A MORPHOLOGICAL PERSPECTIVE ON THE PHYLOGENETIC RELATIONSHIPS OF THE EXTANT PHOCID SEALS (MAMMALIA: CARNIVORA: PHOCIDAE)

by

O. R. P. BININDA-EMONDS & A. P. RUSSELL

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INTRODUCTION

As a group, the true or earless seals (Mammalia: Carnivora: Phocidae) present one of the more interesting puzzles in mammalian systematics. The roughly century-old debate on the position of the phocids within the carnivores (and especially their placement relative to the remaining pinnipeds) has attracted consistent attention, but the internal relationships of the group remain reasonably poorly studied to this day. About the only point of universal agreement is that the phocids are a natural, distinct group. It remains for an all-encompassing study employing a suitably rigorous methodology (such as cladistic analysis) to attempt to resolve the points of contention or uncertainty in phocid systematics.

Characterization of the Phocidae

The phocid seals have been referred to as being among the most specialized of carnivores (Wyss 1988a). Like all pinnipeds, the phocids are amphibious and are characterized by many features that can be interpreted as adaptations to an aquatic environment. These range from a fusiform, streamlined body shape and flippers that enhance aquatic locomotion, to the many specializations of the inner ear required for efficient underwater hearing (see Repenning 1972; de Muizon 1982a), to a simplified homodont dentition to help capture their slippery aquatic prey (see Chapskii 1955a). However, they are clearly distinguished from the remaining pinnipeds (and especially the sea lions and fur seals) by features denoting a greater adaptation to the aquatic environment: the lack of a protruding external pinna (as in the walrus as well), their generally superior diving ability (Costa 1993), and their reliance on the hind limbs for aquatic locomotion. In fact, the modifications associated with this last point are so great as to define perhaps the most definitive phocid characteristic, the inability to turn the hind limbs forward to support the weight of the body on land. Thus, the phocids are restricted on land to some form of crawling locomotion: inchworm-like movements (with or without assistance from the flippers), a modified "swimming" type of locomotion, and/or rolling and sliding (O'Gorman 1963; Ridgway 1972; King 1983).

The phocids inhabit both the northern and southern hemispheres, although they are largely restricted to the polar and sub-polar regions. The limits of their distribution seem to be marked by the 20°C summer isotherm, with only the monk seals (*Monachus* spp.) breaking this rule of thumb to inhabit tropical climes (Davies 1958a; McLaren 1960a; King 1964). The phocids are the only pinnipeds to inhabit Antarctica year-round, with several species being largely tied to the ice along the continent (see King 1968). One curiosity of phocids among pinnipeds is their ability to survive in estuarine and freshwater habitats (King 1983), allowing for the existence of many populations or entire species in land-locked lakes (Doutt 1942; Davies 1958b; King 1983).

The phocids show a tremendous diversity in size, spanning from the largest to among the smallest of all pinnipeds. Smallest of all phocids are the ringed seals (*Pusa* spp.) which average about 1.4 m nose-to-tail length, while the largest is the male southern elephant seal (*Mirounga leonina*) which spans four to five metres in length and can weigh up to 3.6 tonnes (King 1983).

Taxonomic and systematic history

The distinctiveness of the phocids has long been recognized. They were first accorded familial status by Brookes (1828) and, except for minor transient alterations, the membership of the family has remained the same ever since (although species assignments are contentious in some cases; see Appendix A for the list of species recognized here). Monophyly of this group has never been seriously challenged and appears to be universally accepted today (de Muizon 1982a; Wyss 1988a).

The higher level taxonomy of the phocids has been surprisingly stable in view of how historically contentious their placement within the carnivores has been (see below). The phocids are the only extant members of the superfamily Phocoidea (Smirnov 1908), or those pinnipeds that are unable to turn the hind limbs forward on land. Together with the Otarioidea (Smirnov 1908; sea lions, fur seals, walrus, and allied fossil forms), they constitute the Pinnipedia (Illiger 1811). Although their arctoid affinities are readily accepted (Flynn et al. 1988), the distinctiveness of all pinnipeds from the remaining fissiped carnivores has led them to be viewed as a separate order (e.g., Scheffer 1958; Ewer 1973; Corbet & Hill 1991), or, more commonly, as a suborder within the carnivores (e.g., Turner 1848; Flower 1869; Mivart 1885; Simpson 1945; King 1983). However, the possibility of a diphyletic origin of the pinnipeds has led some workers to abandon a distinct Pinnipedia altogether (e.g., McKenna 1969; Mitchell & Tedford 1973).

Taxonomy within the phocids largely reflects the historically poorly described and largely unresolved internal relationships of the phocids. Early taxonomies generally divided the phocids into four main subfamilies [but see Allen (1880) for a more complete review]: the Cystophorinae (Gill 1866; hooded and elephant seals), Lobodontinae (Gill 1866; Antarctic seals), Monachinae (Trouessart 1897; *Monachus* spp.), and Phocinae (Gill 1866; remaining northern hemisphere seals). Although this taxonomy is generally representative of the major phocid types, the granting of equal taxonomic status to each group does not appear to be justified.

Throughout much of their taxonomic history, the Lobodontinae and Monachinae have been alternately separated and rejoined, a fact indicating the general lack of distinctiveness between the two taxa. Scheffer (1958), holding that the only real distinction between the two taxa was one of geography, subsumed the two as tribes (Lobodontini and Monachini respectively) within a newly defined Monachinae.

The next major step involved the dismantling of the Cystophorinae by King (1966). The Cystophorinae were erected largely on the basis of two features: a 2/1 incisor formula and the possession of some form of inflatable nasal proboscis in the adult males [but see King (1966) and Ridgway (1972) for additional minor similarities]. It continued to be recognized despite numerous obvious differences between its two constituent genera (*Cystophora* and *Mirounga*), including the morphology of the nasal sac and manner in which it is inflated (Reeves & Ling 1981; King 1983; Kovacs & Lavigne 1986). Finally, King (1966) argued that the two diagnostic cystophorine features likely arose via convergence and pointed to a suite of 17 other cranial and post-cranial features that allied *Cystophora* with the "northern" seals and *Mirounga* spp. with the "southern" seals. McLaren (1975) later ascribed the convergent cystophorine features [also found in the fossil pinniped *Allodesmus*

(Mitchell 1975)] as being due to feeding specializations and sexual selection. Both genera were later established as members of monotypic tribes within their respective subfamilies (Burns & Fay 1970; de Muizon 1982a).

Thus, two subfamilies are typically recognized today – the Monachinae and Phocinae, corresponding roughly to the seals of the southern (plus *Monachus* spp.) and northern hemispheres respectively – with the previously recognized subfamilies mentioned above largely relegated as tribes within this scheme. Although generally accepted as being paraphyletic, the Cystophorinae are still occasionally referred to, primarily in catalogues of mammalian species (e.g., Ridgway 1972; Hall 1981; Stains 1984; Wilson & Reeder 1993). Considerably less attention has been focused below the tribal level, and the work that has been done possesses numerous shortcomings. As well, the utility of the tribal designations within the Monachinae has recently been questioned (Hendey and Repenning 1972; King 1983), as has the status of the Monachinae as a whole (Wyss 1988a; see below).

Points of contention

Thus, within the taxonomic framework laid out above, we identified five outstanding major problems concerning the systematics of the phocid seals, representing either points of contention or areas that have not been adequately studied. The various opinions expressed by previous workers for each problem may be regarded as hypotheses to be tested here.

The systematic status and interrelationships of the monk seals (genus *Monachus*)

Monachus spp. are nearly universally regarded as the most primitive of the extant phocids, being considerably more primitive morphologically than many fossil forms (Repenning & Ray 1977; Repenning et al. 1979; de Muizon 1982a; King 1983; Wyss 1988a). The three constituent species – *M. monachus, M. schauinslandi*, and *M. tropicalis* – are widely separated geographically, being found in and around the Mediterranean, in the vicinity of Hawaii, and in the Caribbean respectively [although *M. tropicalis* is believed to have been extinct since the early 1950s (Kenyon 1977)]. All three species are poorly known and insufficiently described, especially with respect to their soft anatomy.

The distinctly primitive nature of *Monachus* appears to have contributed to the long standing view that the genus is monophyletic. As well, the differences between the species are apparently so slight that if it were not for their far-flung distribution, all three might be viewed as subspecies of a single species (Scheffer 1958). However, Wyss (1988a) recently put forth the novel suggestion that the genus might be paraphyletic and recognized largely on the basis of the possession of phocid symplesiomorphies. *M. schauinslandi* was held to be the most primitive of the monk seals (and of all phocids), largely on the basis of the anatomy of the ear region (Wyss 1988a). However, this is a relatively recent view [originating with Repenning & Ray (1972)], with earlier researchers, while recognizing the primitive nature of *M. schauinslandi*, regarding it as sharing a common ancestor with *M. tropicalis* to the exclusion of *M. monachus* (King 1956, 1983; Davies 1958b; Kenyon & Rice 1959; King & Harrison 1961; de Muizon 1982a). Altogether, further description and phylogenetic treatment of this genus would be valuable.

The taxonomic status of the genera within the Phocini

The tribe Phocini is comprised of the genera *Halichoerus, Histriophoca, Pagophilus, Phoca*, and *Pusa*. Together, they are apparently clearly distinguished from the remaining phocids by the presence of a white natal coat (lanugo) (McLaren 1960a, 1966, 1975), a reduced karyotype of 2N = 32 (Arnason 1974, 1977), and numerous morphological characters (King 1966; Burns & Fay 1970). Of the five constituent genera, the distinctive nature of *Halichoerus* has long been recognized, it being the first seal to be separated from the original, all-encompassing seal genus *Phoca* (see Chapskii 1955a; Scheffer 1958). *Halichoerus* is the largest of the phocines, and is typified by a long, high, and wide snout which gives it a "Roman nose" in profile (King 1972, 1983; Bonner 1981). Modifications of the nasal region parallel those in *Cystophora* and *Mirounga*, and to such a degree that it is often considered that *Halichoerus* should also possess some form of nasal appendage (King 1972).

Differences between the remaining members of the Phocini are slight. Despite being individually recognizable, the features of the skulls of each genus overlap to such a degree that Burns & Fay (1970) subsumed the four taxa as subgenera within a newly defined *Phoca* (also Doutt 1942). *Halichoerus*, although closely related to the remaining Phocini, was not included in the newly defined *Phoca* due to an insufficient sample size to allow proper re-designation, coupled with sufficient cranial differentiation to allow it to be clearly set apart (Burns & Fay 1970).

However, this exclusion of *Halichoerus* does not appear to be justified. Arnason et al. (1995) note that the cranial characters used to distinguish *Halichoerus* would not merit generic distinction within the terrestrial carnivores, a point conceded by Burns & Fay (1970). In addition, most biomolecular studies indicate either no or equal difference between all the constituent genera of the Phocini (e.g., McDermid & Bonner 1975; Baram et al. 1991; Arnason et al. 1993; Arnason et al. 1995). Perhaps of more importance is the contention that *Halichoerus* is more closely related to the clade of *Phoca* (sensu stricto) and *Pusa* than either genus is to *Histriophoca* and *Pagophilus* (Chapskii 1955a; McLaren 1975; de Muizon 1982a; Mouchaty et al. 1995; Perry et al. 1995), thus rendering *Phoca* (sensu Burns & Fay) paraphyletic. A similar arrangement, with similar consequences for *Phoca* (sensu Burns & Fay), has been suggested infrequently between *Cystophora* and the clade of *Histriophoca* plus *Pagophilus* (de Muizon 1982a; Perry et al. 1995). [In any case, the close morphological similarity of *Histriophoca* and *Pagophilus* has been noted on many occasions (Chapskii 1955a; Davies 1958b; McLaren 1975), but may be based on symplesiomorphies (de Muizon 1982a).] As well, there are reports of interbreeding between *Halichoerus* and either *Pusa hispida* or *Phoca vitulina* in captivity (Chapskii 1955a; Scheffer 1958). In view of recent statements that the generic distinction afforded *Halichoerus* is inappropriate unless it is also applied to the subgenera of *Phoca* (sensu Burns & Fay) (Arnason et al. 1993, 1995), we will use *Phoca* in the strict sense and continue to recognize *Histriophoca, Pagophilus*, and *Pusa* as distinct genera.

In any case, phylogenetic resolution among the Phocini is generally poor. Most authors advocate two roughly equally derived main clades falling along *Halichoerus-Phoca-Pusa* and *Histriophoca-Pagophilus* lines (Chapskii 1955a; de Muizon 1982a; Arnason et al.

1995; Mouchaty et al. 1995; Perry et al. 1995). However, a primitive or ancestral status for either *Pagophilus* or *Pusa* within the Phocini has been suggested by some authors [Burns & Fay (1970) and Shaughnessy & Fay (1977), and McLaren (1966, 1975) respectively].

Altogether, these systematic difficulties within the Phocini likely stem from the relatively recent major radiation of the group [latest Miocene (Arnason et al. 1995) or post-early Pliocene and/or Pleistocene (Ray 1976a)], so that its members are not clearly differentiated from one another. This is especially true for *Phoca vitulina*, a species that has been described as being in the midst of a rapidly evolving "species swarm" (Ray 1976a: 402). Individuals of this species from the Atlantic and Pacific Oceans are readily distinguishable from one another (Allen 1902; Doutt 1942; Chapskii 1955a, 1967; Davies 1958b; Arnason et al. 1995), but there is much debate as to the exact subspecific make-up of the Pacific subgroup [for summaries, see Shaughnessy & Fay (1977) or Bigg (1981)]. This impacts here primarily on the larga seal, a taxon distinguishable from other Pacific *P. vitulina* based on geographical, ecological, behavioural, and morphological grounds (Shaughnessy 1975), but of uncertain taxonomic status. It has variously been regarded as an unnatural, "garbage" taxon (Allen 1902), as a subspecies of *P. vitulina* (Scheffer 1958; Burns 1970; Shaughnessy 1975; Baram et al. 1991), as the species *Phoca largha* (Chapskii 1955a, 1967; McLaren 1966, 1975; Shaughnessy & Fay 1977; Bigg 1981; King 1983; Arnason et al. 1995), or of uncertain status (Allen 1880). As well, the population boundaries of the larga seal are highly contentious, ranging from encompassing all Pacific harbour seals (Chapskii 1955a), to only those inhabiting the western Cis-Asiatic region (roughly from the Chukchi Sea to the coast of China) (Scheffer 1958; Chapskii 1967), to only those in this latter region that breed on the pack ice (Shaughnessy & Fay 1977). For our purposes, we will accept the larga seal as the species *Phoca largha* [species description given in Chapskii (1967)] in order to establish its systematic relationship with *Phoca vitulina*. As well, we will recognize this species as inhabiting the entire western Cis-Asiatic region, a distribution that has become increasingly accepted.

The systematic status of the Monachinae

Since its inception, membership of the subfamily Monachinae has fluctuated from including only *Monachus* spp., to its present status of encompassing all southern hemisphere seals (lobodontines plus *Mirounga* spp.) plus *Monachus* spp. This instability appears to be due simply to an increasing refinement of phocid taxonomy with time, although it may relate to the suggestion of Wyss (1988a) that the subfamily is paraphyletic. This novel suggestion is apparently connected with the paraphyly of *Monachus*, and with the recognition of *M. schauinslandi* as the sister taxon of the remaining phocids in particular (Berta & Wyss 1994; see above). Although a strongly divergent adaptive radiation has been noted for the monachines (Ray 1976b), paraphyly of the subfamily would contradict a number of apparent synapomorphies, particularly among postcranial elements (see King 1966; Hendey & Repenning 1972; de Muizon 1982a), which would have to be re-interpreted as phocid symplesiomorphies. It also clashes with biomolecular evidence (Sarich 1975, 1976), and the finding that the monachines and phocines are equally ancient lineages with distinct representatives of each being found among the first

fossil phocids (Ray 1976a; de Muizon 1982a). The possible paraphyly of the monachines has not been adequately tested since Wyss's (1988a) analysis – studies conducted since have only examined a subset of all monachines, and the only study which corroborates paraphyly for the subfamily (Arnason et al. 1995) does so very weakly – and requires further confirmation.

Phocid phylogeny at the species level

The previous three points are specific, and somewhat contentious, instances of a much more pervasive problem. Overall, the species level relationships for all phocids remain to be fully and adequately elucidated. Much of this can be traced to the paucity of studies performed below the tribal level in phocids, where, of those studies that do, most concentrate on the Phocini at the expense of the monachine tribes. Another hindrance revolves around a similar lack of studies employing a rigorous methodology, and hence some form of testability. Such studies are limited to the morphometric analysis of Burns & Fay (1970); the cladistic studies of King (1966), de Muizon (1982), Wyss (1988a), and Berta & Wyss (1994); and the molecular studies of Arnason et al. (1995), Mouchaty et al. (1995) and Perry et al. (1995). However, these studies all possess one of the two shortcomings mentioned above. Burns & Fay (1970), Mouchaty et al. (1995) and Perry et al. (1995) only examined the phocines or a subset thereof in detail, Arnason et al. (1995) included only half of all monachines, while the resolution is limited in the four cladistic studies as each was essentially performed at the subfamily, generic, generic to tribal, and tribal levels respectively.

Beyond a possible lack of resolution, there is a real danger in performing cladistic analyses above the species level. Such studies tacitly assume the monophyly of the higher level taxa [with monophyly defined here sensu Hennig (1966): all and only the descendants of a common ancestor], something that with the lack of low level systematic studies has not been adequately demonstrated for most phocid taxa. Thus, we may be forcing a less than optimal phylogeny of the phocids as the potential for some taxa to be paraphyletic has not been allowed historically. This is classically demonstrated in the study of Berta & Wyss (1994). Despite their agreement with the earlier findings of Wyss (1988a), they reluctantly took *Monachus* to be monophyletic, causing them to question the validity of their indicated phylogeny for the whole of the monachines (Berta & Wyss 1994: 43). As well, studies assuming the monophyly of higher level taxa tend to make sweeping generalizations concerning character states, often obscuring important, and potentially informative variation within that taxon.

Although cladistic analysis is increasingly the method of choice in phylogenetic analysis (and will be used here), a cladistic solution for a species level phylogeny of the phocids may prove difficult. There is some suggestion that cladistic methodology has a functional lower limit around the species level, based on philosophical considerations of the species and of evolution in general [de Queiroz & Donoghue (1990); Wheeler & Nixon (1990); but see Vrana & Wheeler (1992) for a contrasting viewpoint]. More importantly, however, there may be more immediate methodological problems threatening to impede any potential cladistic solution (Arnold 1981). In any cladistic study, the exclusion of any taxa (whether by choice or through circumstance) may drastically alter the resultant phylogeny.

Although this problem potentially exists at all taxonomic levels, Arnold (1981) holds that it may become more detrimental at the lower levels. As well, as exemplified in the study of de Muizon (1982a), it may be difficult to identify enough shared derived features to adequately establish any species level relationships; Arnold (1981) has suggested that the frequency of synapomorphies likely decreases with decreasing taxonomic level (although molecular data may be more immune to this problem). These practical problems may be offset somewhat as most phocid genera are monotypic. Thus, except for the polytypic genera *Mirounga, Monachus, Phoca*, and *Pusa*, any species differences will essentially translate into generic differences.

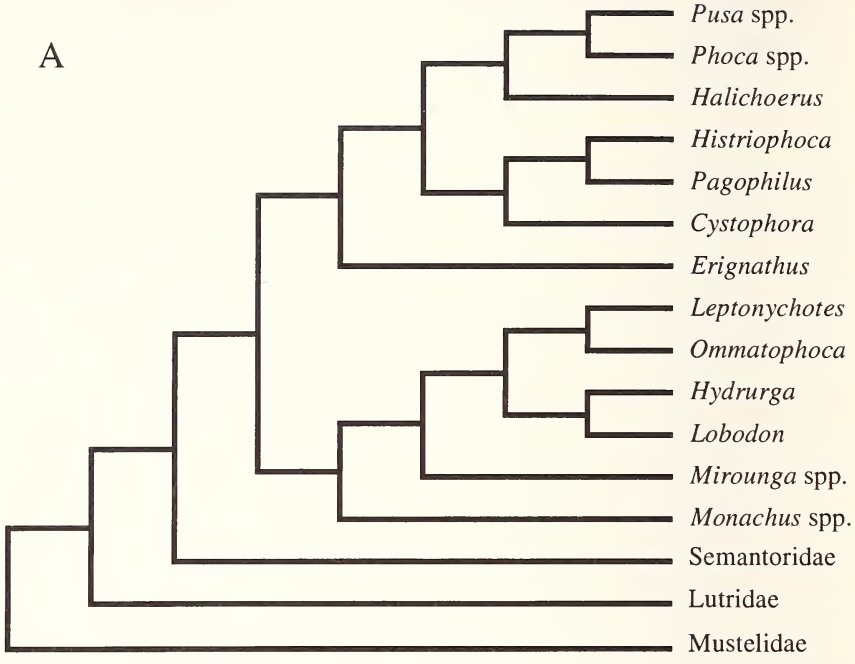
Compounding all these problems is evidence for one or more relatively recent adaptive radiations among phocids. The case for the Phocini has been mentioned above, but Ray (1976a) also indicates that the full modernization of the lobodontines and of the phocines as a whole could have occurred no more than four million years ago, in response to climatic deterioration and adaptation to high latitudes (see also Repenning et al. 1979). With such a comparatively short time for differentiation, achieving full resolution within these groups might be difficult.

Ancestral affinities of the phocids

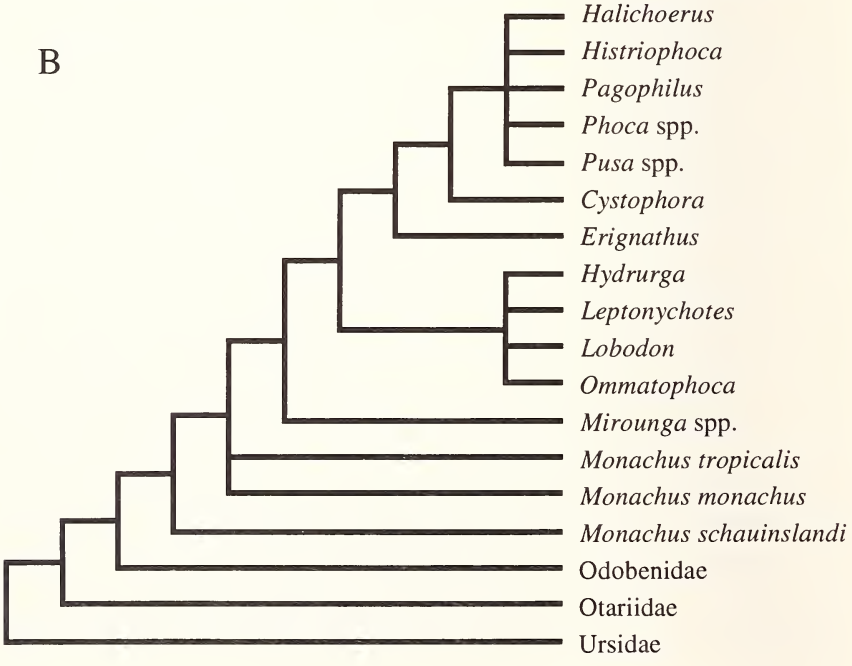
An important historical problem influencing phocid phylogeny is the uncertainty regarding phocid ancestry, a debate that underlies the controversy over whether the pinnipeds have a single or a dual origin. With regard to this latter question, a clear dichotomy is evident in the literature. Although the arctoid affinities of all pinnipeds are not in doubt (Flynn et al. 1988), most morphological, biogeographical, and paleontological studies historically favour a diphyletic origin for the pinnipeds, whereby the phocids are accorded a mustelid (possibly lutrine) ancestry, while the remaining pinnipeds (the otarioids) display ursid affinities (e.g., Flower 1869; Mivart 1885; McLaren 1960b; Hunt 1974; Ray 1976a; Tedford 1976; de Muizon 1982a, Wozencraft 1989; Nojima 1990). In contrast, most biomolecular and karyological studies support a monophyletic Pinnipedia of ursid ancestry, with the phocids and otarioids being sister taxa (e.g., Sarich 1969a, 1969b, 1975, 1976; Arnason 1974, 1977; Haslewood 1978; de Jong 1982; de Jong & Goodman 1982; Wayne et al. 1989; Vrana et al. 1994; Arnason et al. 1995; Lento et al. 1995). The monophyly hypothesis rests on the overall similarity between all pinnipeds in all aspects, including those features representing adaptations to an aquatic existence. Proponents of the diphyly hypothesis dismiss these latter features as being convergent [see especially Mitchell (1967) and Repenning (1990); but see Wyss (1989) for a contrasting viewpoint], and emphasize other, non-aquatically related, similarities between the appropriate taxa. An especially strong argument for the diphyly camp rests with the different centres and timing of the first appearance of the otarioids [North Pacific about 22 million years before present (MYBP)] versus the phocids (North Atlantic about 15 MYBP) in the fossil record (Repenning et al. 1979). The case for diphyly is also strengthened by the suggestion of the fossil taxa *Potamotherium*, and possibly *Semantor*, as putative intermediates between the phocids and their musteloid ancestors (Ray 1976a; Tedford 1976; de Muizon 1982a).

Recently, however, there has been increasing acceptance of a monophyletic Pinnipedia, due not only to molecular work (see above), but also to numerous morphological studies

A



B



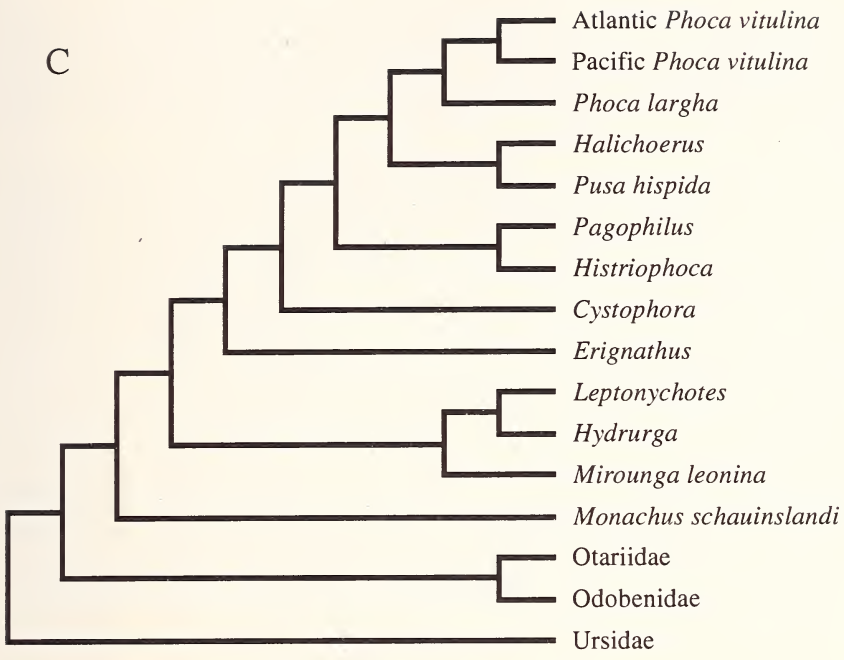


Fig.1: Phylogeny of the Phocidae according to (A) de Muizon (1982a), (B) Wyss (1988a), and (C) Arnason et al. (1995). Adapted from de Muizon (1982a), Wyss (1987, 1988a), and Arnason et al. (1995).

supporting such a scenario (e.g., Wyss 1987; Wolsan 1993; Wyss & Flynn 1993; Berta & Wyss 1994; Hunt & Barnes 1994). But within such a framework, Wyss (1987) held the Otarioidea to be related by symplesiomorphies only, and instead proposed an *Odobenus*-phocid clade with an otariid sister group. This arrangement has since become the dominant view of pinniped phylogeny (e.g., Flynn 1988; Berta 1991; Cozzuol 1992; Wyss & Flynn 1993; Berta & Wyss 1994; Vrana et al. 1994).

Similarly, most workers in this area now also accept the ursids to be the sister group of the pinnipeds, although several morphological or immunological studies persist in proposing a mustelid, and not ursid, ancestry (e.g., Arnason & Widegren 1986; Miyamoto & Goodman 1986; Wolsan 1993). However, much of this discussion may be moot. As Repenning & Tedford (1977) note, considerations of polyphyly are largely dependent on the definitions employed. Additionally, both fossil and molecular evidence indicate that the mustelid, ursid, and pinniped lineages were all diverging at about the same time from the primitive arctoid stock (Sarich 1976; Wayne et al. 1989; C.A. Repenning pers. comm.). Hence, any discussion of mustelid or ursid affinities for the pinnipeds may be irrelevant as these two groups may not have truly existed at the time of pinniped divergence. Thus, the whole question of pinniped ancestry may form part of

an unresolvable polytomy. This was one option put forth by Flynn et al. (1988), the other being an ursid sister group to the pinnipeds. Taken together, this discussion demonstrates that the question of phocid affinities (and those of the remaining pinnipeds) within the Arctoidea should still be regarded as being uncertain, if they are even resolvable to begin with.

Yet, the question of phocid ancestry still bears critical importance to the determination of the internal relationships of the phocids. In cladistic analysis, the accepted method of determining character polarities is through outgroup analysis (Hennig 1966; Arnold 1981; Wiley 1981; Maddison et al. 1984). Normally, this procedure is reasonably straightforward, with the most closely related taxon to the ingroup designated as the outgroup, and thus serving to identify the primitive states for the various characters examined. However, with respect to phocid phylogeny, the uncertainty regarding the ancestral affinities of the phocids complicates the question of designating an outgroup taxon. Yet, rather than employing multiple outgroups and allowing the analysis to dictate the most closely related outgroup taxon (and thus character polarities), most studies examining internal phocid relationships have, to date, either not stated an explicit outgroup, or have assumed either an ursid or mustelid (and occasionally lutrine) outgroup, thus potentially biasing the resultant character polarities [see Maddison et al. (1984) for some of the errors inherent in selecting outgroups and how they can, in turn, affect an analysis using outgroups].

Goals of this project

Currently, most of our knowledge concerning phocid phylogeny derives from the studies of de Muizon (1982a), Wyss (1988a), and, recently, Arnason et al. (1995) (Fig.1). However, each study possesses important shortcomings. All three phylogenies are dependent upon the supposition of a particular arctoid outgroup (lutrine, ursid, and ursid respectively). In the case of Wyss (1988a), we feel that such an assumption was not adequately tested in a prior analysis (Wyss 1987; see also Wozencraft 1989). In de Muizon's (1982a) study, some of the characters used deserve closer scrutiny (e.g., aquatic, high snout, "important" sexual dimorphism), several clades are supported by only a single character, and conflicting (i.e., homoplasious) characters are not mentioned. Yet, despite their limitations and conflicts with each other, these three studies provide the best resolved cladograms of the phocids to date.

