in the fossil taxon is not shared by either of the bracketing taxa. Inference on the behaviour of the fossil taxon in this case is purely speculative.

To Witmer's (1995) three levels of inference, we here define a fourth based on Lauder's (1995) observation that changes in behavioural traits may precede corresponding morphological changes along a phylogenetic trajectory. In this situation, the fossil taxon of interest would share a similar (plesiomorphic) morphological feature with the basally positioned extant bracket for which a known, functionally related, behaviour exists. The other extant bracket, conversely, would possess a different morphology and behaviour. Although the fossil taxon possesses the plesiomorphic morphology, any inference about its behaviour is equivocal (fig. 8D) – it may or may not be similar to the behaviour possessed by the plesiomorphic bracketing taxon. We consider level II and IV inferences to be similar in their level of support.

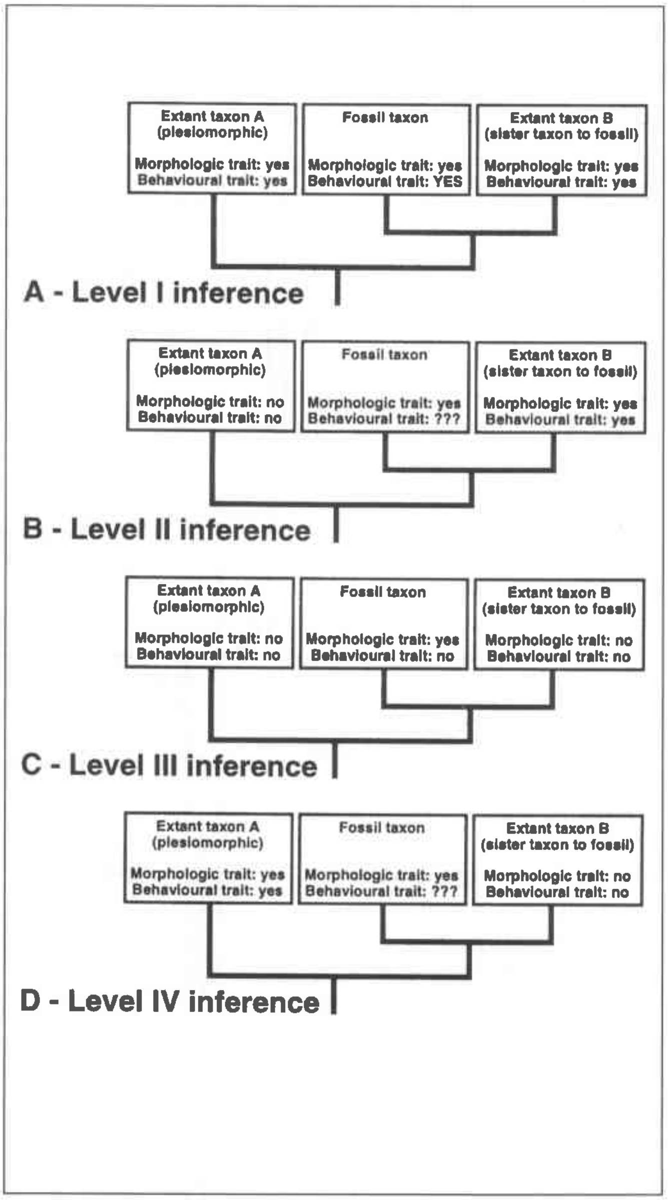


Figure 8. Schematic representation of different levels of inference that can made using the extant phylogenetic bracket method within a phylogenetic framework. See text for further details (A-C adapted from Witmer, 1995; D new inference).

Bearing these cautions in mind, it is possible to evaluate the probable feeding strategies utilized by fossil taxa. Relative to terrestrial carnivorans, pierce feeding in pinnipedimorphs is evidenced by their lack of precise occlusion (character P1), anterior migration of the postcanine dentition (character P2), and tendency towards homodonty (character P3). The stem pinnipedimorphs *Enaliarctos* and *Pteronarctos* still possessed a distinctly carnassial dentition, although other postcanine teeth in these taxa show a trend toward homodonty (fig. 7). This is likely representative of an intermediate condition in the evolution of pierce feeding of later pinnipeds. That extant and fossil pinnipedimorphs pursue(d) prey underwater is further evidenced by their enlarged orbits (character P4) and maxillary branch innervating the vibrissal pad (indicated by enlarged infraorbital foramina; character P5).