Using these three studies as a guide, and bearing the five outstanding problems we have identified above in mind, we present the current state of knowledge regarding phocid phylogeny in Fig.2. The cladogram is characterized by large regions of uncertainty and poor resolution, primarily within the Lobodontini and Phocini, within the polytypic genera, and for the ancestral affinities of the phocids as a whole. One area of strong, almost universal, agreement concerns the most primitive members of each phocid subfamily: *Erignathus* for the phocines (Chapskii 1955a; King 1966, 1983; Burns & Fay 1970; McLaren 1975; Ray 1976a; Wyss 1988a; Berta & Wyss 1994; Arnason et al. 1995; Mouchaty et al. 1995; Perry et al. 1995) and *Monachus* spp. for the monachines (Hendey 1972; Repenning and Ray 1977; Repenning et al. 1979; de Muizon 1982a; King 1983; Wyss 1988a; Arnason et al. 1995; Lento et al. 1995).

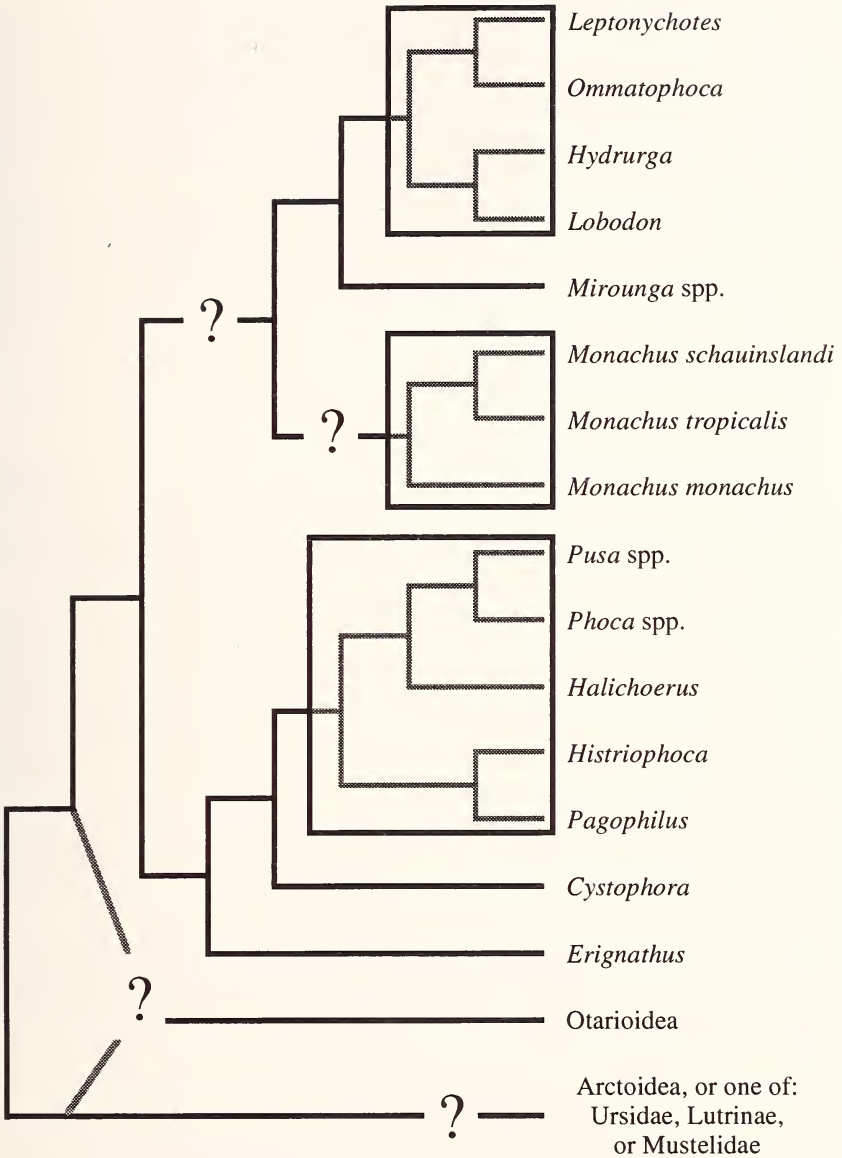


Fig.2: Diagrammatic representation of the current state of knowledge regarding phocid phylogeny. Rectangles indicate monophyletic groups with uncertain internal phylogeny (with the most commonly suggested pattern filled in when possible). Question marks refer to either general uncertainty (outgroup relationships) or to possible instances of paraphyly (ingroup relationships).

The overall goal of this study is to attempt to answer the five outstanding questions regarding phocid phylogeny that we have identified above. This is done via a cladistic analysis (sensu Hennig 1966) based on parsimony, using the outgroup method to determine character polarities. Morphological data are used exclusively. Further assumptions and details concerning this analysis are found in the **Methods and Materials** section, with the results being presented in the **Overall Parsimony** section.

The remainder of this study deals largely with the various means available to judge the robustness of the indicated solution. Attempts to place confidence intervals on phylogenies/taxonomies have been difficult, and thus have only rarely been carried out. One advantage of cladistic analysis in this regard is its ability to roughly indicate the support for a solution (or any portion thereof) by the number of synapomorphies supporting various nodes of the cladogram. However, this measure of support is still somewhat subjective, as it is dependent upon the characteristics of the data set (e.g., the number and type of characters examined) and therefore does not allow for easy comparison between data sets. Cladistics has recently seen the development of statistical and other comparative tools that seemingly allow an even more objective assessment of the quality of a solution, as well as facilitating comparisons between different phylogenetic hypotheses. Again, the tests and assumptions behind them are described in the **Methods and Materials** section, with the results presented in **Statistical Tests** and **Comparative Tools** sections.

With the rise of the use of statistics in cladistics, the realization that any cladistic hypothesis is only as good as the data it is based upon seems to have been forgotten. This point becomes even more crucial when one realizes that the outcomes of most of the newly-developed statistical procedures seem to be consistently misinterpreted (see **Statistical Tests**). Thus, we are left with one real, but increasingly rarely used "test" as to the quality of a solution: an in-depth examination of the characters that were used. This is to be found in the **Character Analysis** section, in which descriptions and historical notes are presented for all the characters examined in this study, together with a description of the evolutionary pathway implied for each character by the overall solution that was found.

Finally, this study concludes by examining such broad-ranging topics as potential sources of error, future lines of research, miscellaneous corroborating evidence (biogeography and timing of parturition), and the taxonomic implications of the proposed phylogeny of the phocid seals advocated herein.

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METHODS AND MATERIALS

Data sources

Specimens

For this study, all extant species of phocid seal plus extant representatives of all major caniform lineages, with an emphasis on putative phocid or pinniped sister groups, were examined (see Appendix A). Although the Caribbean monk seal, *Monachus tropicalis*, is believed to have been extinct since the early 1950s (Kenyon 1977), its persistence well into historical times, its potentially critical role in the resolution of the systematic status of the monk seals (genus *Monachus*) as a whole, and that fact that it is as well-represented in museum collections as any other extant phocid species caused it to be included in this study. Specimens were examined either while they were on loan from or in their respective institutions.

A conscious decision was made to exclude fossil taxa from this study. This was largely due to a lack of available specimens, with most being on loan to other institutions at the time of the museum visits. This is unfortunate as the inclusion of fossil specimens can serve to bridge large gaps between highly divergent extant taxa (Gauthier et al. 1988) such as exist here between the pinnipeds and other arctoid carnivores. Selected fossil forms may also reveal much concerning phocid and/or pinniped ancestry. For example, the advocacy of the lutrine-like fossil *Potamotherium* as an intermediate between the mustelids and phocids is a key argument supporting the hypothesis of a diphyletic Pinnipedia (Ray 1976a; Tedford 1976), or at least a mustelid affinity for all pinnipeds (Wolsan 1993). Likewise, the previously regarded otarioid-like fossil desmatophocids (= *Allodesmus, Desmatophoca*, and *Pinnarctidion*) are now regarded as the putative phocid sister group within a monophyletic Pinnipedia (Wyss 1987; Berta 1991; Wyss & Flynn 1993; Berta & Wyss 1994). Finally, the exclusion of any taxa, whether extant or fossil, from such a low level analysis may have deleterious effects on the resulting cladogram (Arnold 1981). These points are countered somewhat by the admittedly poor fossil record of pinnipeds (Davies 1958b; Hendey 1972; Hendey & Repenning 1972; Ray 1976a), and the generally high preponderance of missing features (and hence data) in fossil specimens. As well, the inclusion of fossil pinnipeds does not seem to alter the phylogenetic relationships of the pinnipeds as determined from the analysis of extant forms alone (Flynn et al. 1988; Berta &

Wyss 1994), although it may alter the implied evolutionary pathway of selected characters. However, given a reasonable degree of completeness (see Huelsenbeck 1991b), the overall potential advantages of including fossil evidence cannot be discounted.

Although there are suggestions in the literature that molecular data may operate more effectively than morphological data at lower taxonomic levels (e.g., Novacek 1993), morphological data were used exclusively. This largely reflects the availability of such data for all the desired species. Among phocids, both *Mirounga* spp. and *Monachus* spp. are CITES-listed animals (Anonymous 1992), and all pinnipeds are subject to the Marine Mammal Protection Act, making the acquisition of fresh samples as a source of molecular data difficult. As well, the full potential of morphological data at low taxonomic levels may not have been properly exploited yet, with the use of non-traditional or multistate characters (see **Character Analysis** and Bryant 1989), possibly derived from techniques such as morphometric analysis (see **Discussion** and **Conclusion**), hopefully improving the effectiveness of this type of data in such cases.

Data were obtained primarily from osteological specimens (see also **Characters** below). This was necessitated by the tendency of museums to preserve mammals as skulls, skeletons, and study skins. Furthermore, as phocids are fairly large mammals, many specimens are represented by skulls alone. Generally, the best available (i.e., most complete and undamaged) specimens for a given species were selected for study while attempting to maintain an equal sex ratio. This latter point was especially important for such grossly sexually dimorphic taxa as *Zalophus californianus* and *Mirounga* spp. Damaged specimens were occasionally employed to view various internal characters of the skull. Missing data were substituted by literature values wherever possible.

Numerous specimens of each taxon were examined in order to take account of intraspecific variation. This was especially important for the pinnipeds, as they apparently display an inordinate amount of intraspecific variation, primarily in their cranial characters (Mivart 1885; Doutt 1942; Davies 1958b; Ray 1976b). With respect to phocids, King (1966) has also commented on how the large intergeneric differences of the skull confound comparisons between the genera, and on the potential problems resulting from the high intraspecific variability of the teeth. (She does add, however, that the tympanic region seems to be relatively stable.) Unfortunately, however, postcranial material, and especially the distal elements of the limbs, were typically only obtainable from a restricted number of specimens. An extreme case is for *Pusa caspica*, where all postcranial observations were derived from a single individual.

Although Hennig (1966) notes that characters can be taken from any life stage of an organism (i.e., any semaphoront), juvenile individuals were also largely excluded from this study. This primarily reflects the very poor representation of juvenile specimens in museum collections. However, this decision secondarily served to minimize the already high intraspecific variation observed in phocids (see above) by avoiding comparisons between vastly different age classes.

Characters

A total of 196 characters were examined in this study (see Appendix B). Characters were selected so that they were at least theoretically observable from the material typically

present in museum collections. The vast majority (191 characters) were osteological, originating from both the cranial (153 characters) and post-cranial skeleton (38 characters). This disposition towards osteological cranial characters reflects both the high information content of the skull in mammals, and the tendency of museums to preserve large mammals as skulls only. The osteological characters were divided according to their general region as follows: snout, 21; orbit and zygomatic arch, 35; palate and ventral side of snout (excluding teeth), 18; basicranial region, 43; bony tentorium and bony falx, 5; dorsal braincase, 4; teeth, 23; mandible (excluding teeth), 3; miscellaneous skull, 1; forelimb, 17; pelvis, 8; hind limb, 12; and miscellaneous post-cranial, 1. Twenty-eight of the originally selected and recorded characters were excluded from the analysis for various reasons (see **Character Analysis**), leaving a functional total of 168 characters. The fact that a character was autapomorphic (including those multistate characters with autapomorphic states) was not considered sufficient grounds for its exclusion (see Yeates 1992). Although such characters do not provide grouping information, their inclusion here reveals cases of unusual and previously undocumented morphologies, or of when our observations do not accord with those of the literature, calling the value of the particular character into doubt. Specific descriptions of all individual characters, including those deleted from the analysis, are found in the **Character Analysis** section.

Data collation

For the 27 taxa used in this study, a total of 286 specimens were examined (see Appendix A). The data editor of MacClade 3.0 (Maddison & Maddison 1992) was used to input the character states for each individual specimen and to generate a consensus set of character states for each species. Polymorphic data (i.e., when a specimen simultaneously possessed two or more states or, more commonly, was intermediate between two supposedly discrete morphologies) were maintained.

Although all variation is important and potentially informative, the large amount of intraspecific variation, primarily among the phocids, required some manner of resolution. Retention of every state indicated for a species by its representative specimens would unnecessarily clutter the analysis (and thereby possibly decrease resolution) with what amount to statistical outliers. Clearly, some states were more predominant than others within a species, and it was these presumably more informative states that needed to be retained. We accomplished this with a modified majority rule algorithm which would hopefully maintain only the more predominant character state(s). For a given taxon and a given character, the consensus state was ordinarily the most frequent state among all specimens for that taxon. Note that polymorphic data, such as when a specimen possessed both states 0 and 1, were treated as a discrete state (the state "01"), rather than independent occurrences of the singular states. However, if the next most frequent state(s) possessed the same frequency, or the same frequency minus one observation (i.e., highest frequency -1), then the consensus state was a combination of these "equally" most frequent states (i.e., the taxon was counted as being polymorphic for that character).

The only exception to the above formula occurred if one or more of the "equally" most frequent states was polymorphic to begin with. In this case, the specimen polymorphisms were "broken", the frequencies for each singular state were counted, and the above

algorithm was reapplied. This was necessitated as the normal polymorphic consensus between the "equally" most frequent states 0 and 01, for instance, is meaningless (i.e., the state "001"), and probably reflects a greater preponderance of state 0 in that particular taxon. However, note that a polymorphic consensus could still result if two or more singular states happened to be "equally" frequent.

The overall effect of this algorithm was to produce many polymorphic taxa, something fairly uncommon in phylogenetic analysis. It is unclear to us exactly why this is the case, but it is likely done (whether through the selection of characters that yield monomorphic taxa, through the algorithms employed to arrive at consensus states for the taxa, or by simply coding polymorphic data as missing) to simplify the overall analysis. However, we believe that the large amount of polymorphism that we observed to be natural and important, with its undue restriction resulting in the loss of a great deal of potential information. This same procedure was employed to collapse species into a higher level taxon for the condensed analysis (see below). The final data matrix appears in Appendix C.

Cladistic analysis

A cladistic analysis (sensu Hennig 1966) of the final data matrix was conducted using the parsimony program PAUP 3.1.1 (Swofford 1993). PAUP was also used to conduct the many statistical tests and comparative tools employed in this study to judge the robustness of the overall solution (see below).

Despite its supposed increased objectivity over other systematic methods, a cladistic analysis still entails a large number of assumptions, both about how the data are to be treated and how the actual analysis is to be conducted. The numerous assumptions we have made concerning the data (both characters and taxa), the implications thereof, and their apparent advantages over alternative assumptions are described first. This is followed by an explanation of both the search criteria and methods of summarizing the output that were used.

Assumptions concerning characters

All characters were assumed to be of equal weight, and multistate ones were held to be unordered. Although either case requires assumptions equal in magnitude to weighted or ordered characters (Sober 1988; Barrett et al. 1991), they were resorted to out of simplicity and/or ignorance. In the first case, equally weighted characters typically imply independence among characters (as co-dependent characters are accordingly down-weighted), and/or characters of roughly equal importance, reliability, or quality [see Underwood (1982) and Bryant (1989) for other uses of weighting]. However, this is not implied here. As we could not objectively determine the degree of character independence, nor relative character importance a priori, we adopted the simplest solution, that of equally weighted characters.

Indeed, we make no pretense as to the independence of our characters. By all being drawn from the same organism, all characters will be correlated with one another to some degree. However, to our knowledge, there has never been a test devised that quantifies the level of character independence or correlation, nor has it ever been explicitly stated what level

of independence is sufficient for a cladistic analysis. As well, mere word play can apparently increase the degree of independence of a group of otherwise highly correlated features. For example, we examined four features of the incisive foramina in this study (roughly size, shape, location, and number; see **Character Analysis**). But, by redefining these characters in terms of other variables (e.g., size of the nasopalatine nerve passing through the foramina, presence of a down-growth of the premaxilla or not, ...), they cease being incisive foramina characters at first glance. Finally, recent evidence indicates that character independence for a single structure may, in some cases, be greater than previously presumed. Atchley & Hall (1991) suggest that the single mammalian dentary bone (as evidenced by the mouse) may, in fact, be composed of up to six separate centres of ossification or condensation, one for each of the ramal, incisor, molar, condyloid process, coronoid process, and angular process regions. Thus, there is at least the potential for each to be acted upon independently during ontogeny, and thus phylogeny. In other words, the mammalian mandible could justifiably be represented by up to six characters (one from each of the regions above) and not violate the independence criterion. Therefore, in selecting a set of characters, the best solution is likely to represent all body regions as much as possible (within the constraints of their relative information content), and not to over-represent any one region or feature to any great extent.

One clarification is required with respect to the phrase "equal weighting". PAUP's algorithms essentially weight characters in proportion to the number of states they possess, thereby artificially attaching greater importance to multistate characters (Swofford 1993). To correct for this, all characters were inversely weighted (base weight = 100) according to the number of states each possessed. So, "equally" weighted will, hereafter, be taken to mean inversely weighted, and not unweighted (i.e., where all characters share some identical weight "x"). Unfortunately, inverse weighting creates rather unwieldy tree lengths, obfuscating discussion and comparison of less than most parsimonious solutions. To compensate for this, discussion is directed towards the number of character state changes (or, equivalently, the number of synapomorphies, both of which equal the number of unweighted steps) along a branch, and not the branch lengths derived from inverse weighting. When this is not possible, "corrected steps" were devised and are referred to. These are simply the absolute number of inversely weighted steps divided by the average character weight of the inversely weighted character set (= 69), rounded up to the next whole number. Both methods appear to be roughly equivalent (i.e., corrected steps appear to be a reasonable estimator of the number of character state changes), based on preliminary comparisons when both were available.

Unordered characters (i.e., Fitch parsimony) were likewise used, as we could not conclusively identify the exact sequence of character transformations based on criteria set out by Hauser & Presch (1991). Thus, all possible transformations were allowed and were considered to be equally probable. In any case, the supposed advantages of ordered characters (e.g., increased resolution and stability, and fewer equally most parsimonious solutions) may be overstated. While ordering may be advantageous for a single character, such is not necessarily the case over an entire matrix due to the interaction of all characters (Hauser & Presch 1991).

Although some authors indicate that both missing data and inapplicable characters (e.g., feather size for mammalian taxa) be coded as "missing" (represented by a question mark) (e.g., Swofford 1993), a distinction was made here between these two cases. Inapplicable characters were instead assigned to a discrete state (state 9), as advocated by Maddison (1993). Largely, this ties in with how PAUP (and other computer algorithms) treat missing data. PAUP will initially treat the missing datum as if it were almost entirely absent from the tree (at least with respect to that character), and then later attempt to infer an appropriate state for any missing data based on parsimony (Maddison 1993). While this latter step is valuable when the state is unknown due to ignorance (creating a valuable hypothesis to be tested in the future), it is clearly inappropriate for inapplicable characters in that PAUP may infer a state that clearly does not apply to the taxon in question (e.g., "large feathers" in mammals when it should really be "feathers absent") (Platnick et al. 1991).

Assumptions concerning taxa

In dealing with the large number of polymorphic taxa, PAUP's multistate taxa option was set at "polymorphism", forcing PAUP to account for all but one of a polymorphic taxon's states in the most parsimonious way possible by invoking changes within this terminal taxon (Swofford 1993). Although the underlying assumption of this setting is that the multistate taxon is a heterogeneous group (i.e., a higher level cluster of morphologically variable taxa), this setting comes the closest to treating the indicated polymorphisms as real and important. The alternative setting, "uncertainty", selects only the most parsimonious state out of the set provided, ignoring the remaining states, and thus the polymorphism, altogether. However, one limitation of "polymorphism" is that PAUP will not form a polymorphic ancestral taxon, even if all of its descendants are identically polymorphic (Swofford 1993). Although this results in the loss of much potential grouping information, it should be noted that the other major phylogeny inference packages (i.e., Hennig86 v1.5 and PHYLIP v3.5) will not handle polymorphic data at all (Sanderson 1990).

The taxa *Canis lupus, Enhydra lutris, Lutra canadensis, Martes americana, Odobenus rosmarus, Procyon lotor, Ursus americanus*, and *Zalophus californianus* (hereafter referred to solely by their generic appellations, as are the monotypic phocid genera) were assigned as outgroup taxa. In so doing, we assumed that each taxon is a representative member of a higher level taxon: canids, lutrines, lutrines, mustelids minus lutrines, odobenids, procyonids, ursids, and otariids respectively. This is almost certainly not the case, but we deemed the alternative, using the presumed ancestral state for each higher level taxon, as less desirable. Such an assessment requires at least some tacit assumptions about both the internal phylogeny and ancestral affinities of the higher taxon. As well, the use of ancestral states may conceal the presence of some potentially important derived subgroups with which the true affinities of the ingroup may lie. In any case, trees were rooted such that the collective outgroup used here was forced to be paraphyletic with respect to the phocids (which were forced to be monophyletic) in accordance with the current views on caniform phylogeny (see Tedford 1976; Flynn et al. 1988; Wyss & Flynn 1993; Vrana et al. 1994).

Search criteria and summarizing output

The number of taxa examined here prevented an exact solution from being found (via exhaustive or branch and bound algorithms). Therefore, PAUP's heuristic search option was used, which although highly effective, cannot guarantee an optimal solution (Swofford 1993). Unless otherwise indicated, all searches were heuristic and used a random addition sequence (with 25 repetitions), TBR branch-swapping on minimal trees only (with steepest descent on), collapsed zero-length branches, and an unlimited number of MAXTREES. This combination of options seemed to be the most effective in finding an optimal solution, and should minimize the analysis becoming trapped in local optima or on islands of less than optimal trees (Maddison 1991: Swofford 1993).

In those cases where multiple equally most parsimonious solutions were found, the rival results were summarized through the use of both strict and majority rule consensus trees. These two methods provide different types of information. By retaining only those groups that are found in all rival solutions, strict consensus trees will identify regions with multiple, conflicting solutions as polytomies. However, within these regions, some groups may occur with a greater frequency than others. The majority rule consensus algorithm, by retaining those groups found in greater than 50% of the rival solutions, will tend to preserve these more frequent groups that are ignored by the strict algorithm.

Character state assignments for internal nodes (see **Character Analysis**) were reconstructed using both accelerated and delayed transformation optimization criteria (ACCTRAN and DELTRAN respectively). With no ambiguity in the reconstruction of a character, both methods will yield identical results. For equally parsimonious reconstructions of a homoplastic character, ACCTRAN optimization will tend to favour an early origin of the derived state, followed by a reversal back to the more primitive state, while DELTRAN optimization will tend to favour later parallel derivations of the derived state (but note that these are not hard and fast rules) (Wiley et al. 1991; Swofford 1993). Thus, the repeated claims of a predisposition towards reversals in phocid (and especially phocine) evolution (e.g., Wyss 1988; Berta & Wyss 1994) may reflect the singular use of ACCTRAN optimization (the default choice in PAUP). A third optimization criterion available in PAUP, MINF, was not employed as its output is often identical to that of DELTRAN optimization (Swofford 1993).

Statistical tests

One of the more active areas in theoretical cladistics in recent years has been the development, and subsequent dissection, of various statistical tests designed to objectively quantify the robustness of a given cladogram. In this section, each of the tests used in this study are described in turn, including their objectives, their shortcomings and/or criticisms, and how they were implemented here.

Goodness-of-fit statistics

The most basic method used to judge the quality of a solution is the use of one or more goodness-of-fit statistics: consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) [see Farris (1989), Wiley et al. (1991), and

Swofford (1993) for definitions and descriptions of each]. These indices can refer either to the fit of individual characters or of the data matrix as a whole (where they are referred to as ensemble indices) to a given tree topology. Unless specified otherwise, the goodness-of-fit statistics quoted herein always refer to the optimal, and not consensus solutions of an analysis.

The utility of the CI (and presumably the HI) is limited by it being inflated by autapomorphic features (which can be corrected for as is done herein), as well as being dependent on both the number of states a character possesses and the size of the data set (Farris 1989; Wiley et al. 1991; Swofford 1993). Both the RI and the RC have been designed to avoid these shortcomings; however, this latter property does allow the calculation of expected CIs for data sets of various sizes (see Sanderson & Donoghue 1989), and hence a means to more objectively judge the quality of a solution.

Although Swofford (1993) indicates that the HI behaves slightly differently when multistate taxa are interpreted with the "polymorphic" option (as change is now allowed within the taxon terminals), this appears to be true for the other three indices as well. Presumably, this derives in part from PAUP's failure to designate multistate ancestral nodes under this option (see above). Therefore, identically polymorphic taxa within a clade will each gain their identical second states by convergence within their respective terminals, rather than via inheritance from a similarly polymorphic common ancestor. However, as this scenario is the proper interpretation for distantly related taxa, the overall effect on a given index will be dependent on the distribution of polymorphisms among the taxa.

It should be pointed out that these indices are merely different ways to indicate levels of homoplasy in a solution. Unfortunately, the tendency in phylogenetic studies based on a parsimony criterion is to automatically equate increased homoplasy with a poorer solution. However, it is reasonable to expect that different groups will be characterized by different levels of homoplasy, so that a high level of homoplasy may be diagnostic of the group under study, rather than of a poor solution. Therefore, these indices should really be limited to comparing different solutions for the same group.

The bootstrap (Felsenstein 1985)

The bootstrap is a non-parametric statistical procedure adopted for use in phylogenetic analysis by Felsenstein (1985). It aims to infer the variability of an unknown distribution (the true phylogeny) from which data were taken (the characters) by resampling with replacement from the data. By taking a large number of replicates, one can estimate the confidence interval of the original unknown distribution. Groups that are supported by a large number of characters will be found in most solutions. The bootstrap frequency indicates the proportion of all solutions that a particular clade was found in.

Despite its widespread use, the bootstrap has shown some problems in its adaptation to phylogenetic analysis. [It apparently has a larger problem in that, despite concerted effort, it has never been demonstrated to be a valid technique for those applications in which it is supposed to be used (L.R. Linton pers. comm.).] These problems derive largely from the key assumption that the data be independently drawn and identically distributed (i.e., a representative, random sample of all possible characters) (Felsenstein 1985; Sanderson

1989). Sanderson (1989) has indicated that this is not likely the case for most systematic studies, so bootstrap frequencies are probably not estimates of the true confidence intervals. The use of replacement during sampling may also artificially increase character non-independence by allowing the same character to be sampled more than once (L.R. Linton pers. comm.). As well, the bootstrap can become problematic when parsimony is used to estimate phylogeny and rates of evolution in the various lineages are greatly unequal (Felsenstein 1985). Thus, the bootstrap solution may differ from the most parsimonious one, a difference that arises from the fact that the bootstrap represents a phylogeny estimated from repeated samplings and not the real one (Felsenstein 1985), and from the properties of consensus trees, of which the bootstrap solution is one (Swofford 1993).

These problems seem to become detrimental to the analysis when more than two topologies are possible (as is usually the case in phylogenetic studies), prompting some algorithmic or procedural corrections (Hall & Martin 1988; Rodrigo 1993; Li & Zharkikh 1994, 1995). However, the only "correction" that we have heeded is Hedges's (1992) suggestion that most studies involving the bootstrap do not use enough replications, with at least 500 replications being required to ensure that the bootstrap frequency is within one percent of the 95% confidence interval. In recognition of all of these difficulties and the varying opinions as to the utility of the bootstrap (see Felsenstein & Kishino 1993; Hillis & Bull 1993), bootstrap frequencies are interpreted here as rough indicators of support for the various nodes of the cladogram, and not as true confidence intervals.

Herein, 1,000 bootstrap replicates were conducted using the heuristic search option of PAUP. Heuristic searches were identical to that detailed above except that taxa were added with the CLOSE algorithm with HOLD = 10, and with only 100 MAXTREES allowed for each replication. Only the 168 included characters were sampled, and with equal probability (i.e., their inverse weights were not used to designate repeat counts of a character). "Irrelevant" characters (primarily autapomorphies here) were retained with the suggestion that they do not adversely affect bootstrap results (Harshman 1994).

Permutation tail probabilities (PTP) (Archie 1989; Faith & Cranston 1991)

The PTP test seeks to assess the degree of phylogenetic structure in a data set based on the amount of cladistic covariation between its characters, as compared to a matrix that possesses random covariation. A data set with an associated solution that is shorter than a statistically significant proportion of those derived from a number of random data sets (e.g., by being within the lower fifth percentile of tree length) is said to possess "significant cladistic structure" (Faith & Cranston 1991). Random data sets are constructed from the original by randomly permutating character states between the included taxa within each character. Outgroup taxa are excluded from this process to maintain polarity assessments. Thus, each random data set maintains most of the characteristics of the original.

Several methods exist to assess the level of significance of a PTP test. The simplest is the PTP statistic which is defined as the proportion of all data sets (original and random) that produce a tree as short or shorter than that derived from the original data set (Faith & Cranston 1991). A critical length value corresponding to the desired level of significance

can also be determined by simply arranging the lengths derived from the random data sets in ascending order and counting off to the appropriate percentile (L.R. Linton pers. comm.).

A serious limitation of the PTP statistic is that it will consistently underestimate the departure of the data from randomness with the low number of randomizations typically employed in phylogenetic PTP analyses (Källersjö et al. 1992). Therefore, Källersjö et al. (1992) have derived two more accurate, albeit slightly conservative measures (α" and α*) for such instances from the standardized Z-scores of the sample of random solutions. However, bearing the conservative natures of all these statistics in mind, Källersjö et al. (1992) recommend using the smallest value obtained from any of the PTP statistic (which they refer to as α'), α", or α*.

Strictly speaking, a PTP test is not sensitive to hierarchical structure in the data set, but merely to patterns of association (Alroy 1994). The tacit assumption then is that the character covariation that the PTP test is sensitive to is due solely to common ancestry, and not to other correlative factors such as character non-independence. Together, this leads to the PTP test being an extremely forgiving and occasionally erroneous test (Källersjö et al. 1992; Novacek 1993). Therefore, it appears that a significant result is not so telling with respect to the PTP test as opposed to a non-significant result.

Another limitation of the PTP test is that it only operates at the level of the solution as a whole, and not for subgroups of interest within it. Although Faith (1991) has suggested an analogous procedure for this latter goal, this topology-dependent PTP test (T-PTP test) is limited to very small data sets for practical reasons. This is because the idea behind a posteriori T-PTP tests for the monophyly of a given clade is to determine how likely it is to form any clade with a similar number of members, and not how likely it is to form that one particular clade of interest. Thus, in order to a posteriori determine whether there is statistical support for a monophyletic Monachinae for instance, we need test not only the monachines, but all clades of nine taxa, for which, for the 19 phocids examined here, there are 92,378 such combinations. It is possible to correct for, rather than test all these possible combinations (see Faith 1991), but for the example given here, a significant result (at the 0.05 level) would still require a P value on the order of 10^{-7}.

The lack of a PTP subroutine in any computer package to date makes use of the PTP test rather labour intensive. Thus, only the minimally suggested number of data sets, 100 (99 permutated plus the original), were analyzed. The permutated data sets were created using the SEQBOOT program of PHYLIP (version 3.52c) (Felsenstein 1993), and subsequently converted to PAUP's NEXUS format to be analyzed using the heuristic search option as detailed above. All three measures of significance – α', α", and α* – were determined for this analysis. As we make no pretense as to the independence of our characters, we will interpret the results of this analysis in terms of character covariation only, and not hierarchical structure.

Skewness (Fitch 1979)

Skewness tests derive from Fitch's (1979) simple observation that distributions of tree length for most phylogenetic data sets possess long left-hand tails (i.e., are left-skewed).

Hillis & Huelsenbeck (1992) suggest that this phenomenon, which indicates the presence of relatively few solutions around the most parsimonious solution, derives from an increased amount of correlation between characters. Therefore, like the PTP test, interpreting a significant left-hand skew to mean significant phylogenetic signal requires the assumption that the indicated correlation derives primarily from common ancestry. So, once again, a non-significant result is more revealing than a significant one (Hillis & Huelsenbeck 1992), although a distribution with a significant left-hand skew does apparently increase the probability that parsimony will correctly identify the actual phylogeny (Huelsenbeck 1991a).

Hillis & Huelsenbeck (1992) also suggested that a significant left-skew for the whole solution may only be an artifact of a particularly strongly indicated subgroup. Therefore, a tree length distribution of all solutions, but with the relationships of this one subgroup constrained, should produce a non-significant skew. Presumably, this is due to the left-hand tail of a left-skewed distribution being composed primarily of solutions containing the indicated subgroup as a clade (but with different combinations of relationships internally).

Despite the work of Huelsenbeck (1991a) and Hillis & Huelsenbeck (1992), the use of skewness (as measured by the g_1 statistic) as an indicator of phylogenetic signal is also not without its problems. Skewness analyses will occasionally give an erroneous outcome due to being influenced more strongly by character state frequency (which in turn affects the pattern of branching) than by correlation between characters, as well as being insensitive to character number (Källersjö et al. 1992). However, this last point is countered by the question of whether support should be measured by the absolute [as in simply tallying the number of synapomorphies, and as Källersjö et al. (1992) apparently feel it should be] or the relative number of characters (as in the bootstrap) supporting a node. Källersjö et al. (1992) also question whether the limited random sample of all possible solutions that skewness statistics are based on for studies with more than 10 taxa can accurately estimate the distribution of all possible solutions, or even sufficiently sample from the attenuated left-hand tail of the distribution. However, Hillis & Huelsenbeck (1992) demonstrate that a random sample of only 10,000 trees does produce a statistically accurate sample, regardless of the number of taxa.

In all but two cases (see below), skewness statistics, g_1, were obtained from a random sample of 1,000,000 trees generated using the RANDOM TREES subroutine of PAUP, and all were compared to critical values published for a given number of taxa and characters (both binary and four-state) by Hillis & Huelsenbeck (1992). Although molecular simulations were used to achieve these critical values, they should, at the very least, give a rough indicator of the level of significance. For those cases when the exact values for either taxa or character number were not present, the next higher category was used, producing a more conservative estimate of the level of significance. However, all skewness results here should be regarded as extremely tenuous as the RANDOM TREES subroutine of PAUP (version 3.1.1) contains major bugs that inhibit the analysis of (inversely) weighted data matrices.

For the "constrained" skewness analysis, the strongly supported subgroup in question (hereafter referred to as the "anti-Phocini" clade) was held to be all taxa excluding

Erignathus, Histriophoca, Pagophilus, Phoca spp., and *Pusa* spp. (hereafter, the "E-Phocini" clade) based on the results of other tests. However, as PAUP cannot produce distributions of truly constrained topologies, distributions were estimated by collapsing the constrained subgroup to its ancestral node. As well, as constrained skewness has not been tested before, reciprocal constraints were analyzed in which the strongly and weakly supported subgroups were alternately collapsed (to nodes 34 and 33 respectively; see Fig.5B) to test whether the collapsing resorted to here had some effect on skewness. If Hillis & Huelsenbeck's (1992) conjecture is accurate, then one would expect the distribution with a collapsed (weaker) "E-Phocini" clade to maintain a significant skew, while that with a collapsed (stronger) "anti-Phocini" clade should possess a non-significant skew. Tests were paired to account for both ACCTRAN and DELTRAN reconstructions of the ancestral node. For the case when the "anti-Phocini" were collapsed only, it was possible to derive the skewness statistic from an exhaustive search of all 135,135 possible trees rather than invoke PAUP's RANDOM TREES subroutine.

Successive approximations (Farris 1969)

Successive approximations is an a posteriori weighting technique that seeks to arrive at a more robust solution (i.e., fewer and more resolved equally most parsimonious solutions) by differentially weighting characters in proportion to how well they have performed in a previous analysis. This procedure is typically recursive, and continues until no further change is observed in either tree topology or character weights (Swofford 1993).

Although the use of successive approximations has increased resolution and decreased ambiguity when applied to some data sets (Novacek 1993), its use is also somewhat problematic. First and foremost, it is not clear how to determine a character's quality. Typically, one of three goodness-of-fit statistics – CI, RI, or RC (see above) – is used, but there appears to be no reason to favour one over another. As well, characters do not fit equally well to all equally most parsimonious solutions, and a decision must be reached whether to reweight characters according to their maximum, minimum, or average value of the goodness-of-fit statistic chosen (Swofford 1993). Other problems include the tendency of missing data to artificially make their characters less homoplastic (thereby contributing more to future analyses), and the obvious circularity of the procedure as a whole (Novacek 1993).

Here characters were reweighted (base weight = 1,000) using all combinations of CI, RI, and RC, and their maximum, minimum, and average values. Fractional weights were rounded off to the nearest whole number. All searches used the heuristic search option as detailed above.

Support analyses (Källersjö et al. 1992)

The general concept of support tests (also known as decay analyses) is to view trees (or their summaries in the form of consensus trees) of increasingly greater length, and thus homoplasy, so as to determine when a clade of interest disappears or is contradicted. Clades that withstand the intrusion of increasing levels of homoplasy to the greatest extent are judged to have the strongest support (Novacek 1991; Swofford 1993). This basic procedure (termed Bremer support by Källersjö et al. 1992) suffers from being dependent on the

different properties of each data set. No objective benchmark has yet been able to delineate strong from weak support [although the confidence intervals may be surprisingly large (see Cavender 1978, 1981)], so all results can only be stated in relative terms (e.g., a clade has stronger support than another, not strong support per se), and only for the data set in question (Novacek 1991). Through the use of permutation, Källersjö et al. (1992) have refined the concept of support to give it a more objective, statistical basis; however, as the calculation of this total support is prohibitive using PAUP, it was unfortunately not examined here.

All trees in increasing increments of 69 steps (= one corrected step; see above) from the most parsimonious tree length were retained using the KEEP command of PAUP in conjunction with the heuristic search procedure described above. As a heuristic search pattern was used, the number of trees retained at each step should be viewed only as a rough estimate of the total number of trees of that length or shorter, rather than an exact figure. Summaries at each length were viewed using both strict and majority rule consensus algorithms (see above for advantages of each). Unfortunately, with the large number of taxa examined here (and concomitant large number of possible trees), PAUP quickly ran into memory limitations, and the support analysis could only be performed for solutions up to and including four corrected steps longer than the most parsimonious length.

All these statistical tests are dependent on the power of the computer and/or the search algorithm employed. In the case of all but skewness, it is important to minimally maintain the searches as robust as the original so that the results will be roughly comparable. For the PTP test, this is especially critical given that any less than optimal solution for the random data sets will increase the probability of generating a significant result (Källersjö et al. 1992). Similar errors can be anticipated for the remaining procedures as well.

Comparative tools

Relatively less attention has been paid to the various non-statistical means of inferring the robustness of a cladogram. Of the comparative techniques described below, only the constraint analyses really qualify as a (non-statistical) means of inferring the robustness of a cladistic hypothesis. Although the remaining four "analyses" do indirectly indicate the strength of the pattern of phocid phylogeny obtained herein, they are, more properly, specific, interesting questions that arose in the course of this study. Each analysis is again described in turn.

Constraint analyses

One invaluable feature of PAUP allows the user to constrain searches to satisfy (or not satisfy) a given topology or range of topologies. Of its many possible uses (see Swofford 1993), topological constraints were used here to view how much less parsimonious a desired set of alternative relationships forced the overall solution to be. In many ways, this procedure is akin to support analyses, except that the shortest solution containing a set of relationships not found in the most parsimonious solution(s) is desired here.

Major competing hypotheses of phocid phylogeny were identified from the literature and tested here. These hypotheses apply to both outgroup and ingroup relations and the

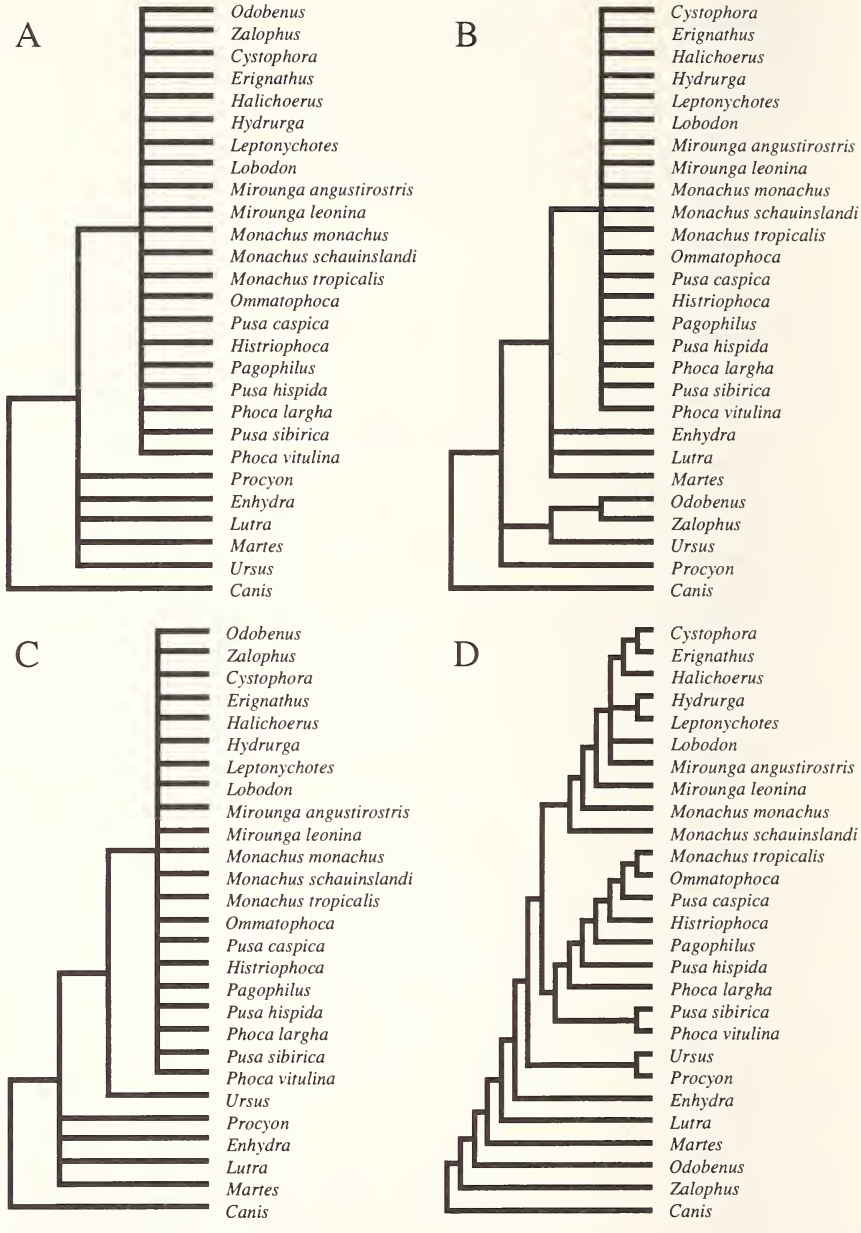

Fig.3A–D: Monophyly constraint trees used to examine various alternative hypotheses of outgroup relationships: (A) (not) monophyly, (B) diphyly, (C) ursid – monophyly, and (D) ursid – diphyly.

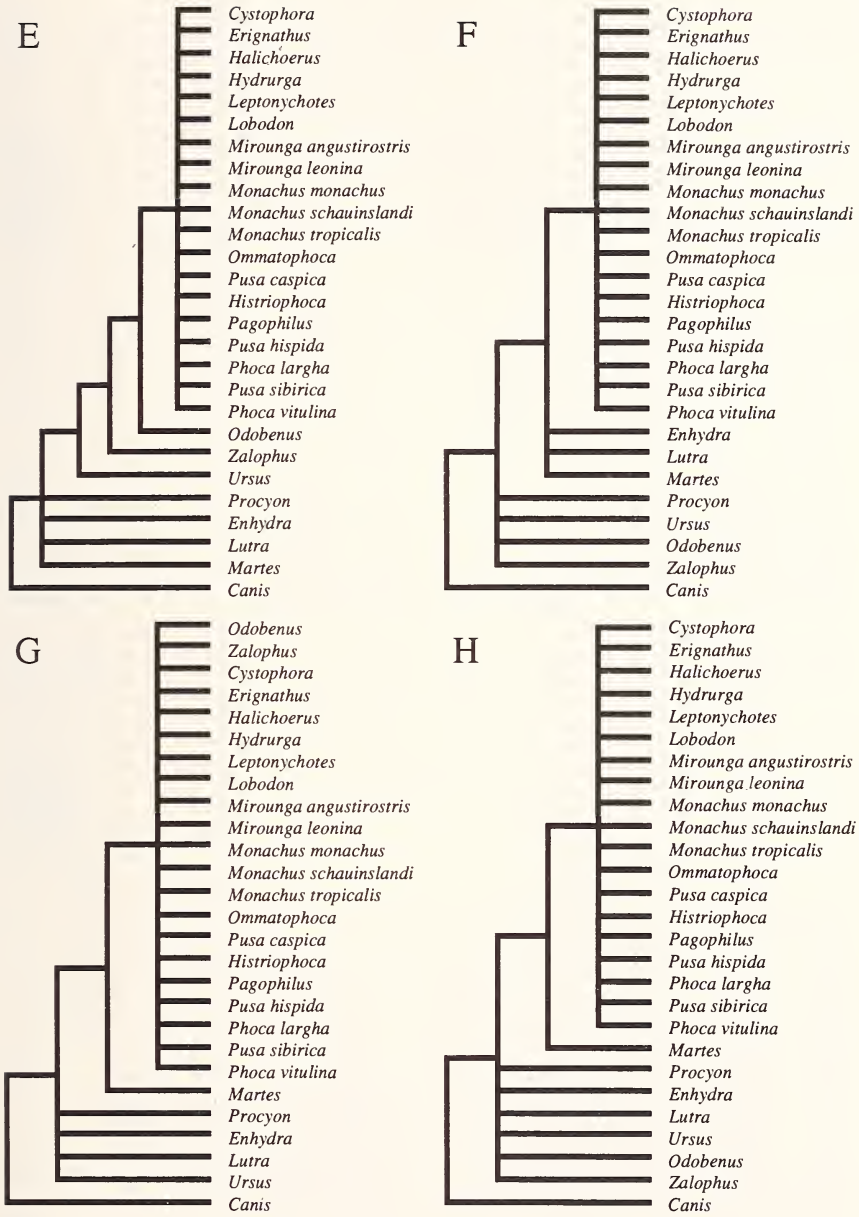

Fig.3E–H: Monophyly constraint trees used to examine various alternative hypotheses of outgroup relationships: (E) ursid – odobenid, (F) mustelid – diphyly, (G) musteline – monophyly, and (H) musteline – diphyly.

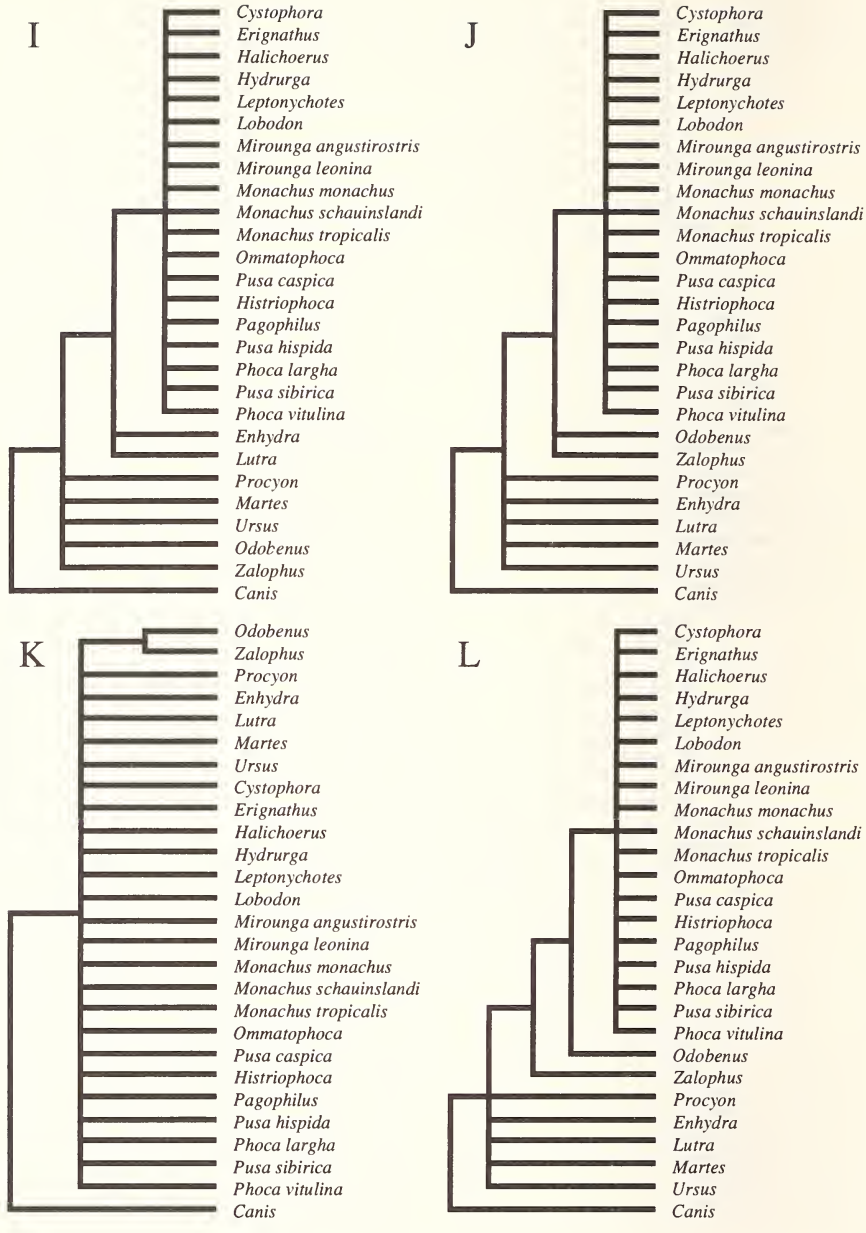

Fig.3I–L: Monophyly constraint trees used to examine various alternative hypotheses of outgroup relationships: (I) lutrine – diphyly, (J) (not) otarioid, (K) (not) otarioidea, and (L) odobenid.

constraint trees as tested are presented in Figs.3 and 4 respectively. Two additional ingroup trees, corresponding to the solutions of the unweighted and condensed analyses (see below), were also tested (Fig.4O and P).

As with Bremer support, constraint analyses suffer from a lack of any explicit statement on how much longer a tree must be for it to be rejected on statistical or other grounds [but again, see Cavender (1978, 1981)]. Thus, we again employ this analysis more in a relative fashion, using it to distinguish between more weakly and more strongly supported solutions. Whénever possible, bootstrap frequencies for the clade being examined were also added as a second, albeit similarly approximate, line of evidence.

All searches employed the heuristic search pattern described above, except for the ingroup constraint trees "de muizon" and "condense", which were analyzed using exhaustive and branch and bound search algorithms respectively (both collapsing zero-length branches), both of which guarantee an optimal solution.

Missing taxa

On the suggestion of Arnold (1981) that missing taxa may have a detrimental effect on low level cladistic analyses, five phocid taxa (*Cystophora, Erignathus, Lobodon, Ommatophoca*, and *Phoca largha*) were selectively deleted and the analysis re-run in order to view the effects of their individual removal, if any. These taxa were selected on the basis of their topological position, various tendencies elucidated by other analyses, or for historical considerations (see **Comparative Tools** section for full details). As the removal of these taxa alters the intrinsic properties of the data matrix, comparisons with other results are primarily limited to comparisons of gross topological changes and various goodness-of-fit-statistics. All searches were conducted using the heuristic search pattern described above.

Condensed analysis

Historical considerations of phocid phylogeny show a strong tendency to assume the monophyly of some higher taxa. However, as this is the first species-level cladistic analysis of the entire family to be performed, some of these assumptions of monophyly will not have been rigorously tested before now. Thus, in order to view the possible historical effects of assumed monophyly on phocid phylogeny, we re-ran the analysis with several species collapsed into one of four higher taxa: the genera *Mirounga, Monachus*, and *Phoca* (sensu Burns & Fay 1970), and the tribe Lobodontini.

Although the paraphyly of three of these four taxa has been suggested, it has not been widely accepted in each case. Certainly, the strongest and almost indisputable case is for *Phoca* (sensu Burns & Fay); however, this taxon is almost universally recognized today. Only Wyss (1988a) has provided evidence for a paraphyletic *Monachus*, something that has not been re-examined to date [although it is endorsed by Berta & Wyss (1994)]. It has been hinted that the Lobodontini may be polyphyletic, or even paraphyletic, but only with the inclusion of fossil taxa (Hendey 1972; McLaren 1975; Ray 1976a; Berta & Wyss

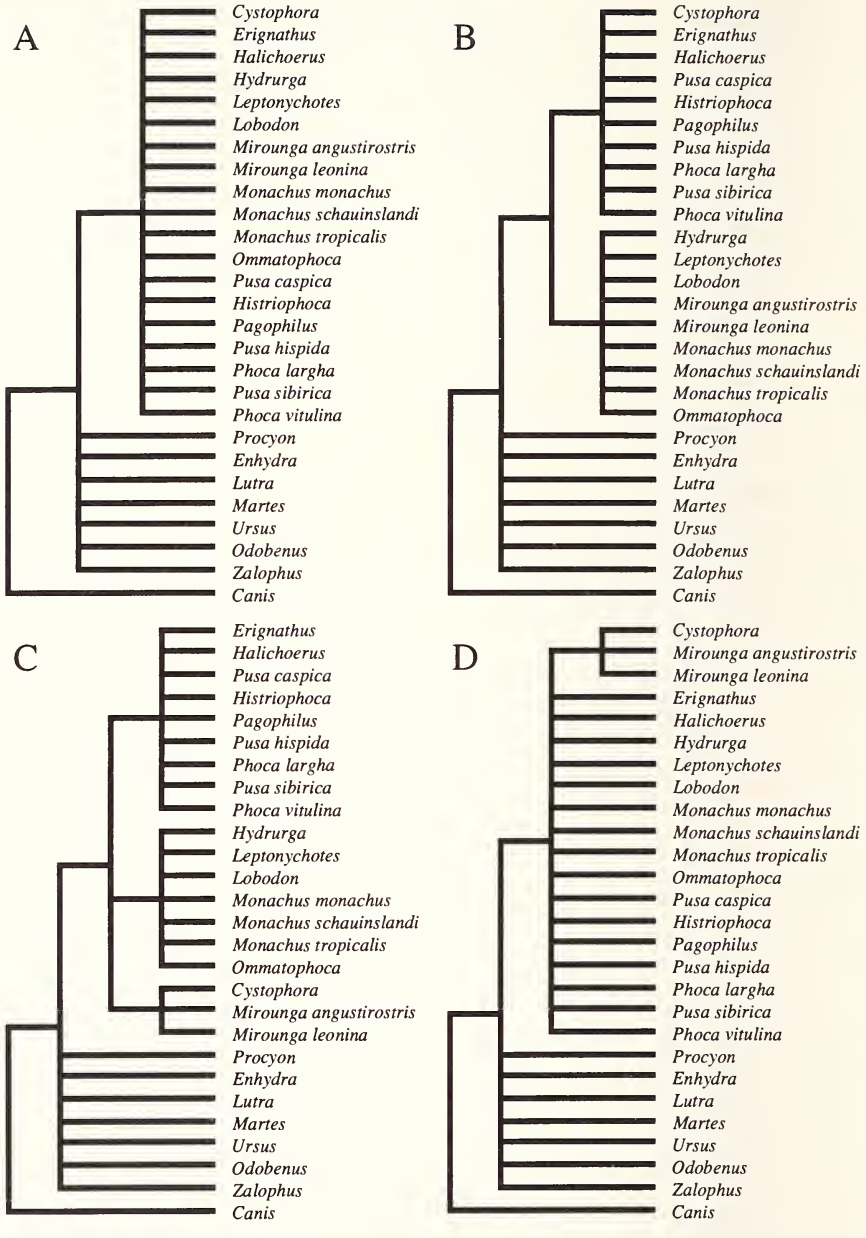

Fig.4A–D: Monophyly constraint trees used to examine various alternative hypotheses of ingroup relationships: (A) (not) phocidae, (B) (not) two subfamilies, (C) three subfamilies, and (D) cystophorinae.

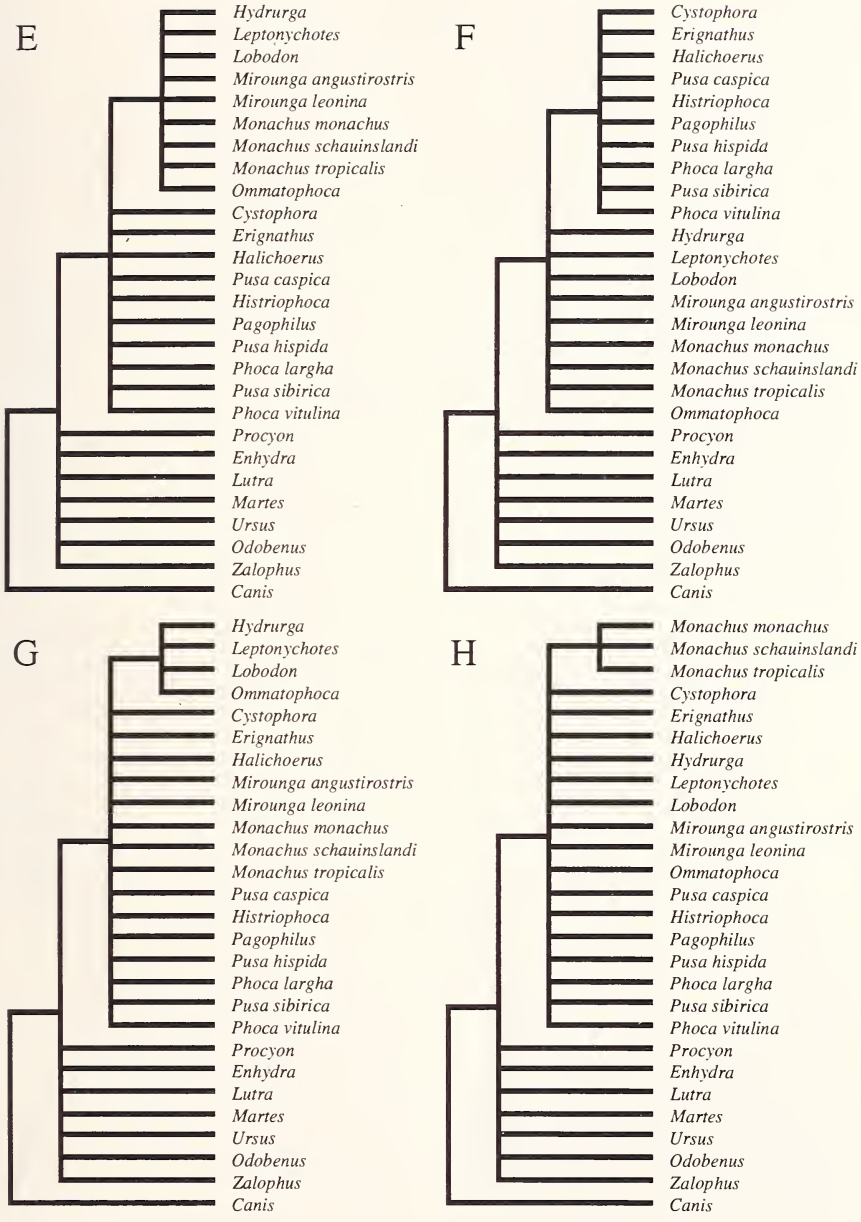

Fig.4E–H: Monophyly constraint trees used to examine various alternative hypotheses of ingroup relationships: (E) (not) monachinae, (F) (not) phocinae, (G) lobodontini, and (H) (not) monachus.