Pierce feeding appears to be plesiomorphic for the Pinnipedimorpha, and is the first evolving prey capturing strategy of pinnipedimorphs when they evolved from arctoid carnivores during the Late Oligocene or earlier. It is also the strategy that characterizes most fossil and living pinnipedimorphs, including the basal taxa *Enaliarctos* and *Pteronarctos* in addition to all otariids (with the exception of *Otaria*), the fossil phocoids *Allodesmus*, *Desmatophoca*, *Pinnarctidion*, *Acrophoca*, *Homiphoca*, and *Piscophoca*, plus all extant phocids except the monachines *Hydrurga* and *Lobodon* and the phocine *Erignathus*, as well as the odobenids *Neotherium*, *Imagotaria*, *Pontolis*, and *Aivukus*. Some of these taxa are, however, also characterized by traits associated with suction feeding, a problem that is discussed later. For *Enaliarctos*, *Pteronarctos*, *Thalassoleon*, and the fossil phocoids *Allodesmus*, *Pinnarctidion*, and *Desmatophoca*, the assignment of pierce feeding is a level II inference in that there is no basal extant bracketing taxon relative to these groups that displays pierce feeding. For the three taxon group including *Acrophoca*, assignment of pierce feeding represents a level I inference in that extant pierce feeding relatives occur both as sister taxa and immediately basal to these fossil forms (*i.e.* among monachine and phocine phocids, respectively). A level IV inference is evoked in assigning *Neotherium*, *Imagotaria*, *Pontolis*, and *Aivukus* to the pierce feeding class, as the only extant bracketing taxon above the node uniting these genera is the modern walrus, which does not possess similar pierce feeding habits or morphology.

Morphologies consistent with filter and grip and tear feeding are found only within the Phocidae. *Lobodon* is unique in having all four filter feeding characters (lattice-like postcanine dental cusps, precise interdigitation of postcanines, high crowned teeth, and postcanine ridges). *Lobodon*'s sister species, *Hydrurga*, is similar in having high crowned, interdigitating teeth in addition to uniquely possessing enlarged incisors and sharp postcanine cusps associated with grip and tear feeding. This suggests that *Hydrurga* also has a limited capacity to filter feed, and that grip and tear feeding evolved from a filter feeding ancestor. The possession of interdigitating teeth in the fossil taxon *Acrophoca*, while superficially indicative of potential filter feeding, must be treated as a level III inference when placed in a phylogenetic framework as it is not immediately bracketed by any extant filter feeding ancestors.

Although not included in this phylogenetic analysis, the western Atlantic fossil seal *Lobodon vetus* (known only from a single tooth) appears to have postcanine dentition that bears striking similarity to *L. carcinophagus* and may place the origin of filter feeding as early as the Miocene. Unfortunately, the dating and taxonomic affinities of this specimen are questionable as the geologic age of deposits on New Jersey's coastal plain are problematic and the holotype specimen has been lost (Ray, 1976). No fossil record exists for *L. carcinophagus* or *Hydrurga*. If the fossil record of *L. vetus* is inaccurate (which is probable), then filter and grip and tear feeding appear to be recent feeding behaviours found only in extant taxa.

Suction feeding is characterized by elongation and vaulting of the hard palate, enlargement of the pterygoid hamuli, and fusion of the mandibular symphysis. Although included above with other characters indicating suction feeding, the loss of incisors does not by itself indicate this type of feeding, as incisors (or lack thereof) do not contribute to the generation of suction forces. Rather, incisor loss in the presence of other suction feeding characteristics indicates that the entrance into the oral cavity is relatively free of obstruction – a feature that would enhance the efficiency of suction feeding. For this reason, the loss of either upper or lower incisors (characters S4 and S5, respectively) were ignored in lineages that did not exhibit other adaptations for feeding by suction (*e.g.* in lineages predicted to feed by piercing prey, mentioned above).