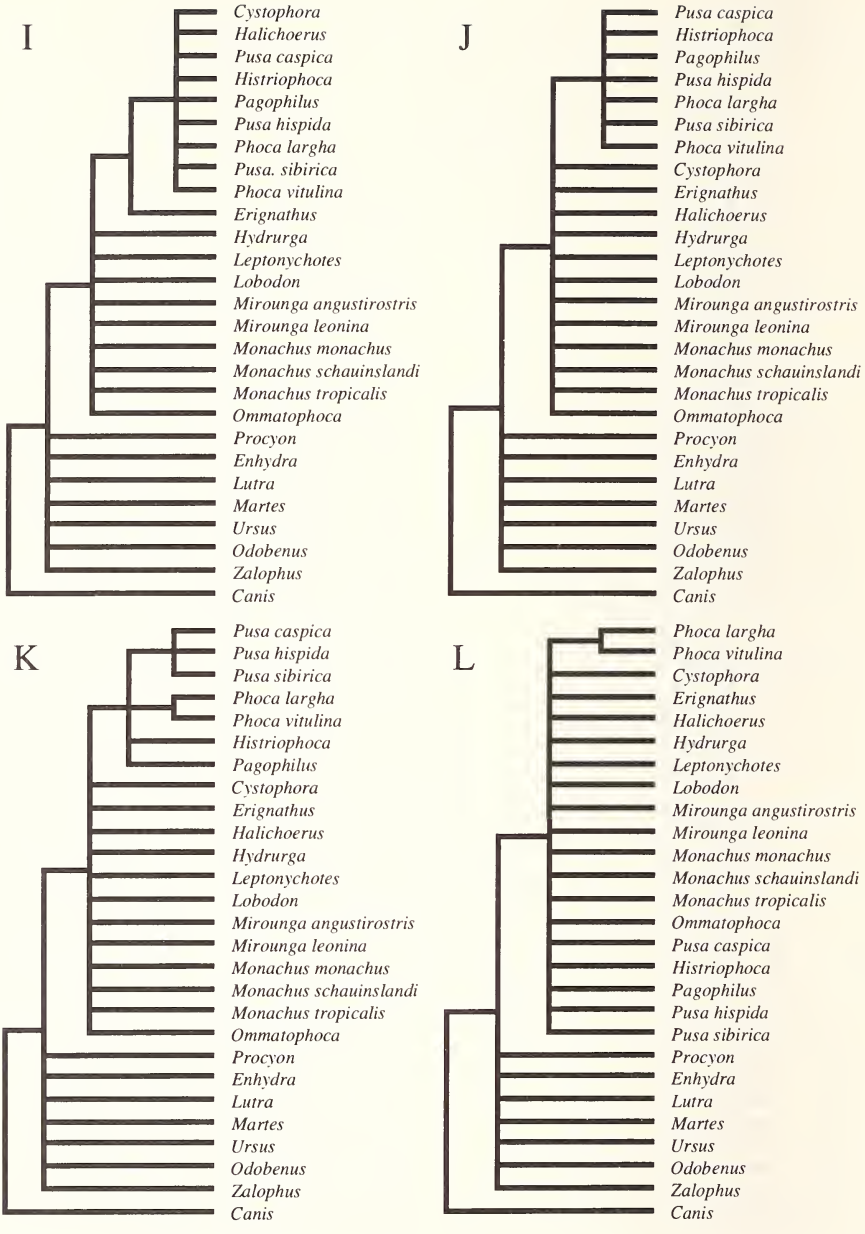

Fig.4I–L: Monophyly constraint trees used to examine various alternative hypotheses of ingroup relationships: (I) erignathus sister, (J) relaxed Burns & Fay, (K) strict Burns & Fay, and (L) phoca.

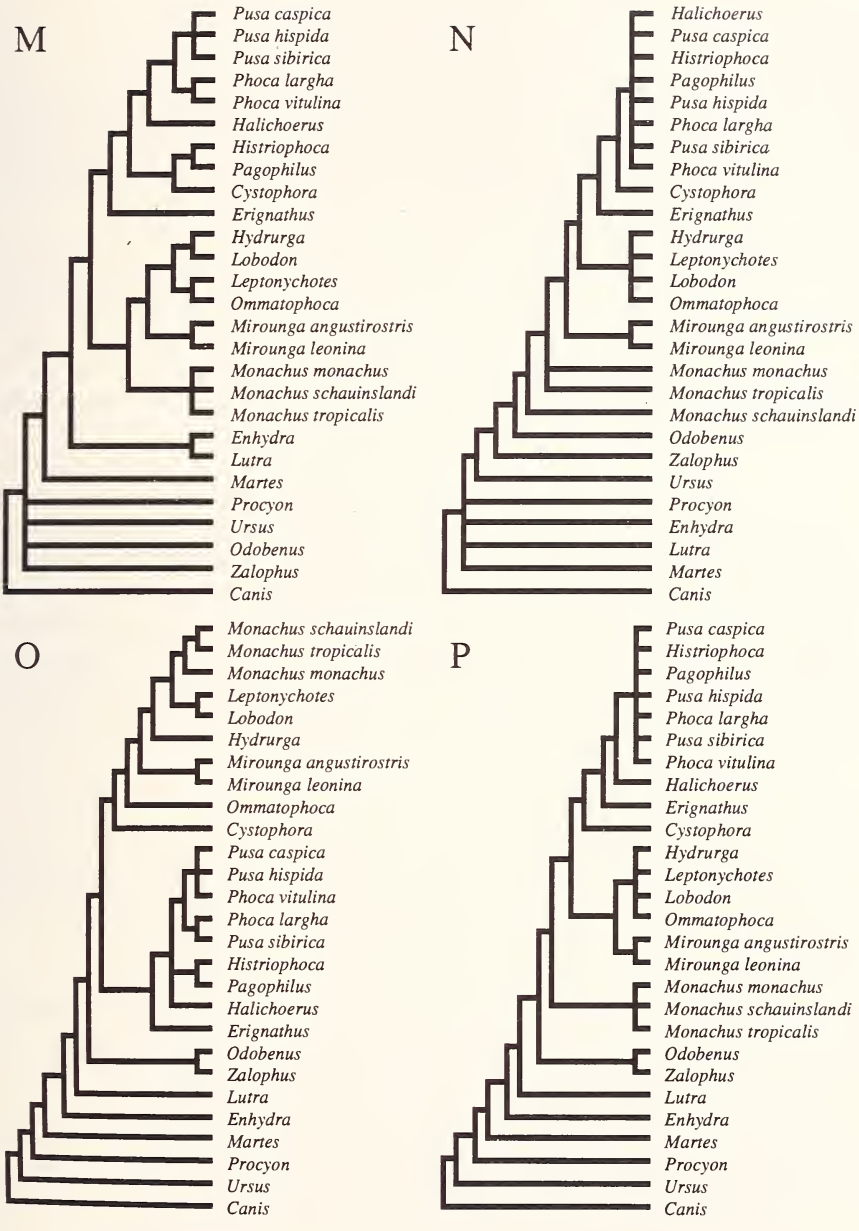

Fig.4M–P: Monophyly constraint trees used to examine various alternative hypotheses of ingroup relationships: (M) de muizon, (N) wyss, (O) unweighted, and (P) condense.

1994). Otherwise, the tribe is almost certainly monophyletic (Wyss 1988:5). To our knowledge, paraphyly of *Mirounga* has never been suggested.

Consensus character states for each higher level taxon were determined from the character states of its constituent species using the same modified majority rule algorithm used to condense specimen observations into the consensus species states (see above; states listed in Appendix B). A heuristic search according to the pattern described above was employed.

Unweighted analysis

The use of inverse weighting for multistate characters is fairly infrequent in phylogenetic systematics (as is the use of multistate characters). Thus, an analysis designed to assess the impact of these different weighting schemes (i.e., inversely versus identically weighted characters) was undertaken. It was performed in exactly the same manner as the overall parsimony analysis except that all characters were unweighted (i.e., each had a weight of 1).

Taxonomic conventions

The ever-changing taxonomy of the carnivores, and especially that within the pinnipeds, reflects the changing opinions on the phylogenetic relationships within this order. Therefore, in order to avoid any confusion, we will refer to the carnivoran taxa as outlined in Tab.1. We will forgo the use of the monotypic phocid tribes Cystophorini (=*Cystophora cristata*), Erignathini (=*Erignathus barbatus*), Miroungini (=*Mirounga* spp.), and Monachini (=*Monachus* spp.) in favour of their constituent taxa. Unless otherwise mentioned, membership of all taxa applies solely to their extant representatives.

Table 1: Indented hierarchy displaying taxonomic conventions employed in this study. Unless otherwise noted, this taxonomy applies only to extant forms. References do not necessarily correspond to the first mention of the group in the literature, but to the manner in which the group is to be recognized here.

Caniformia (Wyss & Flynn 1993) – canids (*Canis*), ursids (*Ursus*), procyonids (*Procyon*), mustelids (*Martes*, *Enhydra*, and *Lutra*), and Pinnipedia
  Arctoidea (Wyss & Flynn 1993) – all caniforms above excluding canids
    Lutrinae (Wozencraft 1993) – otters (*Enhydra* and *Lutra*)
    Mustelinae (Wozencraft 1993) – weasels, marten (*Martes*), wolverine
  Pinnipedia (Illiger 1811) – seals, sea lions, fur seals, and walrus
    Otarioidea (Smirnov 1908) – sea lions, fur seals, and walrus
      Odobenidae (Allen 1880) – walrus (*Odobenus*)
      Otariidae (Gill 1866) – sea lions (*Zalophus*) and fur seals
    Phocidae (Brooks 1828) – phocid seals
      Monachinae (King 1966) – southern seals (*Mirounga* spp., *Monachus* spp., and the lobodontines)
        Lobodontini (Scheffer 1958) – *Hydrurga*, *Leptonychotes*, *Lobodon*, and *Ommatophoca*
      Phocinae (King 1966) – northern seals (*Cystophora*, *Erignathus*, and the Phocini)
        Phocini (Chapskii 1955a) – *Halichoerus*, *Histriophoca*, *Pagophilus*, *Phoca* spp., and *Pusa* spp.

OVERALL PARSIMONY ANALYSIS

The main goal of this section is to present, and preliminarily discuss the robustness of, the solution to an overall parsimony analysis of the data matrix found in Appendix C. The following two sections will then build on this theme by using a number of techniques to more fully examine the support for this cladistic hypothesis. The morphological description of each character is deferred until the **Character Analysis** section, where it can be combined with a description of their evolutionary pathway (i.e., character reconstruction) as inferred from the phylogeny presented and subsequently analyzed in this and the following two sections.

Incidence of polymorphism (Appendix C)

The characters examined in this study, which are primarily osteological and largely relating to the head skeleton, are characterized by a high degree of intraspecific polymorphism, especially among the phocids. Fully 150 of the 196 characters (76.5%) reveal at least one polymorphic taxon. Of these characters, the vast majority demonstrate taxa that maximally possess a two-state polymorphism (124 or 63.6% of all characters), but three- (24 or 12.2%) and four-state (2 or 1.0%) polymorphisms are also present. These ratios are virtually identical in the 168 characters that were retained for analysis – altogether, 129 displayed polymorphic taxa (76.8%), with the taxa in 106 being maximally two-state polymorphic (63.1%), three-state in 21 (12.5%), and four-state in two (1.2%) – indicating that polymorphic characters do not appear to be inferior to monomorphic ones, and that polymorphism appears to be intrinsic to the morphology of these taxa [as intimated for the pinnipeds at least by Mivart (1885), Doutt (1942), Davies (1958b), and Ray (1976b)].

The average number of polymorphic characters for the 27 taxa examined here was 20.8, or roughly 12.4% of the 168 included characters. The range extended from a low of four characters (=2.4%) for *Canis*, to a high of 32 (=19.0%) for both *Leptonychotes* and *Ommatophoca*.

Overall solution (Fig.5)

A parsimony analysis of the 19 extant phocid species (including *Monachus tropicalis*), with eight outgroup taxa, and employing inverse character weighting yielded two equally most parsimonious solutions, each of 69.834 steps (Fig.5A). The differences between these solutions are limited to a subset of the phocines, and arise from the variable placement of *Phoca vitulina* relative to *Erignathus, Histriophoca, Pagophilus* (which consistently form a monophyletic clade), and *Pusa* spp. One solution holds for *Phoca vitulina* being the sister group of all these taxa (with *Pusa* being monophyletic), while the other has *Phoca vitulina* disrupting *Pusa*, rendering it paraphyletic. However, *Pusa hispida* and *Pusa sibirica* remain as sister taxa in both solutions.

Both the strict and majority rule consensus trees for these equally most parsimonious solutions converge on the same cladogram (Fig.5B) with the conflict between the above taxa being visualized as a polytomy within the phocines. The slightly higher length (70,084 steps) of the consensus tree reflects PAUP's use of hard polytomies (which must satisfy

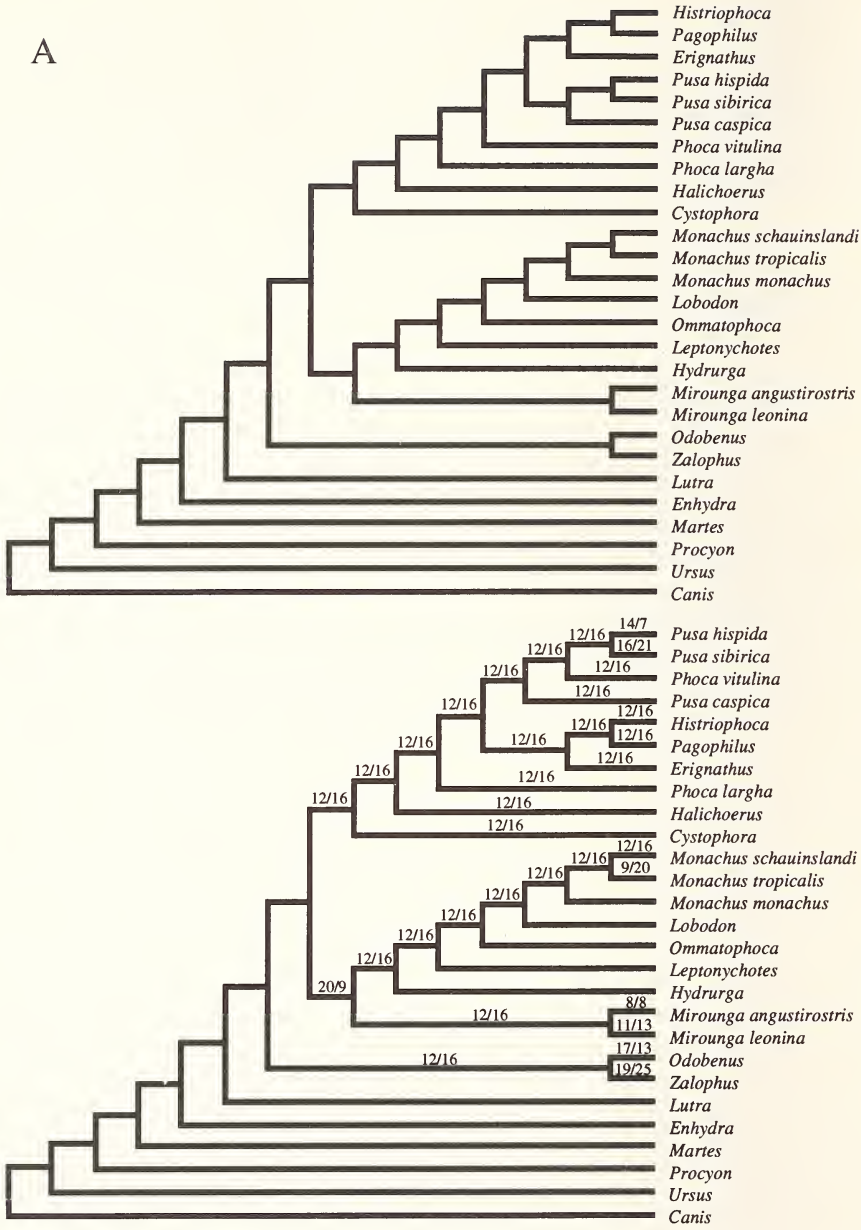

Fig.5A: Cladograms resulting from a parsimony analysis of the inversely weighted data matrix. (A) The two equally most parsimonious solutions (length = 69,834 steps, CI = 0.456, HI = 0.770, RI = 0.629, RC = 0.407).

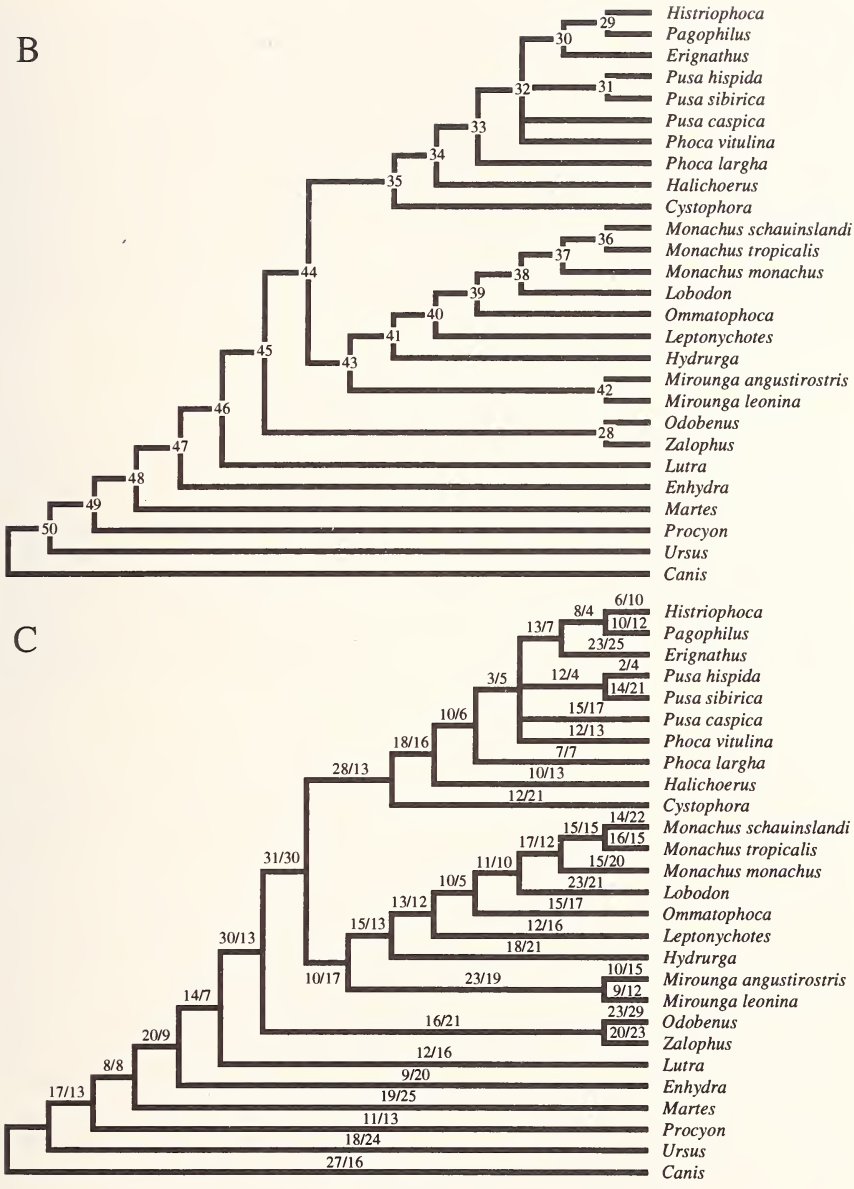

Fig.5B–C: Cladograms resulting from a parsimony analysis of the inversely weighted data matrix. (B) Consensus tree (identical between strict and majority rule algorithms) for the solutions in (A), with internal nodes numbered. All nodes were found in 100% of the equally most parsimonious solutions. (C) As for (B), but with unweighted branch lengths (presented as accelerated transformation / delayed transformation).

multiple independent speciation events from a polytomy) as a computational aid (Maddison & Maddison 1992; Swofford 1993). Although a consensus tree does not necessarily represent an optimal solution for a given data set (Swofford 1993), and does not here, we will refer to the consensus solution as the overall parsimony solution as we believe it to present the best summary of the data set. The consensus solution reflects the conflict present within the phocines, and its single cladogram provides a more efficient discourse. All tree descriptions (see Appendices D through F) are derived from the consensus solution. However, the optimal tree length will be taken to be that of the two equally most parsimonious solutions (69,834 steps) and the various goodness-of-fit statistics will also refer to the optimal solutions (as will be the case for all other analyses as well), unless specified otherwise.

Outgroup relations (Fig.5C)

This analysis confirms a monophyletic Pinnipedia, with the otarioids forming a monophyletic sister group to the phocids. This is in accordance with the recent upswing in support of a monophyletic Pinnipedia among morphological studies (e.g., Wyss 1987; Flynn et al. 1988; Wolsan 1993; Wyss & Flynn 1993), but contradicts the recent contention of an *Odobenus*-phocid clade (Wyss 1987; Wyss & Flynn 1993; Berta 1991; Berta & Wyss 1994; Vrana et al. 1994). However, a monophyletic Otarioidea is among the most strongly supported of all clades, ranging in support from 16 to 21 unweighted steps, depending upon the optimization criterion employed (see Appendix D for weighted branch lengths; the identities of the synapomorphies supporting each node can be found in Appendix E, and are discussed in the **Character Analysis** section).

A somewhat unexpected result was that of a lutrine affinity for the pinnipeds, with *Lutra* being the immediate sister group and *Enhydra* being the sister group to *Lutra* and the pinnipeds. Although many early workers allied the phocids and the lutrines based on superficial similarities [see references in Taylor (1914)], a lutrine affinity for the phocids based on more robust characters has only been suggested by four workers: Flower (1869), Mivart (1885), McLaren (1960b), and de Muizon (1982a). To our knowledge, however, the equivalent scenario has never been postulated for the pinnipeds as a whole, as the otarioids are typically allied with the ursids under this otherwise diphyletic scenario. Most recent studies advocating a monophyletic Pinnipedia (and including both ursid and mustelid outgroups) conclusively indicate an ursid affinity for the pinnipeds (e.g., Vrana et al. 1994; Lento et al. 1995). Only Wolsan (1993) allies a monophyletic Pinnipedia with the lutrine-like fossil *Potamotherium* (which he considers to be a pinniped) within his Mustelida, but his exclusion of any undisputed lutrines [a lutrine affinity for *Potamotherium* has recently come into question (C.A. Repenning pers. comm.; A.R. Wyss pers. comm.)], plus the lack of an ursid outgroup, precludes any definitive statement on lutrine affinities. However, a *Lutra*-pinniped pairing is generally supported here no less strongly than any other outgroup node and is minimally indicated by seven unequivocal synapomorphies. As well, a lutrine affinity also implies a mustelid affinity for a monophyletic Pinnipedia, which, although still rare, is a somewhat more commonly held hypothesis [e.g., Arnason & Widegren 1986; Miyamoto & Goodman 1986 (albeit as the sister group to a mustelid-procyonid clade); Wolsan 1993].

Interestingly, despite Taylor (1914) noting a high degree of convergence between *Enhydra* (but not *Lutra*) and the phocids due to the constraints of their largely aquatic habitats, it is the apparently less aquatically adapted *Lutra* that forms the immediate sister group to the pinnipeds here. The overall implication of this result is that the relationships advocated herein (and especially the historically unusual lutrine-pinniped pairing) are based more on phylogenetically informative characters than on convergent aquatic features.

If the pinnipeds are momentarily ignored, the fissiped outgroups otherwise fall out as is commonly held for the caniforms. The lutrines form a monophyletic clade within the remaining mustelids (*Martes*), with the procyonids (*Procyon*), ursids (*Ursus*), and canids (*Canis*) forming successive sister taxa to the mustelids (see Tedford 1976; Miyamoto & Goodman 1986; Flynn et al. 1988; Wyss & Flynn 1993). Support for the constituent nodes appears reasonably robust, ranging from eight (Mustelidae under either ACCTRAN or DELTRAN optimization) to 27 (Arctoidea under ACCTRAN optimization) unweighted steps (Fig.5C; Appendices D and E). It should be noted, however, that this arrangement is dependent on the somewhat subjective placement of the root of the cladogram (which has *Canis* as the ultimate outgroup). This placement was chosen in accordance with the strong agreement for the canids being the most primitive of the extant Caniformia (Tedford 1976; Flynn et al. 1988; Wyss & Flynn 1993; Vrana et al. 1994; but see Wozencraft 1989), but any alternative placement of the root will disrupt the above pattern of sister taxa relationships. Fortunately, however, these alternative placements will not affect the ancestral state assessment used to determine the pattern of ingroup relationships (Maddison et al. 1984).

Ingroup relations (Fig.5C)

A monophyletic Phocidae enjoys the strongest support of any node in the overall solution, being supported by 30 or 31 synapomorphies (21 of which are unequivocal). However, in contrast to the findings of Wyss (1988a) and Arnason et al. (1995), the overall solution indicates the division of the phocids into two major monophyletic clades: the Monachinae and Phocinae. Support for this arrangement is strong, with the phocines having moderately better support at 13 to 28 unweighted steps (10 of which are unequivocal) versus 10 to 17 (6 of which are unequivocal) for the monachines, depending on the optimization criterion employed (Fig.5C; Appendices D and E). Although the membership of these subfamilies is as expected (see King 1966), some novel internal relations are indicated in both cases.

Relationships within the Monachinae

With respect to the monachines, the elephant seals (*Mirounga* spp.) are held to be basal, a position traditionally accorded to *Monachus* spp. (Hendey 1972; Repenning & Ray 1977; Repenning et al. 1979; de Muizon 1982a; King 1983; Wyss 1988a; Arnason et al. 1995; Lento et al. 1995). Therefore, coupled with the view that *Monachus* spp. is the most primitive of all extant phocids, as well as a good number of fossil forms (Repenning & Ray 1977; de Muizon 1982a), it is surprising to find the monk seals occupying a terminal position deep within the lobodontines. Overall, the indicated topology for the monachines

also speaks against the contention that *Mirounga* is more closely allied to the lobodontines than either is to *Monachus* (Hendey 1972; King 1983; but see Sarich 1976). However, it appears noteworthy that the similarity between *Monachus* and the lobodontines was recognized long before *Mirounga* was added to the Monachinae (see **Introduction**).

Monophyly of *Monachus* is indicated, again in contrast to the findings of Wyss (1988a). As well, this analysis supports the older contention of a sister group relationship between *M. schauinslandi* and *M. tropicalis* (e.g., King 1956; Kenyon & Rice 1959; King & Harrison 1961; de Muizon 1982a), as opposed to the more recent opinion which holds *M. schauinslandi* to be the most primitive member of the genus (if not the phocids as a whole) (Repenning & Ray 1977; Wyss 1988a). Support for both the terminal position of *Monachus* spp. (as indicated by the strength of the *Lobodon-Monachus* spp. grouping) and their interrelationships are marked by a relatively large number of synapomorphies (Fig.5C; Appendices D and E).

The terminal placement of *Monachus* spp. now renders the Lobodontini paraphyletic, which has, at best, only been previously hinted at with the inclusion of fossil forms (Hendey 1972; McLaren 1975; Ray 1976a; Berta & Wyss 1994). However, as again estimated by the strength of a *Lobodon-Monachus* spp. alliance, this paraphyly is strongly indicated. As well, novel internal relationships are proposed for the lobodontines. A *Lobodon-Ommatophoca* pairing is indicated (momentarily ignoring *Monachus* spp.), with *Leptonychotes* and *Hydrurga* forming successive sister taxa to this clade, in contrast to the more traditional *Hydrurga-Lobodon, Leptonychotes-Ommatophoca* split (Hendey 1972; de Muizon & Hendey 1980; de Muizon 1982a; King 1983). Although some of our lobodontine relations are comparatively weak, they are generally supported by more characters than the traditional pairings, which are based primarily on the larger size and more complex morphology of the postcanines in *Hydrurga* and *Lobodon*, or, equivalently, the reduced nature of the postcanines in *Leptonychotes* and *Ommatophoca* (Hendey 1972; de Muizon & Hendey 1980; de Muizon 1982a; King 1983).

Relationships within the Phocinae

As indicated above, support for this subfamily is reasonably strong. Many of the general themes observed for the monachines were also observed here. Again, a novel suggestion for the most primitive member of the subfamily is obtained, with *Cystophora* adopting the traditional placement of *Erignathus*. Although *Cystophora* is generally agreed to be relatively primitive within the phocines [only de Muizon (1982a), Mouchaty et al. (1995), Perry et al. (1995), and possibly Arnason et al. (1995) depart from this view, embedding *Cystophora* well within the Phocini from its traditional sister taxon status, although this result may be peculiar to phylogenies derived from cytochrome b data in particular], to our knowledge, a basal placement for any taxon besides *Erignathus* is unique. The parallel positions of *Cystophora* and *Mirounga* as the basal members of their respective subfamilies hint that some of the similarities between these members of the now abandoned subfamily Cystophorinae might be based on phocid symplesiomorphies, rather than on convergent features (see King 1966). This contention is strengthened by evidence that similar cystophorine features may have been present in *Allodesmus* (Mitchell 1975), a taxon now

felt to be among the fossil sister taxa of the phocids (Wyss 1987; Berta 1991; Wyss & Flynn 1993; Berta & Wyss 1994).

Instead, *Erignathus* is now embedded within the Phocini (rendering the latter paraphyletic), forming the sister taxon to the clade of *Histriophoca* plus *Pagophilus*. Despite the nearly universal agreement on the primitive, almost monachine, nature of *Erignathus* with respect to the remaining phocines (Chapskii 1955a; King 1966, 1983; Burns & Fay 1970; McLaren 1975; Ray 1976a; Wyss 1988a; Berta & Wyss 1994; Arnason et al. 1995), this clade consistently demonstrates the highest number of synapomorphies within the Phocini: seven under DELTRAN optimization (also the number of unequivocal synapomorphies) and 13 under ACCTRAN optimization.

Paraphyly of the Phocini is an extremely uncommon suggestion, speaking against an apparent host of putative chromosomal and morphological synapomorphies (McLaren 1960a, 1966, 1975; King 1966; Burns & Fay 1970; Arnason 1974, 1977; Arnason et al. 1995). To our knowledge, it has only previously been suggested by de Muizon (1982a), Mouchaty et al. (1995), Perry et al. (1995), and possibly Arnason et al. (1995), with *Cystophora* occupying roughly the same position indicated here for *Erignathus*. Yet, there are hints in the literature that *Erignathus* might not be quite as primitive as it is commonly held to be. Ray (1976a) dismisses suggestions of *Erignathus* possessing monachine tendencies, instead preferring to view it as a conservative, partly aberrant phocine. Chapskii (1955a), who supports a basal placement for *Erignathus*, also notes a number of derived features for this genus (mostly pertaining to the feeding apparatus) with respect to the remaining phocines. As well, *Erignathus* displays a number of karyotypic peculiarities that otherwise contradict its plesiomorphic chromosome number (Arnason 1974, 1977). Wyss (1988a) is entirely correct in regarding these features as being autapomorphic and thus phylogenetically uninformative. Nor do they necessarily indicate a paraphyletic Phocini; however, they do potentially hint at a more derived position for *Erignathus* within the phocines. This latter supposition is tentatively supported here by the relatively large number of character state changes (23 to 25 unweighted steps), very few of which indicate a more primitive placement, in the branch immediately leading to *Erignathus*. Within phocids, five of these changes are autapomorphic, 16 are convergent with other phocids, only three are reversals to the plesiomorphic phocid condition, and one is a reversal convergently found in some other phocids (see Appendix E and **Character Analysis**). Nor does *Erignathus* appear to display an inordinate amount of convergence on the monachine pattern. Most of the convergent characters converge on the states found in selected monachines only, and a good number are convergent on the states found in other phocines. On the basis of this evidence, we would suggest that undue attention has been given to the many unusual and prominent attributes of *Erignathus* [which may stem from an accelerated rate of evolution, as has been postulated at the molecular level for *Pagophilus* (Arnason et al. 1995)], at the expense of its many other similarities with the remaining phocines.

Within the Phocini proper, the paraphyly of a number of taxa is indicated. The new position of *Erignathus* now also disrupts the monophyly of *Phoca* (sensu Burns & Fay 1970). As mentioned previously, paraphyly of this taxon is not a new idea, but it is usually attributed to an intrusion by *Halichoerus* [Chapskii 1955a; de Muizon 1982a; Arnason et al. 1995;

hinted at by Arnason et al. (1993)] which is the sister taxon to the remaining Phocini (plus *Erignathus*) here. *Phoca* (sensu stricto) is also paraphyletic, despite the view of some authors that *Phoca largha* is merely a subspecies of *Phoca vitulina* (Scheffer 1958; Burns 1970; Shaughnessy 1975; Baram et al. 1991). The relatively basal position of *P. largha* initially appears weak, as the taxa internal to it are only united by three to five synapomorphies. However, such a position for *P. largha* (with respect to *P. vitulina* at least) is indicated by McLaren (1975) and possibly by Mouchaty et al. (1995). As well, the low number of synapomorphies may be an artifact of the polytomy in this region. With respect to a strictly dichotomous branching arrangement, the polytomy requires that putative synapomorphies for this node (#32; see Fig.5B) satisfy an increased number of descendent lineages (four here). Presumably fewer synapomorphies exist to fulfill this more difficult condition, than for dual descendent lineages (e.g., as in node #30) with the possibility of further changes or reversals further along in the tree. In any case, a clade of *P. largha* and *P. vitulina* is not formed in either of the two most parsimonious solutions.

The polytomy within the Phocini also prevents a clear assessment of the status of *Pusa*. The consensus solution is equivocal; however, one of the two equally most parsimonious solutions does reveal a monophyletic *Pusa* (Fig.5A). At the very least, a sister taxon relationship for *Pusa caspica* is indicated with respect to the remaining *Pusa* spp., as hinted at by Chapskii (1955b). However, the sister taxon status of *Pusa* to the remaining Phocini, as put forth by McLaren (1975), is not supported here.

Histriophoca and *Pagophilus* form a reasonably well supported monophyletic group. This substantiates the long standing, but historically poorly tested claim that the two genera are closely related, or at least very similar to each other (Chapskii 1955a; Davies 1958b; McLaren 1975; de Muizon 1982a; Arnason et al. 1995; Mouchaty et al. 1995). De Muizon's (1982a) hypothesis that any similarity may be exclusively due to symplesiomorphies is not supported.

Summary of ingroup relationships

Overall, the internal relationships of the phocines are comparatively weakly supported in terms of numbers of synapomorphies, especially for those taxa internal to *Halichoerus* (Fig.5C). In fact, the internal relationships of the monachines are generally much better (and more uniformly) supported, despite the weaker support for the subfamily as a whole.

The new relationships proposed within each subfamily are somewhat difficult to reconcile with previous opinion. This is especially true for the phocines, which have been well studied for the most part, and especially for the novel position of *Erignathus* advocated here. The apparent polytomy within the Phocini (plus *Erignathus* here) is suggested by the numerous conflicting taxonomic assessments and biogeographic or systematic hypotheses for this group (e.g., compare Chapskii 1955a; Davies 1958b; McLaren 1966, 1975; Burns & Fay 1970; Ray 1976a; Repenning et al. 1979; de Muizon 1982a; Arnason et al. 1995; Mouchaty et al. 1995; Perry et al. 1995). This lack of resolution is probably traceable to the rapid adaptive radiation of this group in the post-early Pliocene and/or Pleistocene (Ray 1976a), allowing insufficient time for its members to become clearly differentiated (at least morphologically; see Arnason et al. 1995). Evidence from this study

for this line of reasoning lies in the relatively limited number of synapomorphies supporting most nodes in this region, in addition to the polytomy, which is more typical in regions of a cladogram where speciation has occurred via a rapid adaptive radiation (Wagner 1992). The pattern may also be obscured somewhat by a large amount of parallel evolution within the Phocini.

Although the number of proposed systematic alterations for the monachines is greater than for the phocines, this does not seem to present as great a problem. For the most part, this is because the monachines have not been as well studied, possibly due in large measure to the remoteness of most species with respect to the primarily northern hemisphere population of phocid researchers, combined with the seemingly more intuitive relationships of, and tribal allotment within, this subfamily. This seems to be especially true for the lobodontines, whose internal relationships have never been studied in detail, and whose monophyly (despite their obvious morphological differences) has seemingly never been questioned due to their common and distinctive geographic range, coupled with a similar lack of detailed examination. In the end, the novel monachine relationships advocated here may be a consequence of the freedom allowed all species to form the most parsimonious set of pairings, as opposed to previous studies which tended to constrain the monophyly of one or more of the monachine tribes (see **Condensed analysis** in the **Comparative Tools** section), particularly the Lobodontini.

Finally, in contrast to the assertions of Wyss (1988a) and Berta & Wyss (1994), convergences appear to be much more common than reversals in phocid evolution (see Appendix E and **Character Analysis**), a pattern that holds even under ACCTRAN optimization, where reversals are favoured. Of the homoplastic characters (and excluding within terminal changes), 49 / 85 were convergent (numbers given as ACCTRAN / DELTRAN), 16 / 5 were reversals, and 79 / 55 displayed both. Thus, reversals, when present, were typically found together with convergences (although convergent incidences of reversals only accounted for 45 / 29 characters of this subset). Nor was there a discernible pattern of homoplasy [in contrast to Wyss (1988a) and Berta & Wyss (1994) who indicate a distinct pattern of retrogression for the phocines], with convergences and reversals spread throughout the phocids.

Support for the overall solution

Various indicators point to the "good resolving power" of the data set as a whole (see also **Statistical Tests** and **Comparative Tools** sections). On a purely empirical basis, the data set ran surprisingly "cleanly" (only two solutions) and quickly for such a large matrix (27 taxa and 168 characters). In part, this can be traced to the use of inverse character weighting. While similar runs using unweighted characters (see **Comparative Tools** section) produced only four solutions, analysis times were considerably longer, due to a greater number of slightly less than most parsimonious solutions that needed to be searched through. However, the common perception that a low number of most parsimonious solutions implies a good quality to the data set may be an unsubstantiated claim, as some studies suggest that this number is dependent upon the number of characters (and how many states each possesses) and the number of taxa (Hillis & Huelsenbeck 1992; Lamboy

1994). It is unknown what the extent of this is here, as these factors act in opposition to one another, but it would be prudent to rely on other, more robust, indicators of resolving power.

The relatively high values of selected goodness-of-fit statistics (CI = 0.456, RI = 0.629, and RC = 0.407) likewise point to a high resolving power. Benchmarks for evaluating these statistics are rare, and, as these indices estimate the degree of homoplasy, they may be specific for the group under examination (see **Methods and Materials**). However, in the case of CI, the value obtained here is about on a par with the expected value for 27 taxa, 0.461 (Sanderson & Donoghue 1989). These relatively high values are somewhat surprising, as the phocids as a group, and especially the phocines, have been characterized as possessing a reasonably high number of reversals within a monophyletic pinniped framework (Wyss 1988a; Berta & Wyss 1994). Regardless of whether this apparent preponderance of reversals derives from a singular use of ACCTRAN optimization (see above also), the fairly homoplastic nature of the phocids is reflected by the high value obtained for the HI (0.770). However, this value is likely inflated to an unknown extent due to PAUP's failure to designate polymorphic ancestral nodes (see **Methods and Materials**).

Thus far, we have only presented a preliminary assessment of the support for the overall solution. This will be built upon by the results of specific, statistical tests designed to more objectively quantify the level of support (both for the solution as a whole and for the specific clades within it) and of various comparative tools, which are presented in the following two sections respectively. Although the comparative tools are not tests of support per se, their output very often will indicate the robustness of a solution [= how resistant it is to further change; Maddison et al. (1984)], and can be used to corroborate the findings of the true tests of support.

STATISTICAL TESTS

Interpreting statistical results

While the influx of numerous statistical tests has been a great boon to the practice of phylogenetic analysis, the results of these tests seem to be frequently misinterpreted. The case for both the PTP test and skewness is clear and has been mentioned in the **Methods and Materials** section: the degree of character covariation that these tests really indicate is held to equate with the degree of phylogenetic signal in a given data set. Likewise, analyses such as the bootstrap and Bremer support have been, or could be, taken to provide some form of confidence interval on how well a data matrix estimates the one true phylogeny. In reality, these tests merely indicate how well that data matrix presents its own underlying distribution (= hierarchical pattern of relationships), which may or may not coincide with the real distribution. The extension towards how well this underlying distribution estimates the real phylogeny, again, requires additional assumptions.

Most cladists believe that the one true phylogeny is represented by a pattern of shared derived characteristics in organisms and can be reconstructed by interpreting this pattern through some criterion (e.g., parsimony, maximum likelihood). Thus, we attempt to gather

data sets that include only phylogenetically informative characters (see Sanderson 1989; Kluge & Wolf 1993) that are sufficient in number and adequately distributed to reconstruct all portions of the true phylogeny. Given the view that true homoplasy does not exist [as homoplasy merely represents inadequately or improperly described features (see Hennig 1966)], each set of phylogenetically informative characters should yield the true phylogeny (or at least very close to it) under these ideal conditions.

Ignoring any potential flaws in the logic of the cladistic method, the main problem is that we cannot a priori discriminate between characters that have been shaped by evolution via common descent (i.e., are phylogenetically informative) and those that have been influenced by a host of other processes. The variable inclusion of these latter, phylogenetically misinformative, characters will, when they conflict with the informative characters, deflect us away from the true phylogeny to varying extents. This, undoubtedly, is the cause of the many conflicting systematic hypotheses for a given group present throughout the literature. Thus, our data sets probably possess biased estimates of the actual distribution, and the various tests that aim to place confidence intervals on the distribution implied by the data are, in most cases, placing confidence intervals on this biased distribution (but see Felsenstein & Kishino 1993; Hillis & Bull 1993). This is unwittingly illustrated for the bootstrap in Fig.1 of Hillis & Bull (1993). The bootstrap pseudosamples (= replicates here) are one step too far removed to be able to estimate the true phylogeny (without the additional assumption that all the characters are phylogenetically informative).

Yet, Hillis & Bull (1993) indicate that, under certain circumstances, the bootstrap actually provides a conservative estimate that an indicated group is also found in the known true phylogeny. (The phylogeny was known in this instance as it was computer generated or created in the laboratory using viruses.) But, if this is the case, then how does one explain equally high (and sufficiently high so as to indicate the reality of the clade with some confidence) bootstrap frequencies in conflicting solutions? To illustrate this point, we have run bootstrap analyses equivalent to the one performed here for the "rival" hypotheses of Wyss (1987, 1988a), Wyss & Flynn (1993), and Berta & Wyss (1994). [Where possible, the data matrices were analyzed as indicated in the respective study. The only changes we made were to include all-zero state ancestors for Wyss (1987; 1988a) to polarize the characters, and to change state 9 ("known, but not described") to a question mark for Wyss (1987). This coding more properly reflects that the data are really missing, whereas Wyss's (1987) coding implies that the act of not having a known state described is a putative homology. These changes did not result in a different most parsimonious solution for either study.] In each case, the bootstrap generally supported the findings of the respective conflicting parsimony analyses with bootstrap frequencies about on a par with those observed here (Figs.6 and 8 respectively). This apparently anomalous result of equally (and sufficiently) supported, but highly contrasting solutions supports our contention that at least the bootstrap, and probably most of the remaining tests are merely elucidating how strong the underlying, potentially biased distribution is in each set of characters, and not how well each data matrix estimates the actual phylogeny.

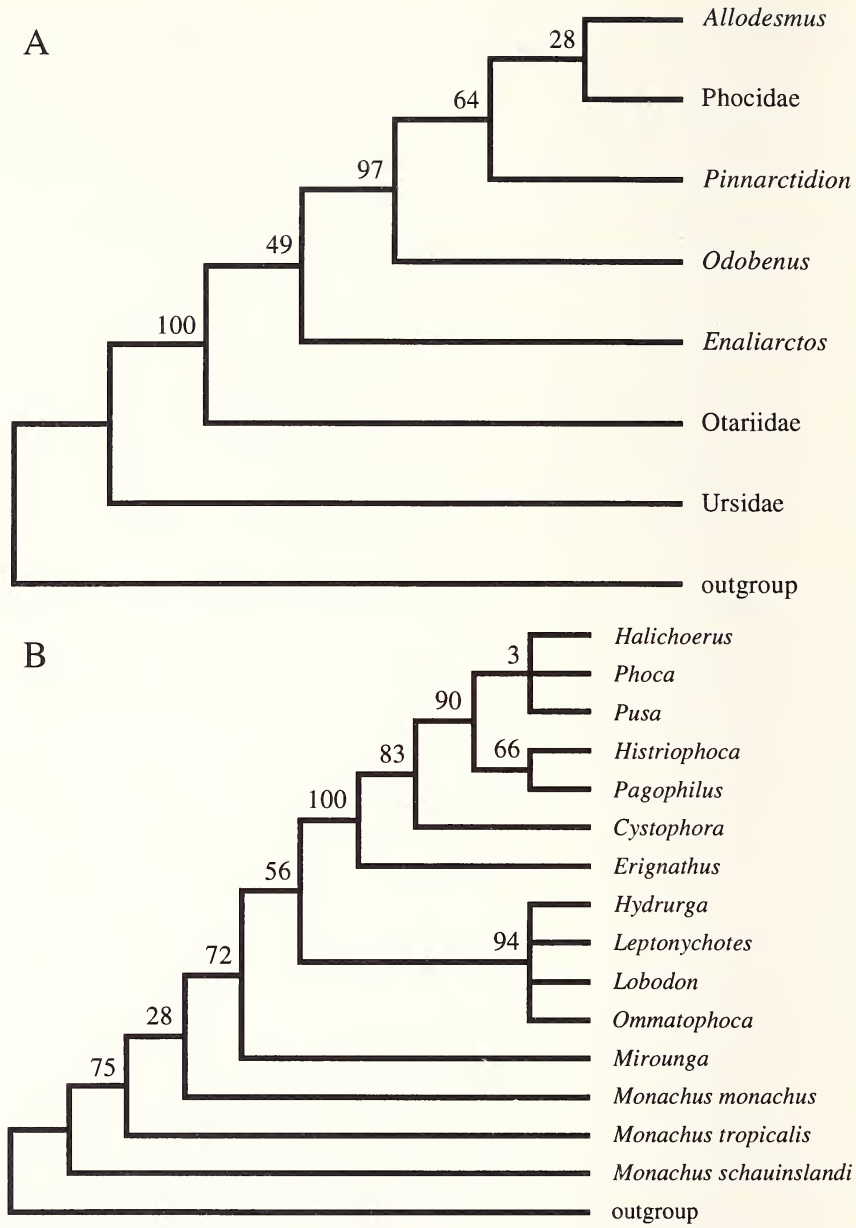

Fig.6A–B: Majority rule consensus solutions with bootstrap frequencies resulting from bootstrap analyses (1,000 replications) of various "rival" data matrices for examining pinniped phylogeny: (A) Wyss (1987) and (B) Wyss (1988a).

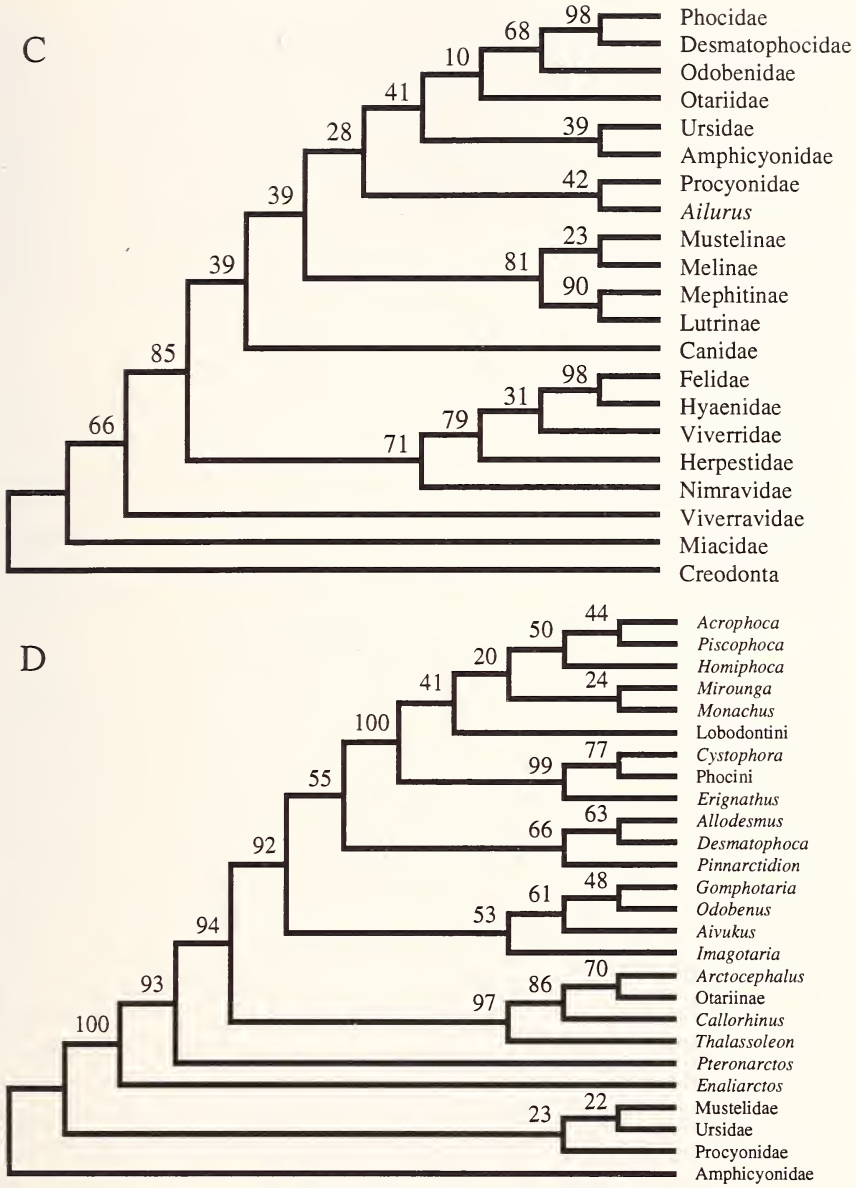

Fig.6C–D: Majority rule consensus solutions with bootstrap frequencies resulting from bootstrap analyses (1,000 replications) of various "rival" data matrices for examining pinniped phylogeny: (C) Wyss & Flynn (1993) and (D) Berta & Wyss (1994).

The solution then seems to be not the accumulation of data matrices with only phylogenetically informative characters (which may be impossible to determine), but of matrices that represent a random sample of the universe of all possible characters. This is based on the assumption that of the many possible signals influencing the form of a character, the phylogenetic signal will be the strongest (otherwise, a systematic analysis based upon phylogenetic principles would appear to be unrealizable). Thus, by taking a random sample, the phylogenetically informative characters will hopefully predominate and point towards the one true phylogeny. As well, in such a case (where the signal within the data matrix closely approximates the true phylogeny), the various statistical tests mentioned above will be more likely to be placing confidence intervals on how well we have reconstructed the true phylogeny.

A simple analogy involves a universe of (scattered) points that roughly indicate a square in space. Through some biased sampling (which emulates the inclusion of increasing numbers of non-phylogenetically determined characters), we could achieve data sets whose underlying distributions are of a straight line and a circle respectively. [Note that this is also possible under random sampling, but should be far less likely to occur. Likewise, biased sampling could also indicate a square (e.g., sample only from the corner regions), but, again, this is unlikely.] By employing tests based on each data matrix, or some sample thereof, we cannot help but observe something along the lines of a line and a circle each time.

Although all of our current tests provide valuable information, they may be erroneously focused. These tests indicate only the signal strength in our samples, with no indication as to the accuracy of that signal. They are similarly hampered by being based, to varying degrees, on the same tree constructing methods (and thus the same potential biases) that were used to generate the cladogram under examination. As stressed by Sanderson (1989), more tests that are independent of the various tree constructing methods are required. Although it is unlikely to ever be developed, what we really require is a statistical test measuring the randomness of our sample of characters, for it is presumably only with a random sample that our data matrices will estimate the true phylogeny to various degrees (which our current tests could then delineate). Unfortunately, even with such a test we would be left with a discrepancy between what it really indicates (randomness of the character set) and what we would interpret it to mean (the potential accuracy of the character set in predicting the true phylogeny). Note that this desired test is subtly, but meaningfully different from our current PTP and skewness tests. In a universe of characters shaped largely by evolution, a random sample thereof should covary significantly, except now this covariation would be primarily due to common descent with modification. The characters need not be completely independent either (and in all likelihood they would not be), merely a random sample. Without such a test for randomness, all that we are left with is a critical examination of the characters used to achieve a given result, something that has, unfortunately, become increasingly rare with the influx of statistics into cladistics.

The total evidence approach, where different data sets are combined into one larger data set (see Kluge 1989; Kluge & Wolf 1993), is one step towards reducing the bias present in our character sets. Disregarding potential problems such as how to combine characters

from very different sources (e.g., morphological versus molecular data), or whether or not one can even justifiably pool data matrices of very different signals (see Bull et al. 1993), total evidence does, in principle, provide the advantage of a more varied data set that presumably provides a better and/or wider representation of the suite of all possible characters. However, we are left with the same dilemma, now only one step further removed. So long as the set of characters is non-random, the tests we currently have will not place confidence intervals on the true phylogeny.

Therefore, we will interpret our results according to what the various tests maximally indicate: character covariation (PTP and skewness tests), or how strongly our data present some underlying distribution which may or may not be the true phylogeny (bootstrap and support analyses, as well as successive approximations and constraint analyses). The true "test" lies in the **Character Analysis** section, where the set of characters producing this distribution are individually presented and described. Implications as to the overall accuracy of our solution (with respect to the one true phylogeny) are not intended. But, since we naturally feel that our data set is one of the best available in terms of taxonomic rank examined, number of taxa (both ingroup and outgroup), range of morphological characters (with the acceptance and inclusion of polymorphic data), and general inclusiveness, we feel that it provides one of the better estimates of the true phylogeny of the phocid seals. However, with no knowledge as to how random our character set is, we make no pretense as to the accuracy of our solution.

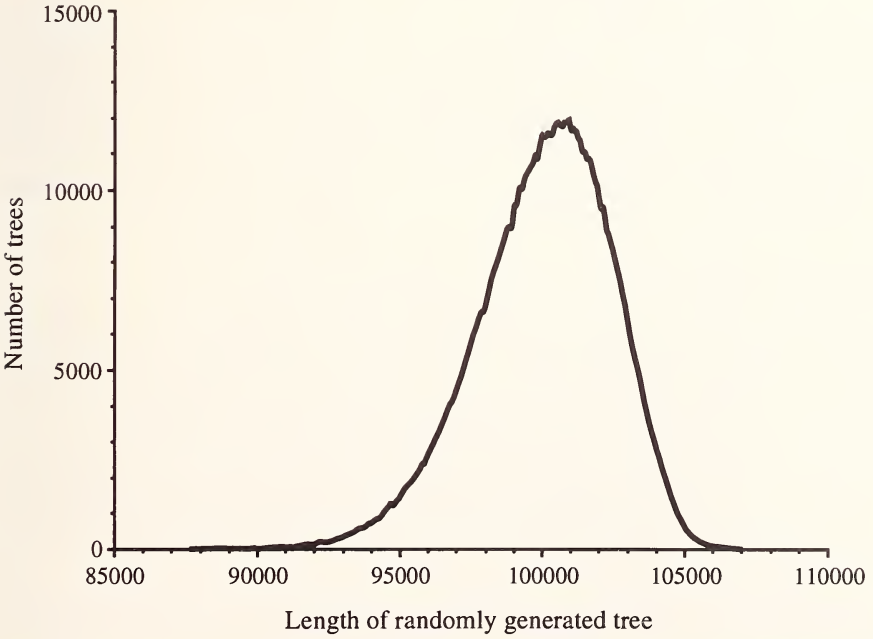

Fig.7: Frequency distribution of tree lengths for a random sample of 1,000,000 trees generated from the inversely weighted data matrix. Skewness statistic (g_1) = -0.503.

Character covariation within the data set

Both the PTP and skewness tests produced highly significant results, indicating very strong character covariation within the data set. Using 99 randomly permutated data matrices, the PTP statistic (or α') was calculated as 0.01. The more accurate estimates proposed by Källersjö et al. (1992) showed even lower values: 6.0×10^{-4} for α" and 2.2×10^{-18} for α*. In accordance with Källersjö et al. (1992), this last, lowest value is held to be the best estimate of the level of significance here. The critical PTP length value corresponding to the 0.05 level was determined to be 79,619 steps, some 9,785 steps (142 corrected steps) longer than the overall parsimony solution. The shortest and longest trees derived from the permutated matrices were 79,227 (+ 9,393 steps / 137 corrected steps) and 80,605 steps (+ 10,771 steps / 157 corrected steps) respectively.

Skewness tests echoed the findings of the PTP test. A frequency distribution of tree lengths from a random sample of 1,000,000 trees possessed a value of -0.503 for g_1 (Fig.7). This was judged to be significant at the 0.05 level based on a critical value for g_1 (25 taxa and 250 binary or four-state characters) of -0.08 (Hillis & Huelsenbeck 1992). The shortest random tree obtained, 85,170 steps, was 15,336 steps (223 corrected steps) longer than the overall solution. As suggested by Källersjö et al. (1992), the sample size used here was apparently not sufficient to sample trees from the attenuated left-hand tail of the distribution.

Regional support within the overall solution

While the previous subsection demonstrated significant character covariation throughout the data set as a whole, not all regions within the resultant solution will necessarily be equally supported by this set of covarying characters. The remaining statistical tests show considerable agreement as to the regional localization of stronger and weaker signal within the data set. This more localized signal, it appears, is sufficiently strong and/or widespread to override regions of weak support and be manifested at the level of the entire solution (see above).

Bootstrap analysis (Fig.8)

The majority rule consensus tree obtained from a bootstrap analysis of 1,000 replicates (Fig.8A) agrees quite strongly with the overall parsimony solution. The various goodness-of-fit statistics are virtually identical between the two solutions, and the bootstrap solution at 70,006 steps is only 172 steps (= three corrected steps) longer than the overall solution. Only two major topological differences were observed, one in each phocid subfamily. In the monachines, *Leptonychotes* moved to a more terminal position to form a clade with *Lobodon*. This clade now becomes the sister group to *Monachus* spp. In the phocines, the clade composed of *Erignathus, Histriophoca*, and *Pagophilus* moved basally to form the sister group to *Phoca* spp. plus *Pusa* spp. Within this latter clade, *Pusa* is indicated to be monophyletic, with *Pusa caspica* again being held to be basal to the remaining species of the genus. *Phoca* remains paraphyletic and related by symplesiomorphies, with *Phoca largha* maintaining its more basal status within the genus. However, as the bootstrap solution is based on statistical considerations and not parsimonious ones (as well as being

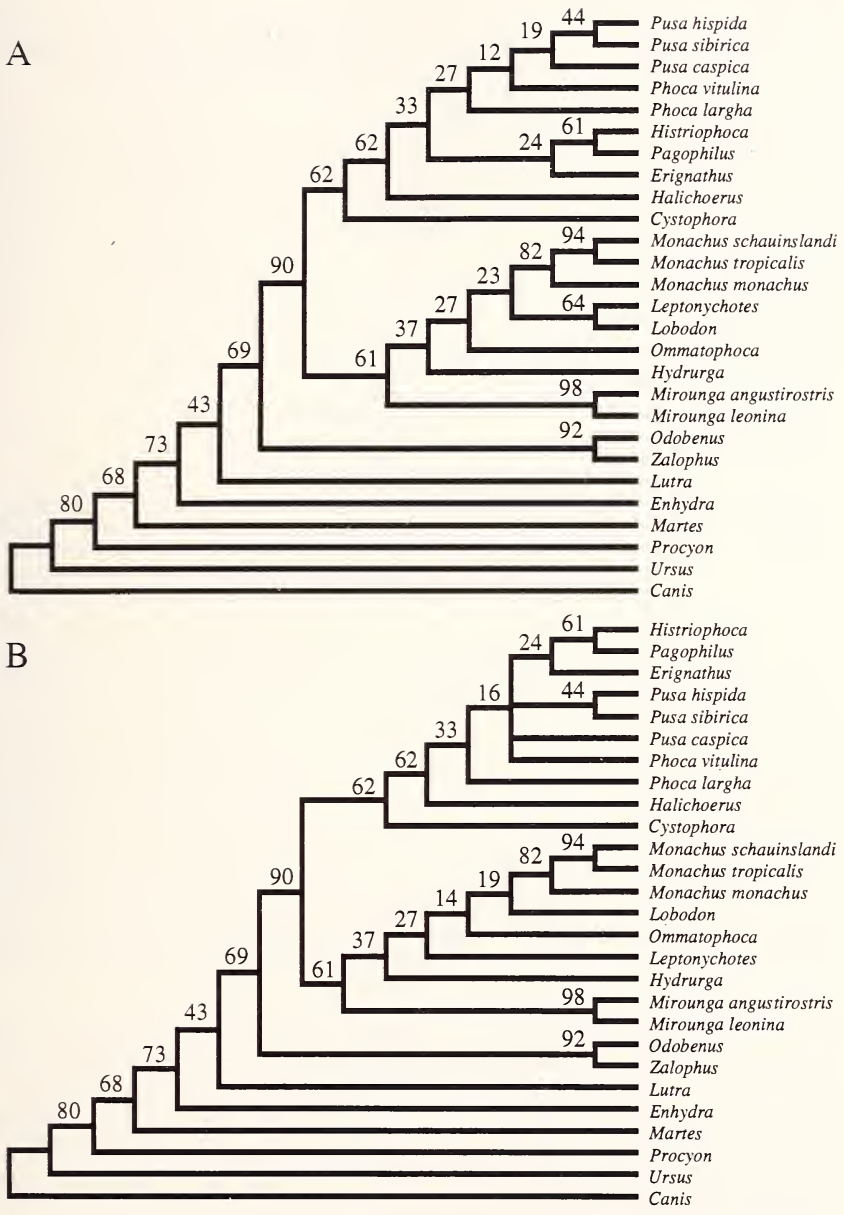

Fig.8: Results from a bootstrap analysis (1,000 replications) of the inversely weighted data matrix. (A) Majority rule consensus tree from bootstrap analysis (length = 70,006 steps, CI = 0.456, HI = 0.770, RI = 0.626, RC = 0.405). (B) Overall parsimony solution with bootstrap frequency of each node.