A trend towards suction feeding is observed in a number of independent pinniped lineages. Among the odobenids, fossil members of both the dusignathine and odobenine lineages appear to have independently adapted to suction feeding (a level II inference). As previously noted by Barnes and Raschke (1991), *Gomphotaria* shows several adaptations consistent with suction feeding, including an elongate and transversely arched palate and the loss of two upper and all three lower incisors. *Dusignathus* has a similarly transversely arched palate, has lost one upper incisor, and in addition has a fully ankylosed mandibular symphysis. With the exception of *Aivukus*, all odobenine walruses share enlarged pterygoid hamuli (unknown in *Protodobenus*), elongated hard palates and, with the exception of *Protodobenus*, have deeply vaulted palates. *Valenictus* and *Odobenus* also have fully ankylosed mandibles. All odobenines have lost some or all (*Valenictus*) of the incisors, with the exception of *Protodobenus*.

In addition to the odobenids, adaptations for suction feeding (not considering incisor loss) are also seen in the extant southern sea lion (*Otaria*) and the bearded seal (*Erignathus*). Unfortunately, neither basic descriptions nor behavioural studies of feeding in *Otaria* have been published, and it cannot be confirmed whether or not this sea lion is able to feed by suction. Deméré (1994*a*) and Burns (1981) both indicate that *Erignathus* is an efficient suction feeder, although behavioural studies confirming this have not been conducted. As such, designating either species as a suction feeder requires a level III inference, as neither is immediately bracketed by a known suction feeding taxon. However, several characters associated with suction feeding in pinnipeds are also found in suction feeding ziphiid whales (Heyning and Mead, 1996). Given the taxonomically broad-ranging commonality of these characters, we postulate that both *Otaria* and *Erignathus* do indeed have a limited capacity to suction feed, although their abilities are unlikely to be as strong as has already been observed in the walrus. This hypothesis is readily testable, as both species are extant (although such a study is beyond the scope of this paper). In addition to behavioural studies, examination of recently ingested prey recovered from the stomachs of these species may shed some light on how the prey were captured.

DIET OF FOSSIL PINNIPEDIMORPHS

As noted above, the diet of extant species is generally well known. Given that we know the diets of living pinnipeds and have generated hypotheses for the different feeding strategies used to capture their prey, what can we predict about the diet of fossil taxa? In *lieu* of alternative methods for determining the diet of fossil taxa (*e.g.* preserved stomach contents), we must rely on analogies with the functional morphology associated with different feeding strategies and diet in living taxa. This method requires secondary speculations (*i.e.* diet) to be drawn from primary speculation (*i.e.* feeding behaviours), and the compounded sources of error require that predictions of diet in fossil forms be treated with considerable caution. Indeed, the unfortunate answer to the question posed above is that even among extant species there appears to be only loose correlation between specific diets and different feeding strategies.

For example, suction feeding has been demonstrated for the walrus and is predicted here for both *Otaria* and *Erignathus* based on similarities in craniodental functional morphology. These taxa, however, feed on very different food items. Both the walrus and *Erignathus* feed on the soft portions of benthic bivalve mollusks, while the latter also feeds on epibenthic crustaceans (Lowry *et al.*, 1980). In contrast, *Otaria* eats comparatively larger and more mobile fish and squid (George-Nascimento *et al.*, 1985; Koen Alonso *et al.*, 1999). Thus, suction feeding appears to be an efficient method for capturing and consuming a wide variety of food items, and predictions of diet in fossil taxa using functional morphology must take this into consideration.

The diet of *Protodobenus japonicus* has previously been predicted to be primarily fish and squid, based on the observation that this species has well developed upper incisors that would have precluded bivalve dismemberment as seen in the modern walrus (Horikawa, 1994: p. 325). This prediction parallels the observed morphology and known diet of *Otaria*.

However, *Erignathus* also possesses upper incisors and is efficient at removing the foot of clams (*Serripes* sp.), presumably because the foot is exposed when the clam is excavated. In light of a broader taxonomic survey, the diet of *Protodobenus* cannot accurately be predicted. Similar arguments can be made for Deméré's (1994*b*: p. 97) postulation that the sympatric odobenids *Valenictus chulavistensis* and *Dusignathus seftoni* fed on benthic invertebrates and fish or squid (respectively) and Barnes and Raschke's (1991: p. 10) prediction of molluskivory for *Gomphotaria pugnax*.