Table 2: Bootstrap frequencies indicating support within the inversely weighted data matrix for a monophyletic grouping of various outgroup taxa and either the phocids alone or the pinnipeds as a whole. Numbers given as the total number of trees (out of 1000) / percentage of all trees.

Alternative outgroup	For phocids alone	For all pinnipeds
arctoid	< 0.08 / << 1	1000* / 100*
procyonid	1.00 / < 1	1.00 / < 1
ursid	< 0.08 / << 1	21.00 / 2
mustelid (including lutrines)	115.50 / 12	680.50 / 68
musteline	4.00 / < 1	43.67 / 4
lutrine (both *Enhydra* and *Lutra*)	219.67 / 22	729.33 / 73
Enhydra alone	11.25 / 1	41.00 / 4
Lutra alone	119.93 / 12	428.67 / 43
otarioid	687.00 / 69	n/a
Odobenus alone	59.00 / 6	n/a
Zalophus alone	24.50 / 2	n/a

* Due to *Canis* being the ultimate outgroup, this arrangement was necessarily found in all bootstrap replicates.

a consensus solution; see **Methods and Materials**), we should look instead to the overall solution.

When bootstrap frequencies are determined for the nodes present in the overall solution (Fig.8B), a clear dichotomy in support can be observed. Outgroup relationships tend to be moderately to strongly supported, with only the node for *Lutra* plus the pinnipeds falling below a bootstrap frequency of 50%. However, this merely reflects an equally strong tendency for the two lutrines to form a monophyletic sister group to the pinnipeds (bootstrap frequency = 39%), in essence a minor alteration. A monophyletic Otarioidea is particularly strongly indicated. Bootstrap frequencies for alternative outgroup arrangements are noticeably smaller, especially for those postulating a diphyletic Pinnipedia (Tab.2).

The monophyly of both the phocids as a whole, and of each of its two subfamilies, show comparable bootstrap frequencies to the outgroup nodes. Beyond this, support for the relationships within each subfamily was distinctly weaker. Only the species clusters of *Histriophoca* plus *Pagophilus, Mirounga* spp., and *Monachus* spp. (and *M. schauinslandi* plus *M. tropicalis* within this) display bootstrap frequencies greater than 50%. A monophyletic Phocini (plus *Erignathus*) is also relatively strongly indicated (bootstrap frequency of 62%), giving further support to the basal position of *Cystophora* within the phocines. In fact, *Cystophora* displays an unusually strong tendency to cluster with the monachines (bootstrap frequency of 31%), something that might be expected more of the supposedly more monachine-like *Erignathus*, but was not supported here (bootstrap frequency of <1%).

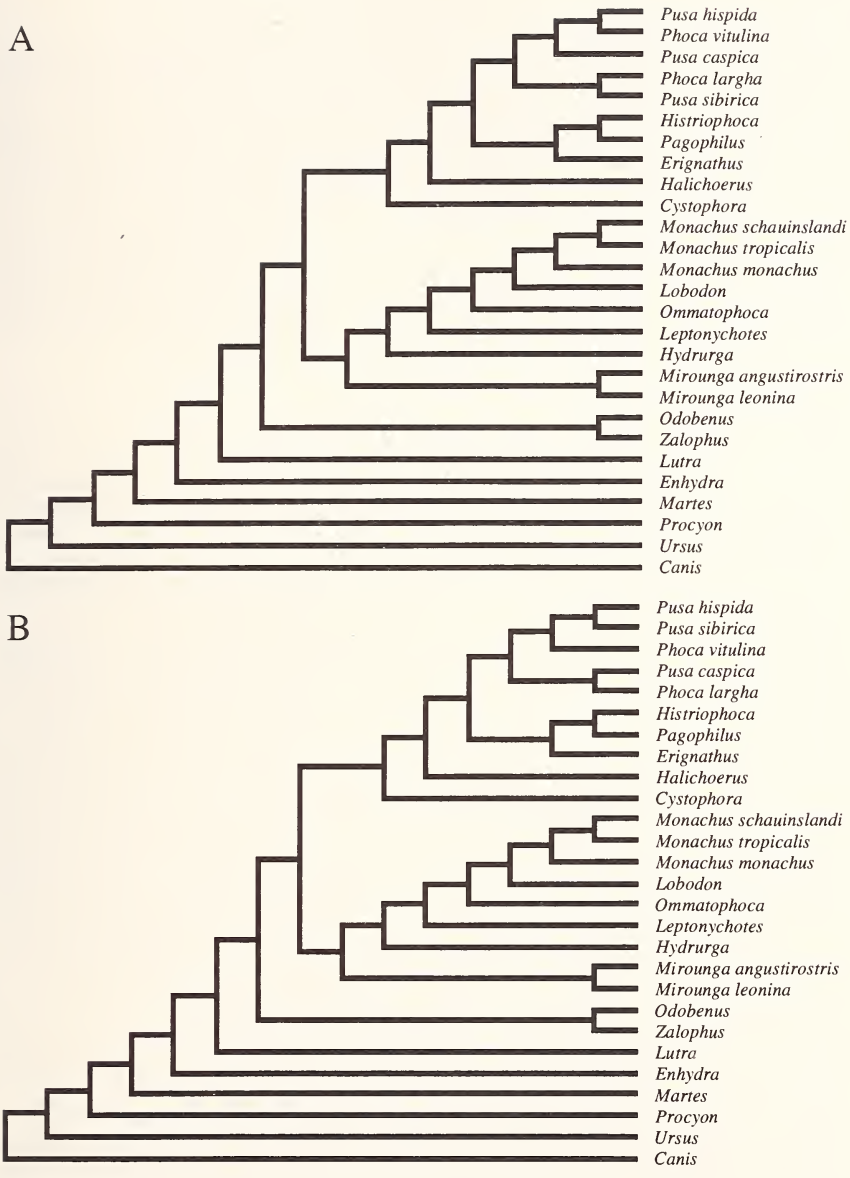

Fig.9: Cladograms resulting from a successive approximations analysis. Characters were reweighted according to their (A) CI and (B) RI or RC from the overall parsimony analysis (with each solution being identical between maximum, minimum, and average fit of the respective goodness-of-fit statistic). Both trees of length = 69,842 steps, CI = 0.456, HI = 0.770, RI = 0.629, RC = 0.407.

Successive approximations (Figs.9 and 10)

The a posteriori weighting of the characters based on one of three goodness-of-fit statistics (CI, RI, or RC) converged on either of two solutions (Fig.9). Each solution, when constrained with the original set of inversely weighted characters, was only very slightly longer than the overall solution at 69,842 steps (= 7 steps / 1 corrected step longer). Topological differences between these two solutions, and between either and the overall solution were found solely within the Phocini (plus *Erignathus*) and limited to the interrelationships between *Phoca* spp. and *Pusa* spp. This conflict is reflected by the strict consensus tree of both solutions [Fig.10A; the majority rule solution (Fig.10B) is the same as that produced by either the RI or RC] where the species of both genera are the sole members of a completely unresolved polytomy.

Support analysis (Fig.11)

Interpreting the results of the support analysis varies according to the form of consensus tree that is viewed, with the strict and majority rule consensus algorithms treating conflicting solutions relatively more severely and more forgivingly respectively (see **Methods and Materials**).

The strict consensus trees show a steady decrease in resolution as increasingly homoplasious solutions are retained. At only one corrected step longer than the most optimal solution (Fig.11A), resolution within the Phocini (plus *Erignathus*) is almost completely lost. Resolution is also lost for the lutrines, reflecting the equally large tendency for these two taxa to form a monophyletic sister group to the pinnipeds (see above). An increase of an additional corrected step (Fig.11B) shows a partial degradation of lobodontine relationships, which becomes complete at the next step (Fig.11C). At this latter step (three corrected steps longer), resolution is completely lost for the Phocini (plus *Erignathus*) as well, and the integrity of the monachines is also lost. Finally, at the limits of the analysis (Fig.11D), almost all structure within the phocids is lost. Only the clades of *Mirounga* spp. and *Monachus* spp. (and within *Monachus*) retain unanimous support. As well, structure is lost for the pinnipeds as a whole, with the otarioids and phocids, although still distinct clades, forming a polytomy with the lutrines. Another polytomy was also formed between *Procyon, Martes,* and the lutrine-pinniped clade.

In contrast, the majority rule consensus trees show virtually complete and unaltered resolution, even at the limits of the analysis. Only a progressive degeneration of Phocini (plus *Erignathus*) structure was observed, although the support within the phocids as a whole (as visualized by the percentage of solutions supporting each node) gradually decreased with increasing length (except for most strongly supported species clusters). Among outgroup relationships, only support for the *Lutra*-pinniped and *Martes*-lutrine pairings were observed to decrease, albeit only slightly, with increasing length.

Overall conclusions

Altogether, the findings of these statistical tests largely corroborate those of the parsimony analysis conducted in the previous section. This could be an artifact of all these tests

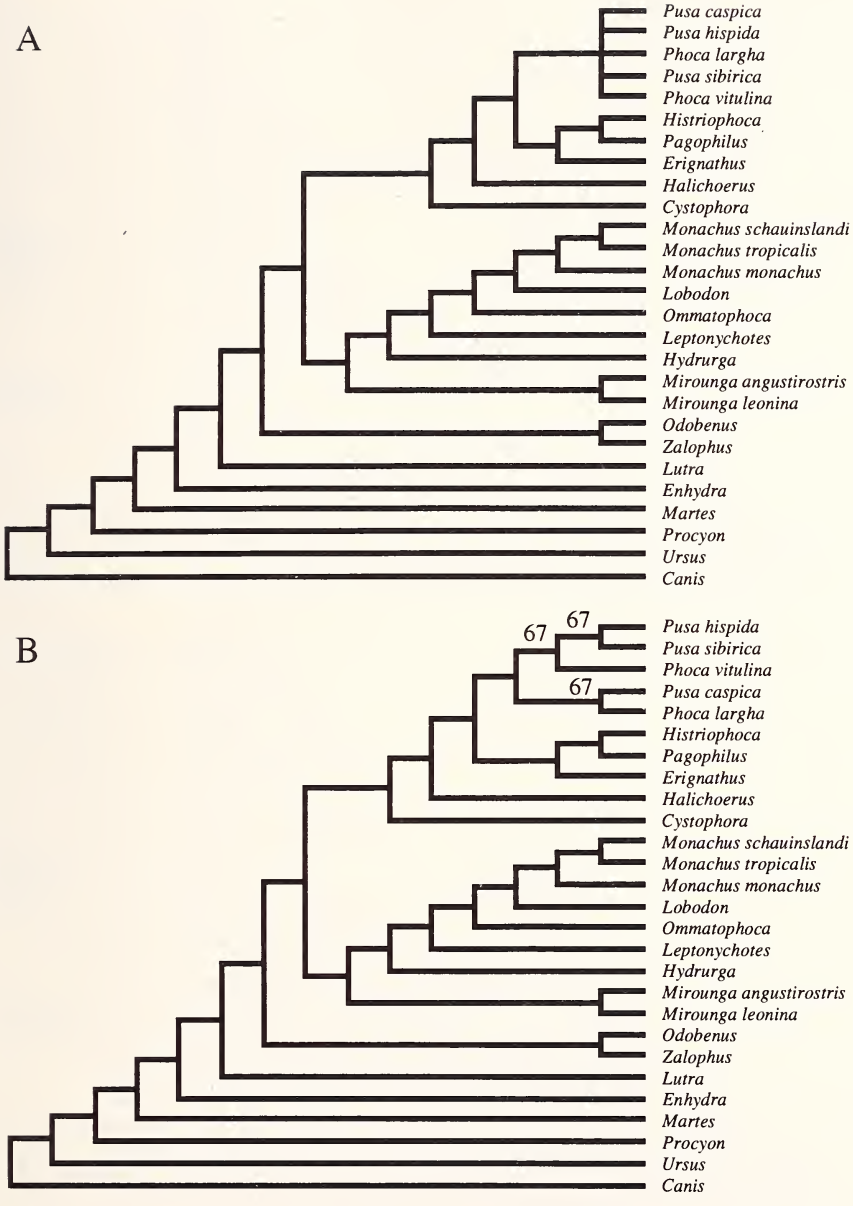

Fig.10: Strict (A) and majority rule (B) consensus solutions for cladograms resulting from successive approximations analyses based upon CI, RI, and RC. Unless otherwise indicated, all nodes in (B) were found in 100% of the equally most parsimonious solutions.

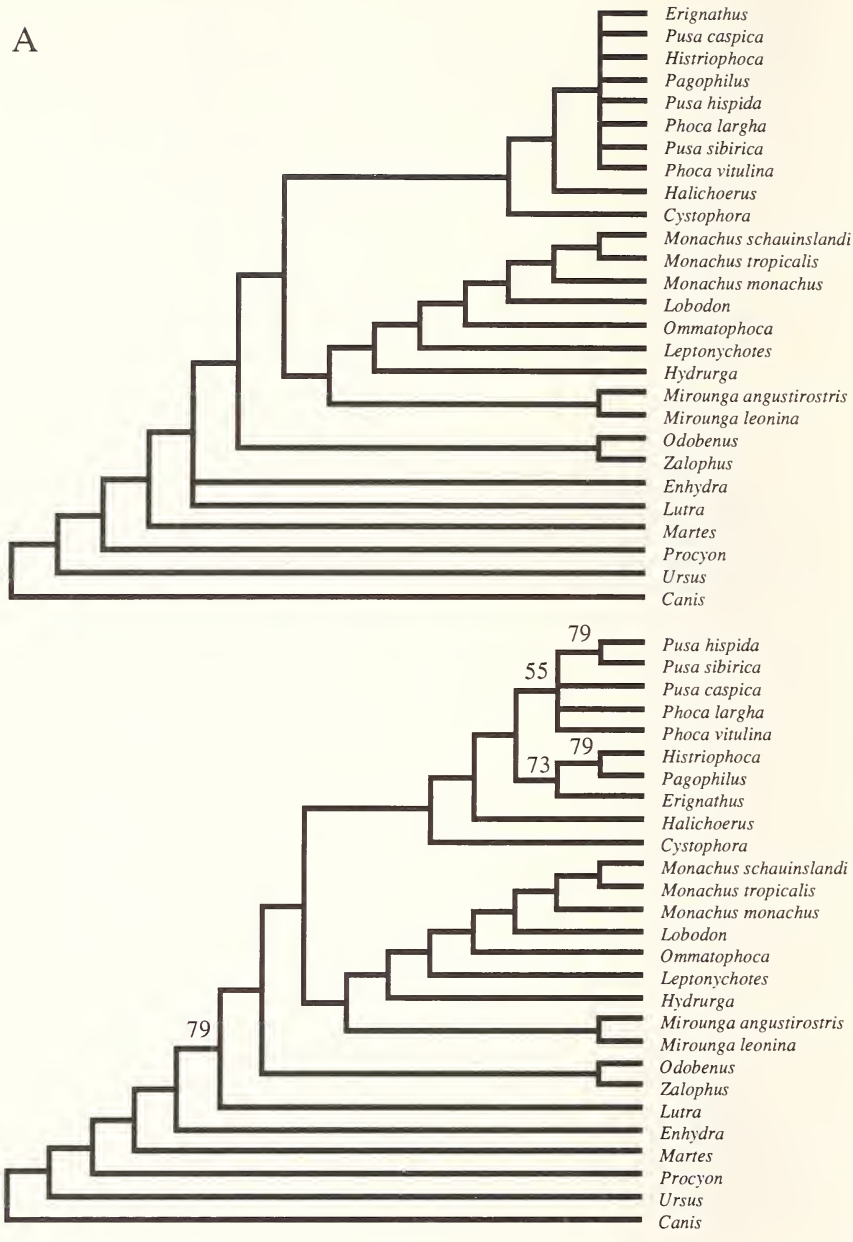

Fig.11A: Strict (top) and majority rule (bottom) consensus solutions resulting from a support analysis of the inversely weighted data matrix. (A) All trees of 69,903 steps or less (n = 33).

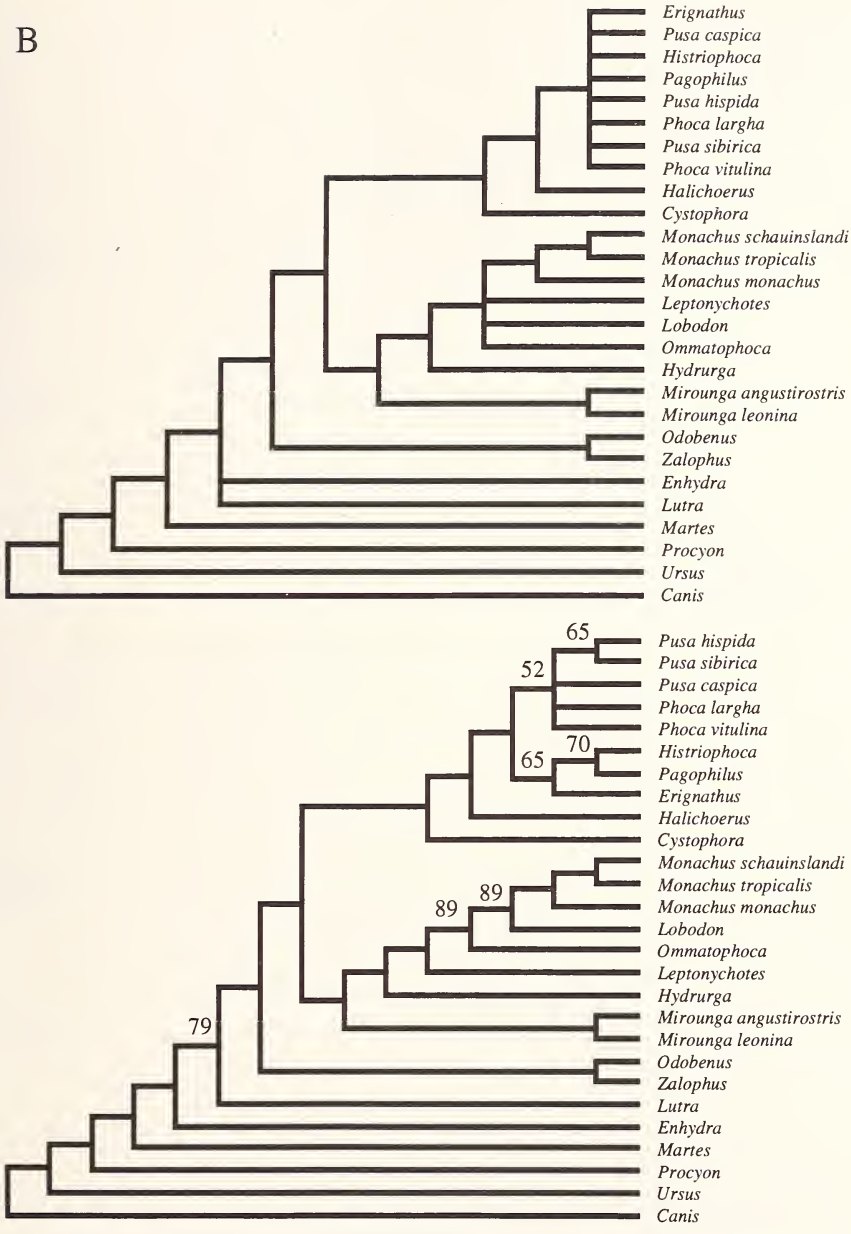

Fig.11B: Strict (top) and majority rule (bottom) consensus solutions resulting from a support analysis of the inversely weighted data matrix. (B) All trees of 69,972 steps or less (n = 187).

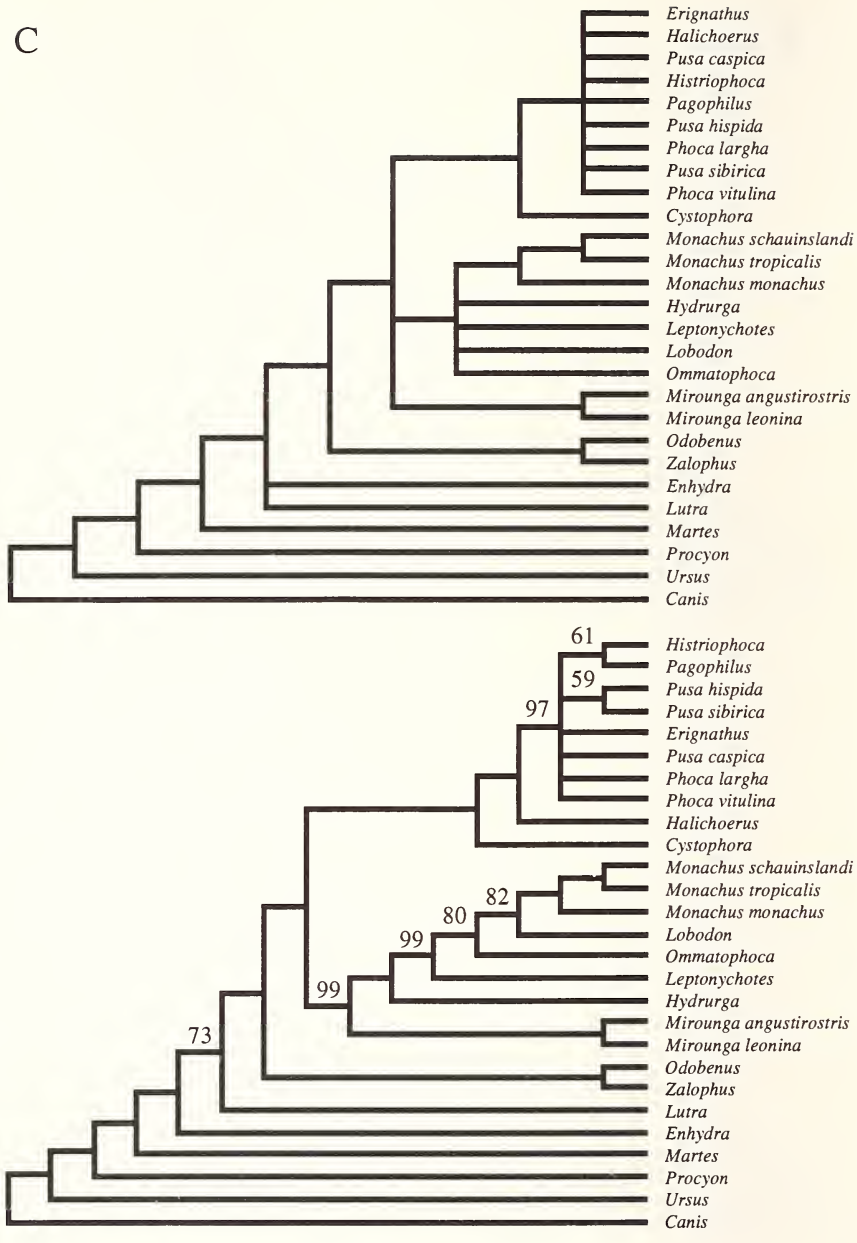

Fig.11C: Strict (top) and majority rule (bottom) consensus solutions resulting from a support analysis of the inversely weighted data matrix. (C) All trees of 70,041 steps or less (n = 917).

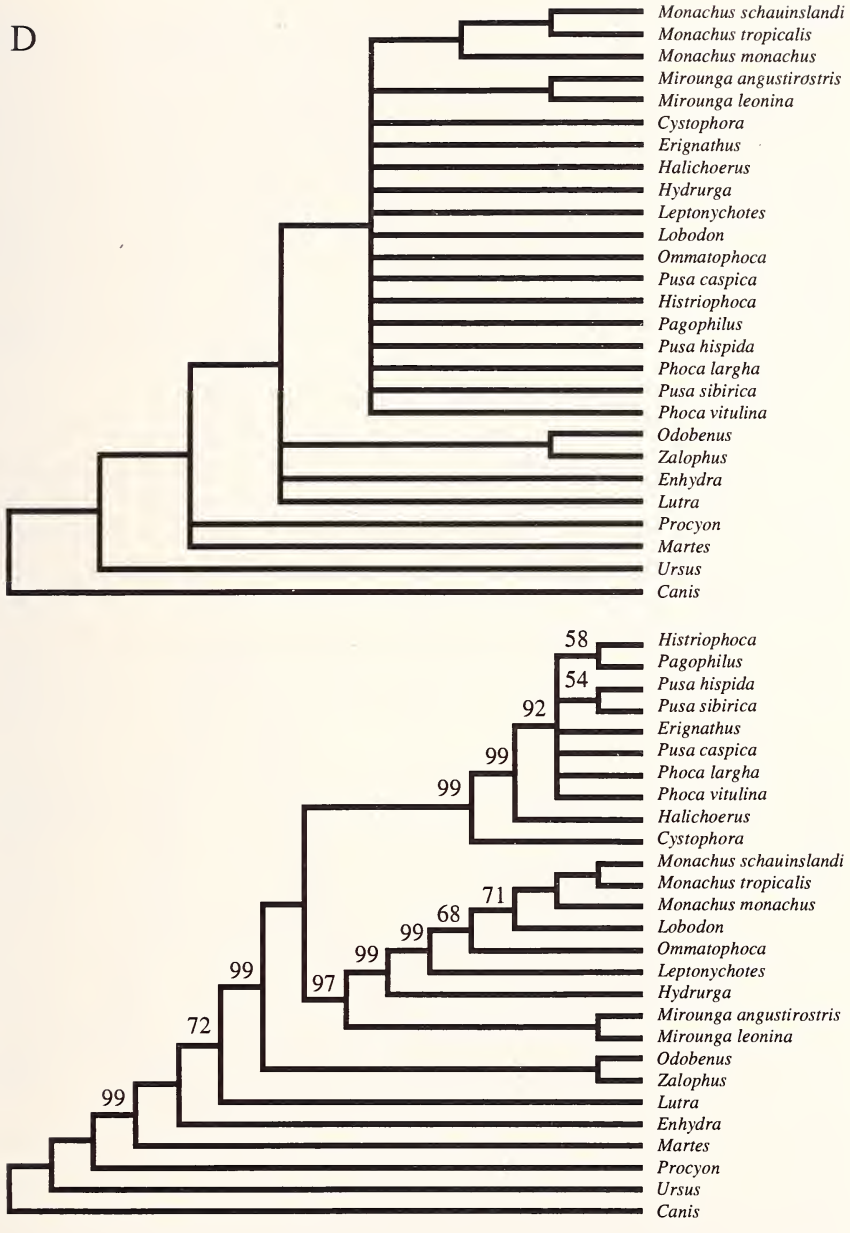

Fig.11D: Strict (top) and majority rule (bottom) consensus solutions resulting from a support analysis of the inversely weighted data matrix. (D) All trees of 70,110 steps or less (n = 3,409).

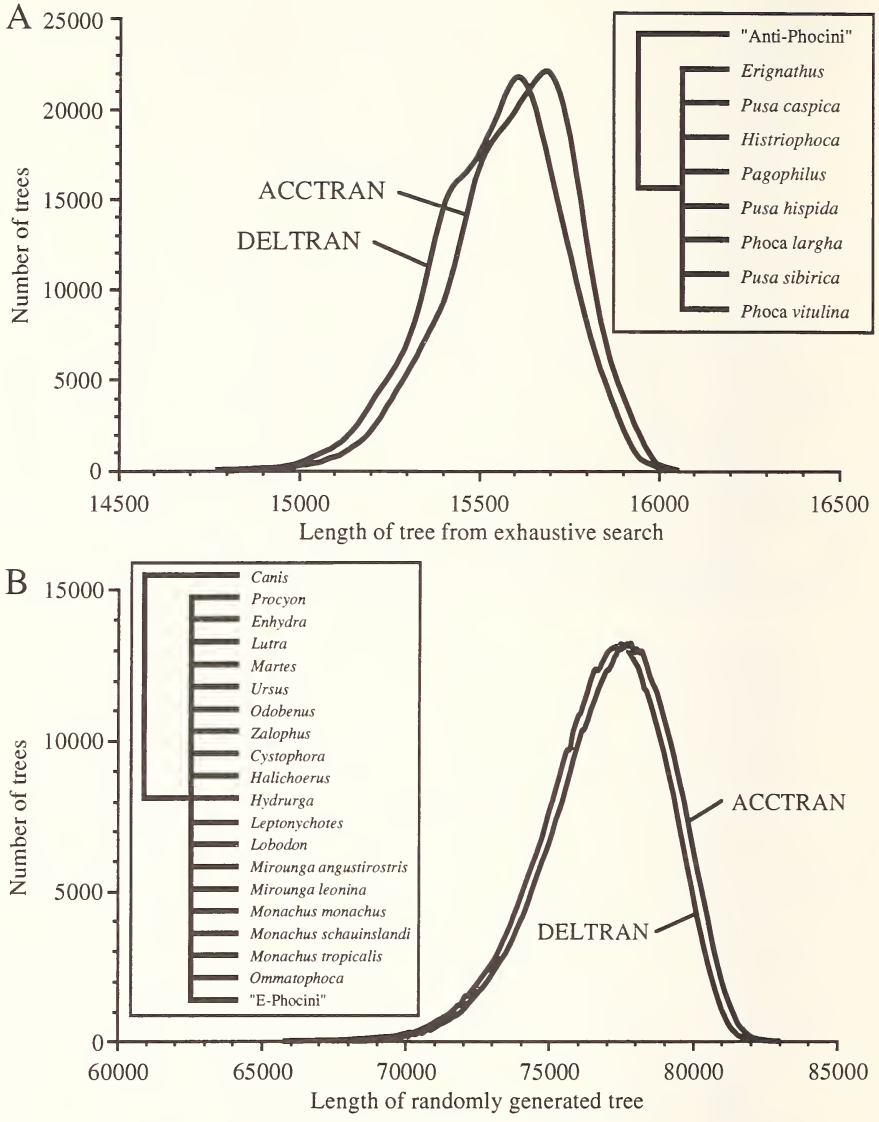

Fig.12: Frequency distributions of tree lengths generated from the inversely weighted data matrix with some regions topologically constrained. (A) Clade "anti-Phocini" collapsed (see insert) according to either accelerated (ACCTRAN; g_1 = -0.483) or delayed transformation (DELTRAN; g_1 = -0.368) criteria. (B) Clade "E-Phocini" collapsed (see insert) according to either ACCTRAN (g_1 = -0.540) or DELTRAN (g_1 = -0.541) optimization. Distributions are of either all 135,135 possible trees (A) or of a random sample of 1,000,000 trees (B).

(including the overall parsimony analysis) being based on the same data matrix, or some sample(s) thereof. Combined with all of the procedures using some form of parsimony criterion, it is not too surprising that they all indicate roughly the same solution, as they are merely summarizing the underlying distribution of the matrix in slightly different ways.

As exemplified by the results of the bootstrap analysis, the common finding is for relatively strongly supported outgroup relations, with support dropping off markedly within each phocid subfamily (some fairly robust species pairs therein notwithstanding). However, we would postulate that the region of weaker signal is limited even further to that portion of the cladogram near the polytomy within the Phocini (plus *Erignathus*). Despite the comparably weak bootstrap frequencies generally present in both subfamilies, the pattern advocated in the previous section for the monachines appears to be remarkably robust and survives largely intact in both the support and successive approximations analyses. A monophyletic *Monachus*, in particular, seems to be very robust. In contrast, the pattern within the Phocini (plus *Erignathus*) is more labile, with almost every analysis holding for a slightly different set of relationships. Although the membership of the group in question (*Erignathus, Histriophoca, Pagophilus, Phoca* spp., and *Pusa* spp.) is constant, as is its monophyletic status, only the *Erignathus, Histriophoca*, and *Pagophilus* clade appears to have any consistent support. Overall, this set of conclusions could also be reached by merely examining the number of synapomorphies supporting the various nodes within each phocid subfamily (Fig.5C). The nodes within the Monachinae are more strongly supported in this respect than are those within the Phocinae, and especially those within the Phocini (plus *Erignathus*).

Therefore, it was somewhat surprising that a test aimed directly at elucidating this weak region (constrained skewness) did not identify it as such (Fig.12). Constraining the stronger, and therefore supposedly more informative, "anti-Phocini" (Fig.12A) did not eliminate a significant left-hand skew in the distribution as expected [g_1 = -0.483 (ACCTRAN) or -0.368 (DELTRAN); critical g_1 = -0.29 or -0.22 at the 0.05 level for nine taxa and 250 binary or four-state characters respectively]. Thus, there would appear to be greater support (i.e., character covariation) within the Phocini (plus *Erignathus*) than the remaining tests indicate, as skewness seems to be very sensitive to minute amounts of covariation (Hillis & Huelsenbeck 1992). As well, the g_1s for the "anti-Phocini" test are approaching their respective critical values to a greater extent than we have ever witnessed in a skewness test, indicating some reduction in the level of character covariation, but not to non- significant levels. Finally, the constrained skewness test does appear to be working properly (within the suspect nature of PAUP's RANDOM TREES subroutine), as the reciprocal constraint of the weaker "E-Phocini" (Fig.12B) produced the expected significantly left-hand skewed distribution [g_1 = -0.540 (ACCTRAN) or -0.541 (DELTRAN); critical g_1 = - 0.08 at the 0.05 level for 25 taxa and 250 binary or four-state characters]. However, in order to more rigorously test this last supposition, random clades of a fair size (say six or seven taxa) should be constrained, and the skewnesses of the resulting distributions analyzed.

COMPARATIVE TOOLS

Constraint analysis

Outgroup constraints (Figs.3 and 13, and Tab.3)

All outgroup constraints, which forced an alternative set of outgroup relationships to those found in the overall solution, produced cladograms that were longer than the overall solution (Fig.13 and Tab.3). However, in relative terms, these increases were almost negligible, as even the longest solution (from the constraint tree "ursid - diphyly") of 1,388 extra steps (21 corrected steps) only amounts to an increase of 0.77% over the most parsimonious length (of the overall solution) of 69,834 steps. Given such slight increases in length, corresponding bootstrap frequencies for the specific clade(s) under examination were surprisingly low (all below 22%). This might indicate that although very few individual characters directly support the various alternative outgroup relationships, the

Table 3: Summaries of searches of the inversely weighted data matrix with certain topological constraints of outgroup relationships imposed (see Fig.3). MPT = most parsimonious trees. Bootstrap frequencies for the desired monophyletic group are given whenever possible. When a constraint tree imposes multiple monophyletic groups, the bootstrap frequency indicated is that of the least supported major clade (indicated by an asterisk).

Constraint tree	Absolute length	Extra steps relative to overall solution (absolute / corrected)	No. of MPT	Bootstrap analysis frequency	(%)
Pinnipedia					
– monophyly	69834	(+0 / +0)	2	687.00	(69)
– (not) monophyly	70067	(+233 / +4)	3	–	–
– diphyly	70334	(+500 / +8)	2	115.50*	(12)*
Ursidae					
– ursid - monophyly	70374	(+540 / +8)	1	21.00	(2)
– ursid - diphyly	71222	(+1388 / +21)	1	< 0.08	(<< 1)
– ursid - odobenid	70374	(+540 / +8)	1	–	–
Mustelidae					
– mustelid - monophyly	69834	(+0 / +0)	2	680.50	(68)
– mustelid - diphyly	70334	(+500 / +8)	2	115.50	(12)
Mustelinae					
– musteline - monophyly	70225	(+391 / +6)	2	43.67	(4)
– musteline - diphyly	70708	(+874 / +13)	2	4.00	(< 1)
Lutrinae					
– lutrine - monophyly	69834	(+0 / +0)	2	729.33	(73)
– lutrine - diphyly	70067	(+233 / +4)	3	219.67	(22)
Miscellaneous					
– (not) otarioid	70067	(+233 / +4)	3	–	–
– (not) otarioidea	70234	(+400 / +6)	2	–	–
– odobenid	70234	(+400 / +6)	2	59.00	(6)

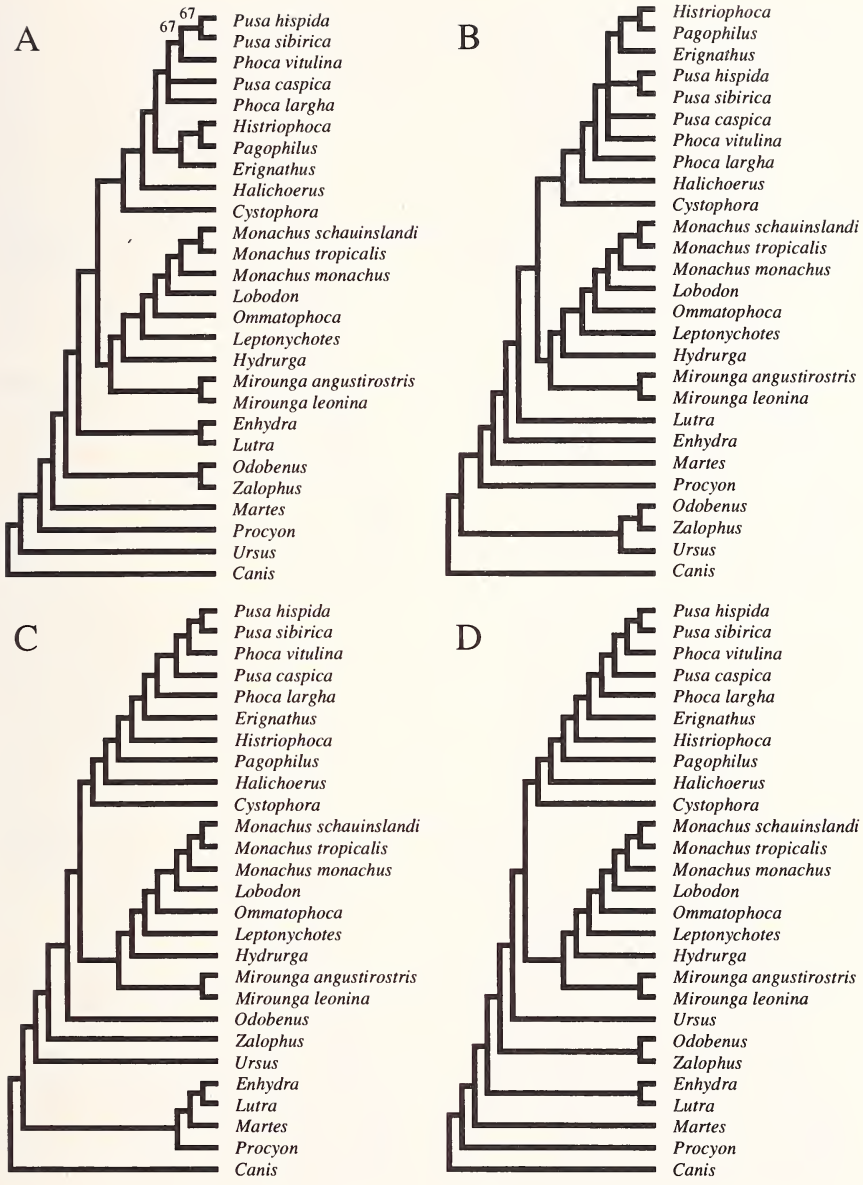

Fig.13A–D: Cladograms resulting from a constraint analysis examining various alternative hypotheses of outgroup relationships: (A) (not) monophyly *, (B) diphyly *, (C) ursid – monophyly, and (D) ursid – diphyly. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.3 and Tab.3.

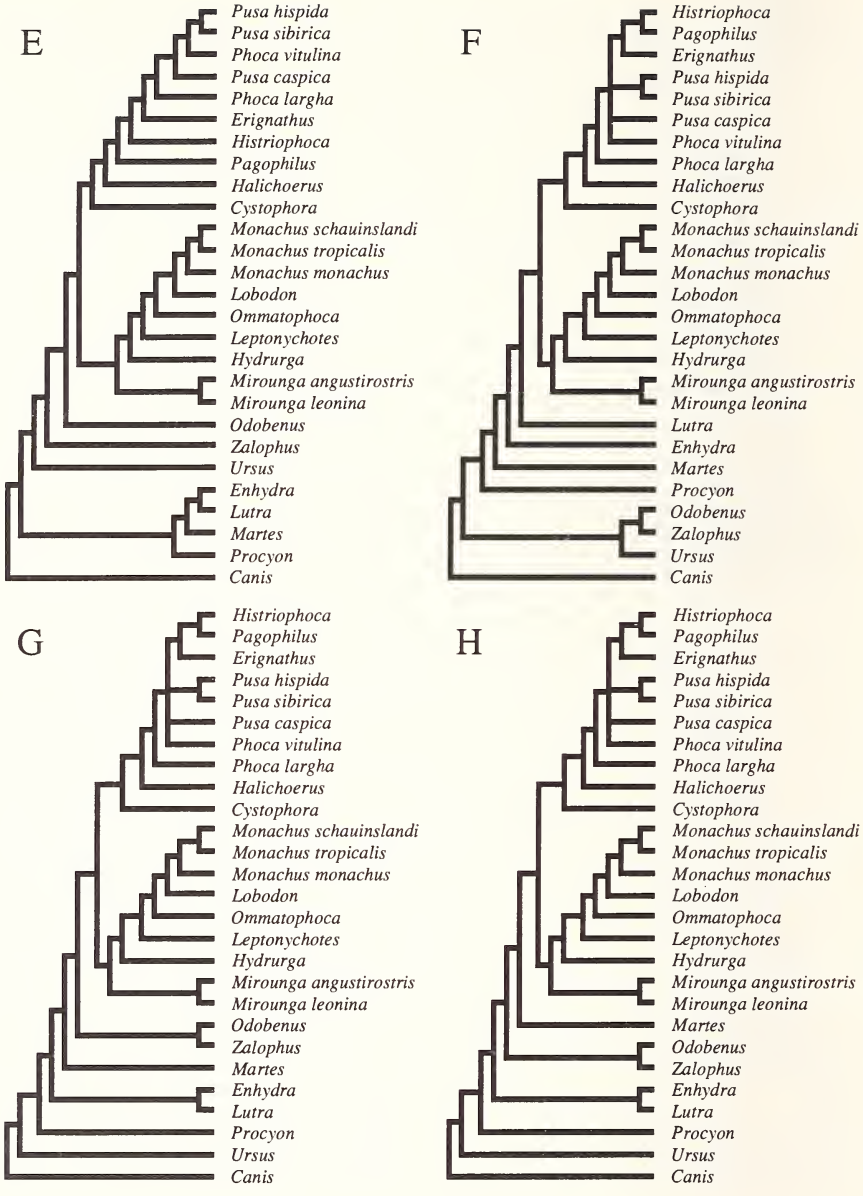

Fig.13E–H: Cladograms resulting from a constraint analysis examining various alternative hypotheses of outgroup relationships: (E) ursid – odobenid, (F) mustelid – diphyly *, (G) musteline – monophyly *, and (H) musteline – diphyly *. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.3 and Tab.3.

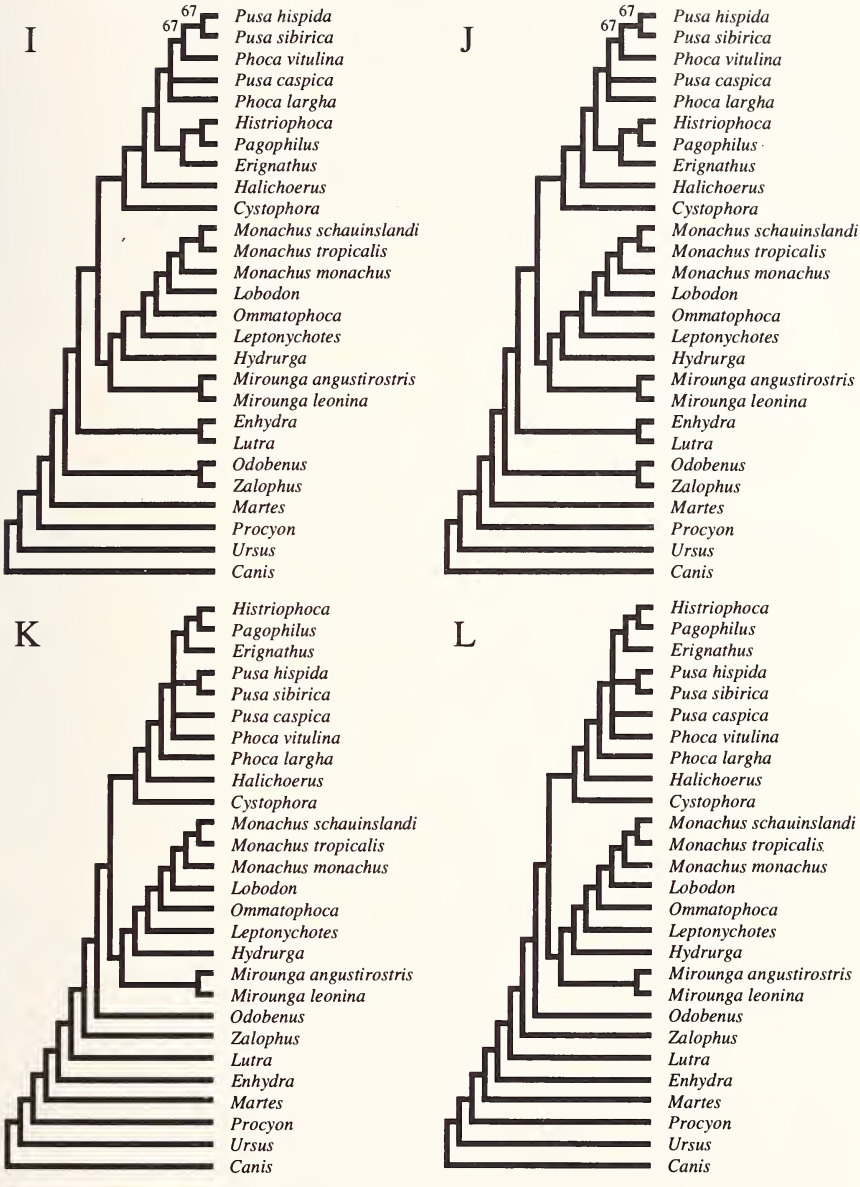

Fig.13I–L: Cladograms resulting from a constraint analysis examining various alternative hypotheses of outgroup relationships: (I) lutrine – diphyly *, (J) (not) otarioid *, (K) (not) otarioidea *, and (L) odobenid *. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.3 and Tab.3.

overall matrix can accommodate them with a minimal amount of extra homoplasy (see Overall conclusions – possible effects of polymorphic data below).

Despite these minimal increases in length, some clear patterns did arise in this analysis (Tab.3). Of the paired constraint trees, those advancing a diphyletic Pinnipedia always resulted in a longer and, as measured by the corresponding bootstrap frequency, more weakly supported solution (see also Tab.2). Additional support for a lutrine affinity for the pinnipeds under this data matrix is provided by the observation that the lutrines always form the sister group to the phocids and/or pinnipeds as a whole (Fig.13), unless other sister taxa were specifically constrained for. Numbers of most parsimonious trees were again very low for such a large data set (Tab.3), once again roughly indicative of good resolving power (but see **Overall Parsimony Analysis**; Hillis & Huelsenbeck 1992).

More importantly, relationships within the phocids were identical with those of the overall solution in most cases, or, at most, only slightly altered within the Phocini (plus *Erignathus*). Only those constraint trees supporting an ursid ancestry for the pinnipeds ("ursid - monophyly", "ursid - diphyly", and "ursid - odobenid") produced major disruptions within the phocids. Again, this was limited to the Phocini (plus *Erignathus*), and amounted to a basal shift of *Histriophoca* and *Pagophilus* to form successive sister taxa to the clade of *Erignathus, Phoca* spp., and *Pusa* spp. Thus, the possibility of a symplesiomorphic relationship between *Histriophoca* and *Pagophilus* (see de Muizon 1982a) only appears to arise under the assumption of an ursid affinity for the phocids.

Of the individual solutions (see Fig.13), the constraint of a non-monophyletic Otarioidea – as advocated by Wyss (1987), Berta (1991), Wyss & Flynn (1993), and Berta & Wyss (1994) – converged on the same solution as that resulting from a forced *Odobenus*-phocid pairing. However, while this common solution might point to some affinity between *Odobenus* and the phocids [it only required an extra 400 steps (six corrected steps) over that of the overall solution], such a pairing has very weak support in the data matrix (bootstrap frequency of 6%).

Altogether, the negligible increases in length resulting from the constraint of the various alternative outgroup relationships, coupled with their minimal effects on internal phocid phylogeny point to the potential bias from assuming one outgroup taxon over another for the phocids as being very small. The apparently inherently less stable Phocini (plus *Erignathus*) notwithstanding (see **Statistical Tests** section), the selection of any major arctoid lineage (e.g., lutrines, mustelids, otarioids, or ursids) will apparently all give roughly the same set of internal relationships for the phocids, as was also claimed for the phocines by Perry et al. (1995). This finding might ensue from the early history of the arctoids, whereby the fact that all of these lineages (including the phocids) were diverging at about the same time (Sarich 1976; Wayne et al. 1989; C.A. Repenning, pers. comm.) largely renders the designation of sister taxa as irrelevant, or even erroneous. Thus, the supposition herein of a lutrine affinity for the pinnipeds might be artifactual (i.e., a consequence of this particular biased data set), and an artificial resolution of a real polytomy. Although an intriguing possibility, and preliminarily substantiated by Perry et al. (1995), this question should remain open until more paleontological and/or molecular evidence is accumulated.

Internal constraints (Figs.4 and 14, and Tab.4)

The various alternative ingroup relationships tested in this study likewise all resulted in cladograms that were longer than the overall solution (Tab.4). The increases were again virtually negligible, with most amounting to an increase in length of less than 0.72% (506 extra steps or eight extra corrected steps). The constraints of a monophyletic *Phoca* (both sensu stricto and Burns & Fay 1970) were accommodated with minimal amounts of extra homoplasy in particular. Surprisingly, not even the disruption of one of the most strongly supported nodes in the overall solution, that of a monophyletic Phocidae, produced a tangibly longer solution. Only the very specific constraints of "de muizon" and "wyss" and, to a lesser degree, those requiring a monophyletic Cystophorinae ("three subfamily" and "cystophorinae") yielded noticeably longer solutions (but still well under a 5%

Table 4: Summaries of searches of the inversely weighted data matrix with certain topological constraints of alternative ingroup relationships imposed (see Fig.4). MPT = most parsimonious trees. Bootstrap frequencies for the desired monophyletic group are given whenever possible. When a constraint tree imposes multiple monophyletic groups, the bootstrap frequency indicated is that of the least supported major clade (indicated by an asterisk).

Constraint tree	Absolute length	Extra steps relative to overall solution (absolute / corrected)	No. of MPT	Bootstrap analysis frequency	(%)
At family level					
– (not) phocidae	70340	(+506 / +8)	2	–	–
At subfamily level					
– (not) two subfamilies	70028	(+194 / +3)	1	–	–
– three subfamilies	70779	(+945 / +14)	4	3.00*	(< 1)*
– cystophorinae	70779	(+945 / +14)	4	3.00	(< 1)
– (not) monachinae	70028	(+194 / +3)	1	–	–
– (not) phocinae	70048	(+214 / +4)	9	–	–
Within Monachinae					
– Lobodontini	70283	(+449 / +7)	1	50.55	(5)
– (not) monachus	70279	(+445 / +7)	2	–	–
Within Phocinae					
– erignathus sister	70140	(+306 / +5)	2	–	–
– relaxed Burns & Fay	69991	(+157 / +3)	3	44.33	(4)
– strict Burns & Fay	70041	(+207 / +3)	1	64.06*	(6)*
– phoca	69892	(+58 / +1)	1	64.06	(6)
Within Phocinae					
– de Muizon	71831	(+1997 / +29)	1	–	–
– Wyss	72406	(+2572 / +38)	1	–	–
Miscellaneous					
– unweighted	70048	(+214 / +4)	2	314.00*	(31)*
– condense	70453	(+619 / +9)	5	44.33*	(4)*

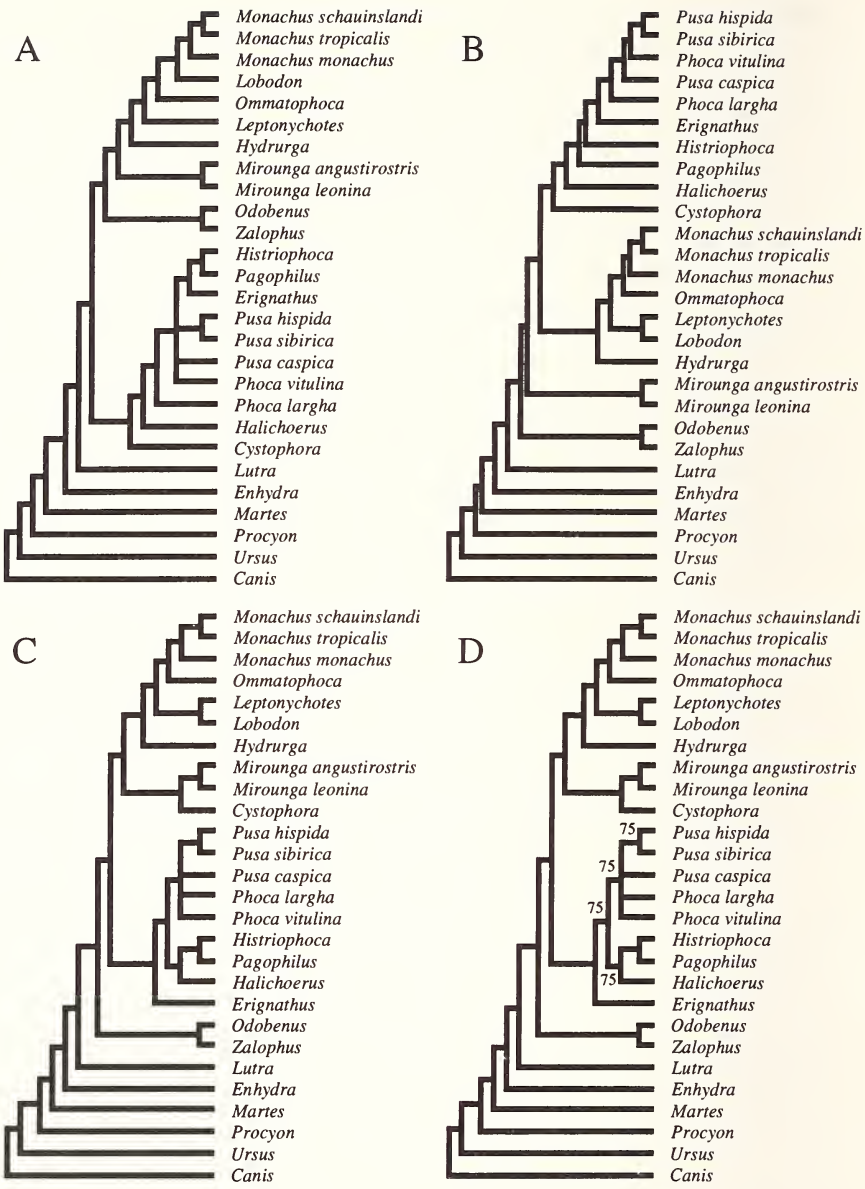

Fig.14A–D: Cladograms resulting from a constraint analysis examining various alternative hypotheses of ingroup relationships: (A) (not) phocidae *, (B) (not) two subfamilies, (C) three subfamilies *, and (D) cystophorinae *. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.4 and Tab.4.

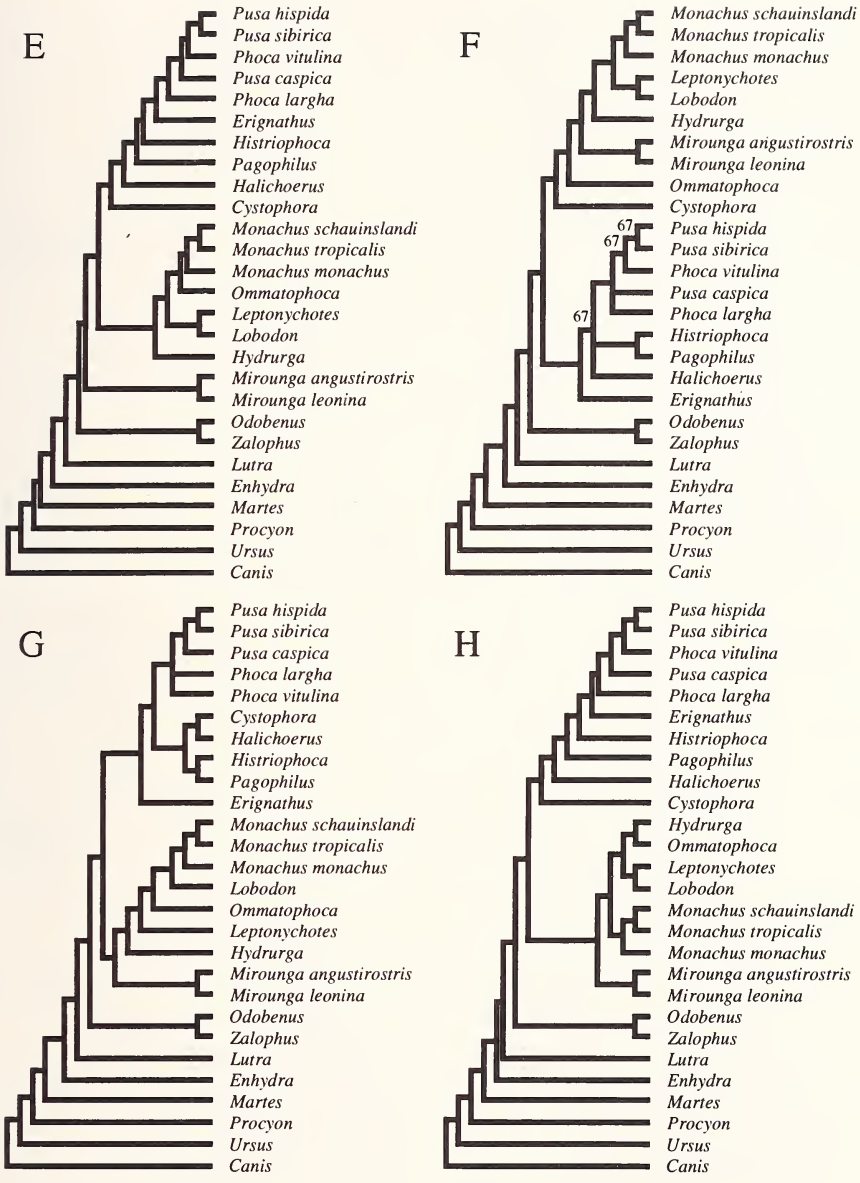

Fig.14E–H: Cladograms resulting from a constraint analysis examining various alternative hypotheses of ingroup relationships: (E) (not) monachinae, (F) (not) phocinae *, (G) erignathus sister *, and (H) lobodontini. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.4 and Tab.4.