In a similar fashion, filter feeding is a specialization of the crabeater seal (*Lobodon*) and, to a lesser extent, the leopard seal (*Hydrurga*). Krill constitutes a large proportion of the known diet in these seals, and it might be surmised that fossil taxa exhibiting characters consistent with a filter feeding strategy fed on krill. However, krill also constitutes a large portion of the diet of the Antarctic fur seal (*Arctocephalus gazella*), a species that shows no characters consistent with filter feeding. Furthermore, *A. gazella* and other piscivorous/teuthophagous members of the *Arctocephalus* clade are so similar in craniodental features that distinguishing skulls from individual species of the genus is problematic (Repenning *et al.*, 1971). Given this similarity, it is improbable that the distinct diet of *A. gazella* could have been accurately predicted from craniodental features alone.

SUMMARY AND FUTURE DIRECTIVES

We have shown that although commonly employed morphologic features of the skull and teeth may be used to predict the feeding behaviour of pinnipeds, extending these observations to predict the diets of fossil or unknown taxa warrants considerable caution. Among living species, pierce feeding is most commonly associated with piscivorous or teuthophagous diet. However, a pierce feeding morphology is also sufficient for capturing zooplankton, as observed in *A. gazella*. Similarly, the apparent specializations of the stenophagous *Lobodon* for filter feeding do not preclude other species from a zooplanktonic diet. A suction feeding morphology, although commonly associated with a benthic invertebrate diet (*e.g. Odobenus* and *Erignathus*), is also found in the fish- and squid-eating *Otaria*. Previous predictions of diet for fossil taxa based on morphology may or may not be correct in light of this broader taxonomic survey and phylogenetic framework.

Given these problems, how can we progress to better resolve the diet of fossil pinnipeds? Certainly the strongest arguments will be those that utilize all available sources of evidence. We recommend that an important first step is the assessment of the above characters in the fossil species to assess potential feeding behaviour. It is also possible that other, as yet undescribed, craniodental features might reveal clues to the diet of extinct pinnipeds. For example, a comparative biomechanical analysis of lever arms of the masseter and temporalis muscles acting on the lower jaw in relation to feeding behaviour or diet has not yet been conducted for the pinnipedimorphs. Similarly, we observed reduced (relative to other pinnipeds) orbital size in all odobenines with the exception of *Aivukus* - this might be expected of species that do not rely solely on visual cues for detecting sessile prey (*i.e.* benthic invertebrates). However, too little is known about the visual systems in pinnipeds at present to infer how the structure and orientation of the eyes might contribute to the capture of different types of prey. In looking for new characters to predict diet, however, we stress that any study should be comparative and should sample broadly those taxa described above as having different feeding behaviours and/or diets. The use of a phylogenetic framework will also benefit such a study to assess whether the morphology in question (and perhaps diet) is the result of homology or homoplasy.

Clues from the environment at the time of deposition should also be taken into consideration. For example, sediments associated with a given fossil pinnipedimorph, and the potential prey that they contain, should be examined. As noted earlier, however, pre-depositional transport of carcasses presents problems in that predator-prey interactions cannot be assumed. Examination of multiple, independent specimens of the fossil taxon would help to reduce ambiguity.

Barnes and Raschke (1991) additionally used features of swimming behaviour to infer the probable diet of *Gomphotaria pugnax*. The specimen of *Gomphotaria* that they described (LACM 121508) is pathological in that the right elbow is ankylosed due to an arthrosis of unknown origin. They speculated that due to the pathology, in life the specimen would have been unable to produce the fine movements required to capture agile prey and was therefore restricted to shallow water where it fed on benthic invertebrates (Barnes and Raschke, 1991: p. 11). Although their interpretation appears to be flawed in that walruses use the hind limbs for generating thrust during fast swimming and forelimbs for fine movement at low speeds (Gordon, 1981), an exploration of locomotor ability and other aspects of the biology of pinnipedimorphs may very well contribute to a better understanding of potential diet in some fossil taxa.

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