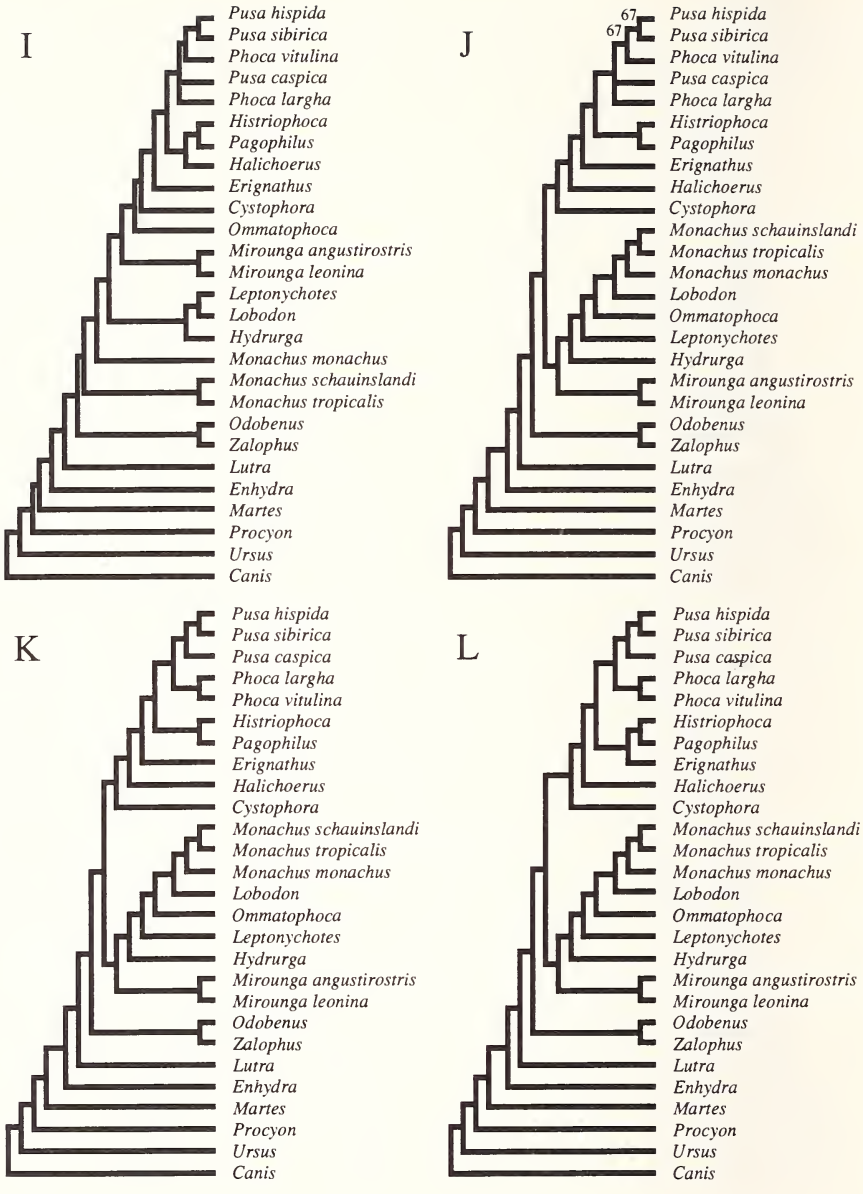

Fig.14I–L: Cladograms resulting from a constraint analysis examining various alternative hypotheses of ingroup relationships: (I) (not) monachus *, (J) relaxed Burns & Fay *, (K) strict Burns & Fay, and (L) phoca. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.4 and Tab.4.

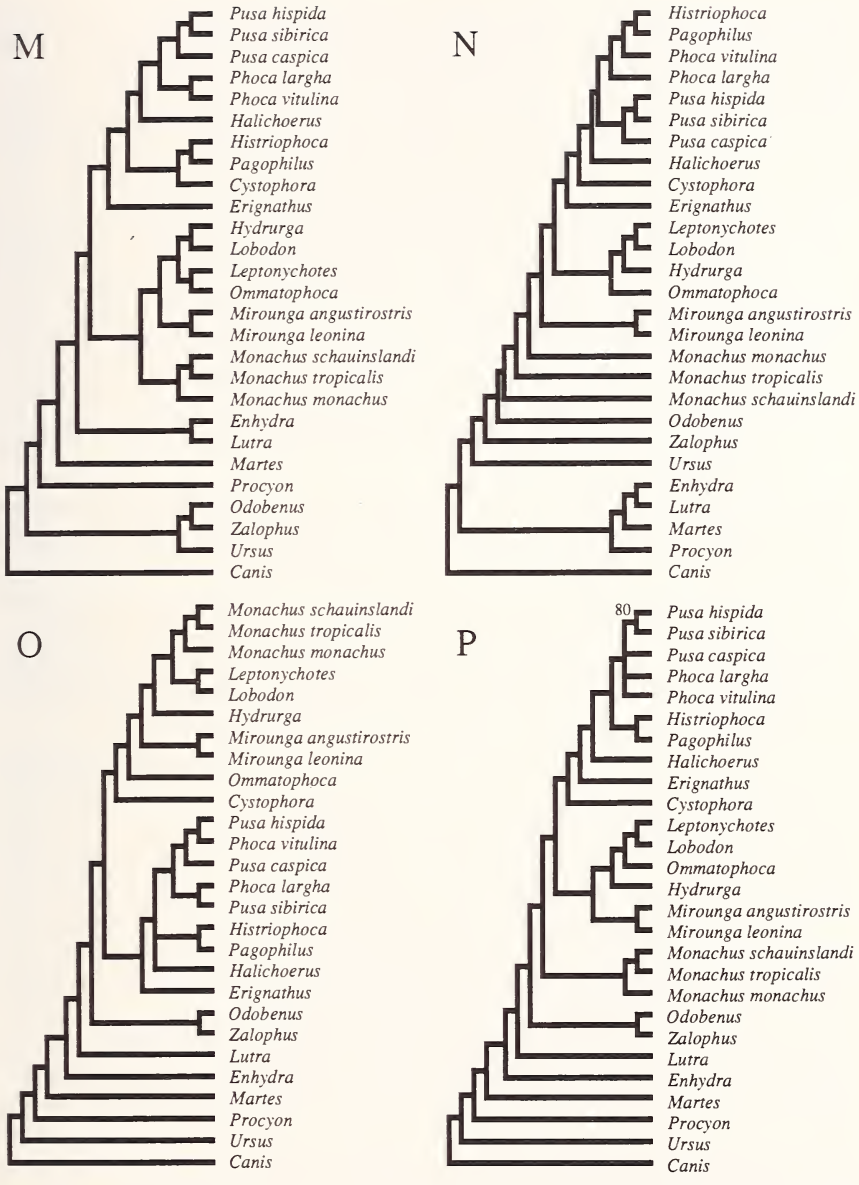

Fig.14M–P: Cladograms resulting from a constraint analysis examining various alternative hypotheses of ingroup relationships: (M) de muizon, (N) wyss, (O) unweighted *, and (P) condense *. An asterisk indicates a majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions. See also Fig.4 and Tab.4.

increase in length). Low bootstrap frequencies (all below 32% and most below 7%) again denote weak support for these alternative groupings, while the small number of most parsimonious solutions likewise hints at good resolving power in the data set.

Of more interest than the magnitude of the increases in length, however, are the topologies resulting from the various constraint conditions (Fig.14). Disruption of a monophyletic Phocidae resulted in the otarioids forming a monophyletic sister group to the monachines, reiterating the late convergence of the latter group on the former (Repenning 1990). Of the two subfamilies, paraphyly of the Monachinae was easier to achieve, as might be expected with the slightly weaker support noted earlier for this entire subfamily (see **Overall Parsimony Analysis** and **Statistical Tests** sections). The constraint of a paraphyletic Phocinae or a monophyletic Cystophorinae, meanwhile, again demonstrates the strong tendency of *Cystophora* to join the monachines. The enforced paraphyly of *Monachus* produced a topology much like that advocated by Wyss (1988a), again demonstrating that a paraphyletic Monachinae is dependent upon a paraphyletic *Monachus* to some degree (Berta & Wyss 1994).

Additional observations support some of the more contentious, non-traditional relationships indicated by the overall solution. Monophyly of *Monachus*, as well as its terminal position within the lobodontines, was extremely robust and was only disrupted when specifically forced to do so. Likewise, paraphyly for the lobodontines was always indicated, even when *Monachus* was disrupted. A more terminal position for *Erignathus* (or, equivalently, a basal position for *Cystophora*) within the phocines was also always observed, when not specifically constrained otherwise. *Erignathus* was typically embedded within the Phocini, but it always clustered internal to *Cystophora* in any case.

Finally, one curious phenomenon was observed in this portion of the analysis. Changes forced within the monachines altered not only the topology elsewhere within this subfamily, as would be expected, but often within the phocines as well. These were largely localized within the Phocini (plus *Erignathus*), and typically amounted to a basal shift of *Histriophoca* and *Pagophilus* to form successive sister taxa to the remaining Phocini (plus *Erignathus*). However, the complete absence of the equivalent reciprocal situation again hints at the comparatively weaker support for the Phocini (plus *Erignathus*) within the phocids (see **Statistical Tests** section). Monachine interrelationships, although comparably weak with respect to a bootstrap analysis (see **Statistical Tests** section), appear to be exceptionally robust by all other indications. Only changes forced directly within the Monachinae seem to be able to disrupt the interrelationships of this subfamily indicated in the overall solution.

Overall conclusions – possible effects of polymorphic data

The fact that no constrained solutions were substantially longer than the overall solution might derive from the high amount of polymorphic data in this analysis (see **Overall Parsimony Analysis**). The flexibility allowed by the alternative states of the polymorphisms likely permitted the very different competing topological hypotheses to be satisfied with a minimal amount of extra homoplasy. In contrast, those data matrices with less polymorphic data (e.g., Berta & Wyss 1994) would presumably be more rigid, and meeting

the requirements of very different topologies would require a larger amount of extra homoplasy. But, in view of the unexpectedly low number of equally most parsimonious solutions (and slightly less than most parsimonious; see skewness analysis in the **Statistical Tests** section) entailed by this supposedly more flexible data matrix, the effects of polymorphic data on parsimony analyses need to be investigated further.

Missing taxa (Fig.15)

The impetus for this analysis initially stemmed from taxonomic considerations within the Phocini (plus *Erignathus*). In a preliminary parsimony analysis, all of the constituent genera except for *Phoca* (sensu stricto) were monophyletic. However, the presence of *Phoca largha* in this study is contingent on the somewhat debatable species status granted it here. Subordinating *P. largha* as a subspecies of *Phoca vitulina* (as advocated by Scheffer 1958; Burns 1970; Shaughnessy 1975; Baram et al. 1991) would effectively render the now monotypic *Phoca* monophyletic. But, as Arnold (1981) suggests that the absence of some taxa might seriously affect the outcome in a low level cladistic analysis, we desired to investigate the effects of the removal of *P. largha* from the analysis. Subsequent analyses also saw the individual removal of *Cystophora, Erignathus, Lobodon*, and *Ommatophoca* in order to view the effects of their deletion. *Cystophora* was chosen due to its basal position within the phocines, combined with its strong tendency to join the monachines. *Erignathus* was likewise selected due to the novel position indicated for it here, and because of its position within the labile Phocini clade (as with *Phoca largha*). The removal of *Lobodon* provided an insight into the effects of the deletion of a rather topologically unspectacular and undistinguished taxon. Finally, *Ommatophoca* was deleted as it appears to be one the more unstable taxa in the otherwise fairly robust Monachinae (see **Unweighted analysis** below).

As would be expected, the removal of each taxon yielded a shorter solution than that obtained when all taxa were present. Single most parsimonious solutions were the norm, with only the matrix lacking *Erignathus* producing dual equally most parsimonious solutions. However, the degree of shortening in each case was much greater than would be achieved by merely "pruning" the single species branch in question from the tree. For example, the removal of *Phoca largha*, which effected virtually no topological changes, resulted in a solution some 1,452 steps (22 corrected steps) shorter than the overall solution. As the length of the branch leading to *P. largha* was only 383 steps (seven unweighted steps), the removal of taxa must decrease homoplasy elsewhere in the tree. This is demonstrated by the generally reduced branch lengths around the region that the removed taxon formerly occupied (compare Figs.5C and 15 for all removed taxa). Branch lengths within the outgroups were virtually unchanged. As well, the various goodness-of-fit statistics are slightly altered to reflect this decrease in the overall level of homoplasy.

Although major changes in topology were generally not evident in this analysis, the removal of taxa again demonstrated how the topology of one region of a tree can affect the topology of another, supposedly distinct region. This was especially evident with the removal of either of the two monachines. The deletion of either *Lobodon* or *Ommatophoca* produced minor, if any, topological changes within the monachines, but generated more substantial changes within the phocines (Figs.15D and E). Again, these latter alterations

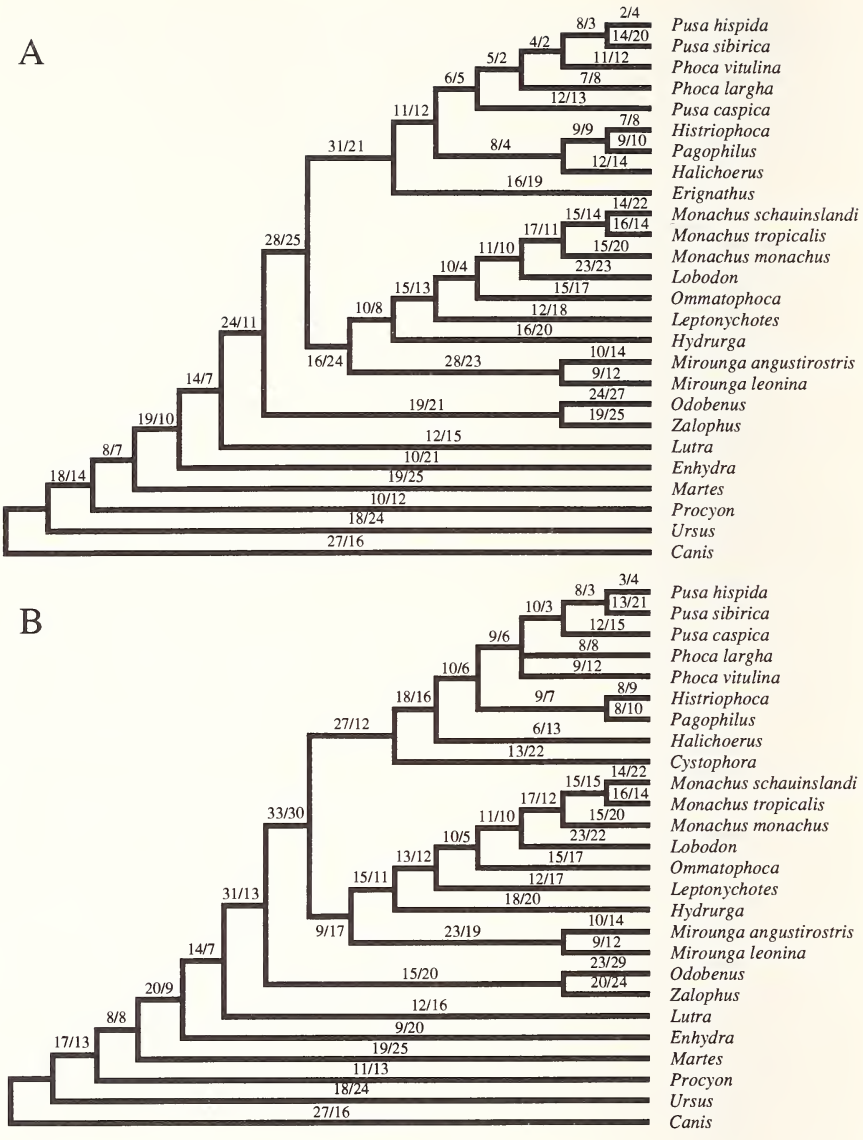

Fig.15A–B: Cladograms resulting from a parsimony analysis of the inversely weighted data matrix with a selected phocid species deleted: (A) *Cystophora* (length = 67,348 steps, CI = 0.461, HI = 0.761, RI = 0.635, RC = 0.414) and (B) *Erignathus* (length = 67,421 steps, CI = 0.462, HI = 0.763, RI = 0.638, RC = 0.419). Unweighted branch lengths presented as accelerated transformation / delayed transformation. Note that (B) is a consensus solution with all nodes found in 100% of the two equally most parsimonious solutions.

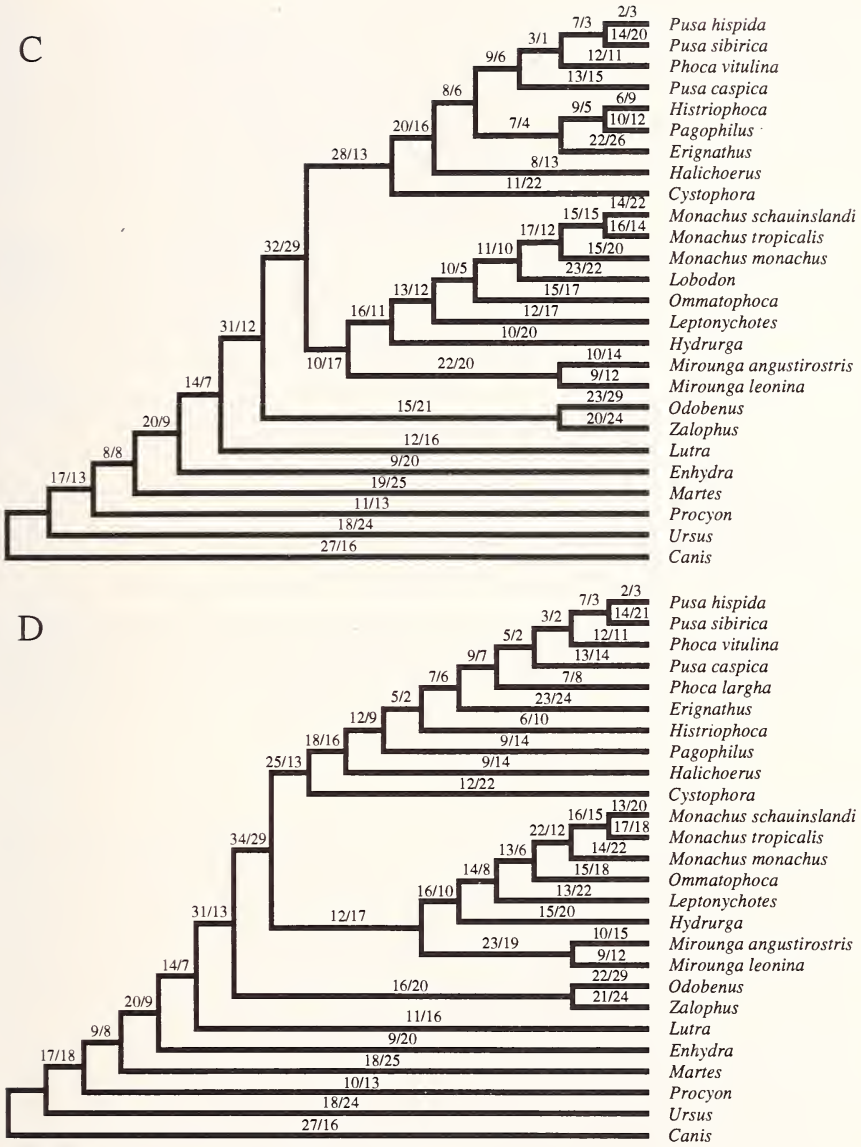

Fig.15C–D: Cladograms resulting from a parsimony analysis of the inversely weighted data matrix with a selected phocid species deleted: (C) *Phoca largha* (length = 68,382 steps, CI = 0.458, HI = 0.765, RI = 0.629, RC = 0.408) and (D) *Lobodon* (length = 67,333 steps, CI = 0.461, HI = 0.763, RI = 0.626, RC = 0.410). Unweighted branch lengths presented as accelerated transformation / delayed transformation.

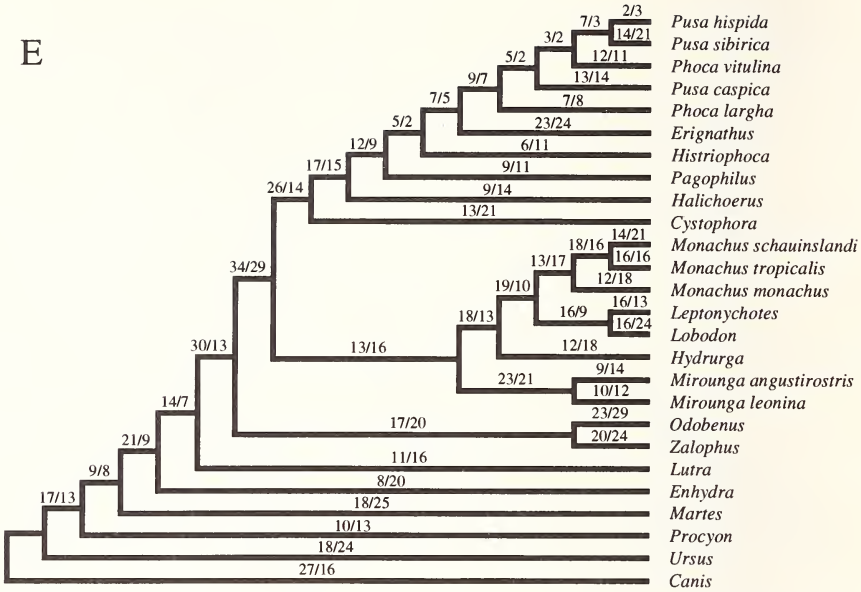

Fig.15E: Cladograms resulting from a parsimony analysis of the inversely weighted data matrix with a selected phocid species deleted: (E) *Ommatophoca* (length = 67,017 steps, CI = 0.460, HI = 0.760, RI = 0.630, RC = 0.409). Unweighted branch lengths presented as accelerated transformation / delayed transformation.

amounted to a basal shift of *Histriophoca* and *Pagophilus* within the Phocini (plus *Erignathus*), so that they became related by symplesiomorphies. However, like the constraint analyses, the removal of any of the three phocines affected only phocine interrelationships. As mentioned, the removal of *Phoca largha* yielded virtually no changes. In fact, the cladogram obtained (Fig.15C) is identical with one of the two equally most parsimonious solutions (Fig.5A) with *P. largha* merely pruned off. The removal of *Cystophora* caused *Erignathus* to regain its traditional role as the sister taxon to the remaining phocines (Fig.15A). The Phocini, however, remain paraphyletic, as *Halichoerus* now occupies the former position of *Erignathus* (although compared to the overall solution, this analogous clade is shifted basally with respect to the clade composed of *Phoca* spp. and *Pusa* spp.). *Histriophoca* and *Pagophilus* likewise move basally with the absence of *Erignathus* (although they remain as a clade) (Fig.15B), hinting that the supposedly primitive and monachine-like *Erignathus* is responsible for the more terminal position of this clade, and of the other two genera in particular, in the overall solution. This is also substantiated by the constraint analyses, where disruptions to the structure within the Phocini were due primarily to the movement of *Histriophoca* and *Pagophilus*; *Erignathus* generally maintained its relatively terminal position. Again, perhaps too much has been made of some of the more primitive features of *Erignathus* (see **Overall Parsimony**).

Thus, although this analysis into the effects of missing taxa cannot directly indicate the robustness of a given solution, it did indicate results in common with several analyses that could. As in the constraint analyses, the resistance of the monachine topology to changes directed within the phocines again points to the greater stability of this subfamily. As well, this analysis gives further cause to question the historically primitive role typically assigned to *Erignathus*.

"Unweighted" solution (Fig.16)

A parsimony analysis employing identically weighted characters (regardless of the number of character states) was also undertaken, yielding four equally most parsimonious solutions of 1,253 steps each. The consensus solution (identical between strict and majority rule algorithms) is presented in Fig.16.

The outgroup relations for this solution are identical with those of the overall solution; however, large differences are indicated within the phocids. The most striking difference

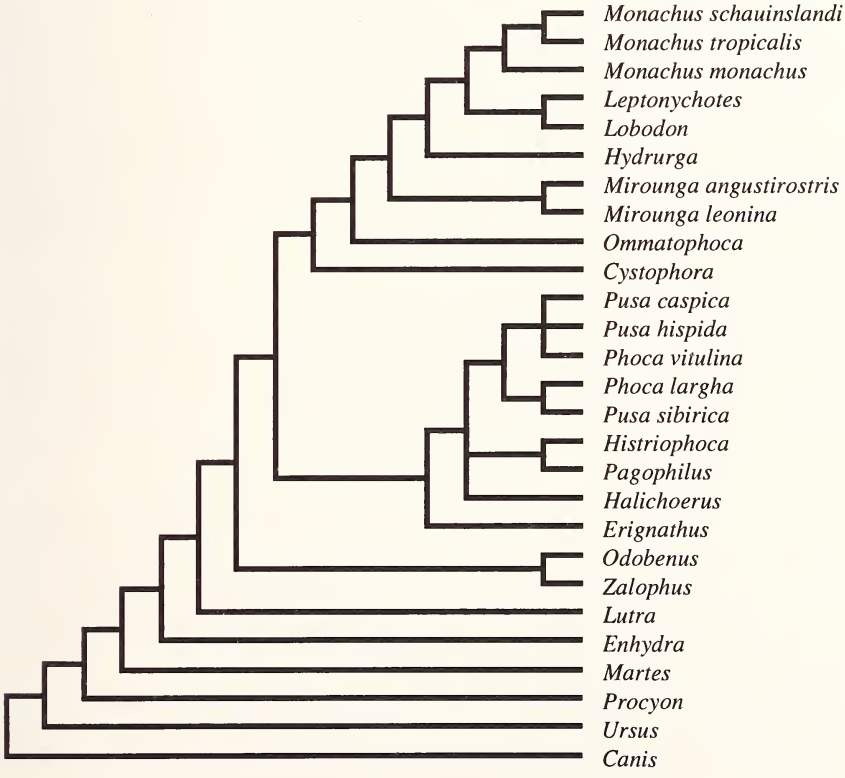

Fig.16: Consensus solution (identical between strict and majority rule algorithms) of four cladograms resulting from a parsimony analysis using identically weighted characters (length = 1,253 steps, CI = 0.460, HI = 0.772, RI = 0.603, RC = 0.396). All nodes were found in 100% of the equally most parsimonious solutions.

is the disruption of the two subfamilies as they are commonly recognized. Two distinct clades are still present, but *Cystophora* is now seen to cluster with the monachines, forming the sister taxon to this subfamily. This result is fairly labile, however, with cladograms of only one additional step finding *Cystophora* back as the sister taxon to the remaining phocines (results not shown). However, as indicated by the bootstrap, *Cystophora* displays a strong tendency to join the monachines even in the inversely weighted data set (bootstrap frequency of 31%).

This tendency on the part of *Cystophora* likely reflects its similarities, be they convergent or symplesiomorphic (with respect to all phocids), with *Mirounga*. The failure of *Mirounga* spp. to show an analogous predisposition (bootstrap frequency of only 2%) relates in turn to a third taxon, *Ommatophoca*. Together, these three genera are uniquely characterized among phocids by nasal processes of the premaxilla that distinctly fail to reach the nasal bones (see **Character Analysis**, character #12). Although this morphology is not as developed in *Ommatophoca*, together with the large number of characters used to describe the nasal region (see **Character Analysis**, characters #5-12), it is apparently sufficient to have all three taxa occupying the basal positions within the one clade. (These same characters, being predominantly multistate, exhibit less of an influence in the inversely weighted data matrix. However, note that even under such ameliorating conditions that *Cystophora* still displays a marked tendency to cluster with the monachines.) In fact, the tendency for all three genera to group together is demonstrated by the inclination for both *Mirounga* spp. and *Ommatophoca* to join the phocines (bootstrap frequency of 9%) being marginally higher than of *Mirounga* spp. alone. This also reflects the surprisingly high tendency of *Ommatophoca* to join the phocines (bootstrap frequency of 14%), presumably to cluster basally with *Cystophora*.

Within the monachines proper, the paraphyly of the lobodontines is even more pronounced with the shift of *Ommatophoca* to its basal position between *Cystophora* and *Mirounga* spp. As well, the traditional lobodontine relationships (i.e., paired *Hydrurga-Lobodon* and *Leptonychotes-Ommatophoca* clades) are contradicted further with *Leptonychotes* and *Lobodon* forming a monophyletic clade. Monophyly of *Monachus* is still indicated, however.

The loss of *Cystophora* to the monachines results in *Erignathus* resuming its traditional sister taxon status to the remaining phocines. Resolution within the now monophyletic Phocini is again limited, but paraphyly of *Phoca* (sensu Burns & Fay 1970), *Phoca* (sensu stricto), and *Pusa* are all indicated, with some novel relationships presented between *Phoca* spp. and *Pusa* spp. *Histriophoca* and *Pagophilus* continue to constitute a clade although, again, it is shifted basally with the loss of *Erignathus*.

This analysis is mentioned primarily as a curiosity into the effects of character "weighting" on this data matrix. As mentioned previously, the uncorrected use of binary and multistate characters will not result in equally weighted characters (as desired here) due to the algorithms used in PAUP (Swofford 1993). However, the results from this analysis do mirror the general conclusions from the analysis of the inversely weighted data set: strongly supported relations for the outgroup taxa and at the level of the phocid subfamilies, and weakly supported/resolved relations within the subfamilies (albeit

apparently somewhat stronger within the monachines). Differences with the overall solution are limited exclusively to within the phocid subfamilies, which demonstrate how labile the relationships at this level are with respect to which characters are used, and/or how they are used. Finally, as demonstrated by a constraint analysis (Fig.14O and Tab.4), the inversely weighted data matrix can accommodate the "unweighted" solution with a minimal amount of extra homoplasy: 214 extra steps (four extra corrected steps). The bootstrap frequency for the least supported major clade of this solution (estimated at 31%) is also remarkably high compared to those of the remaining constraint analyses.

Condensed analysis (Fig.17)

The constrained monophyly of four higher level phocid taxa – *Mirounga, Monachus, Phoca* (sensu Burns & Fay 1970), and Lobodontini – resulted in some rather major topological changes within each phocid subfamily, with respect to the overall solution.

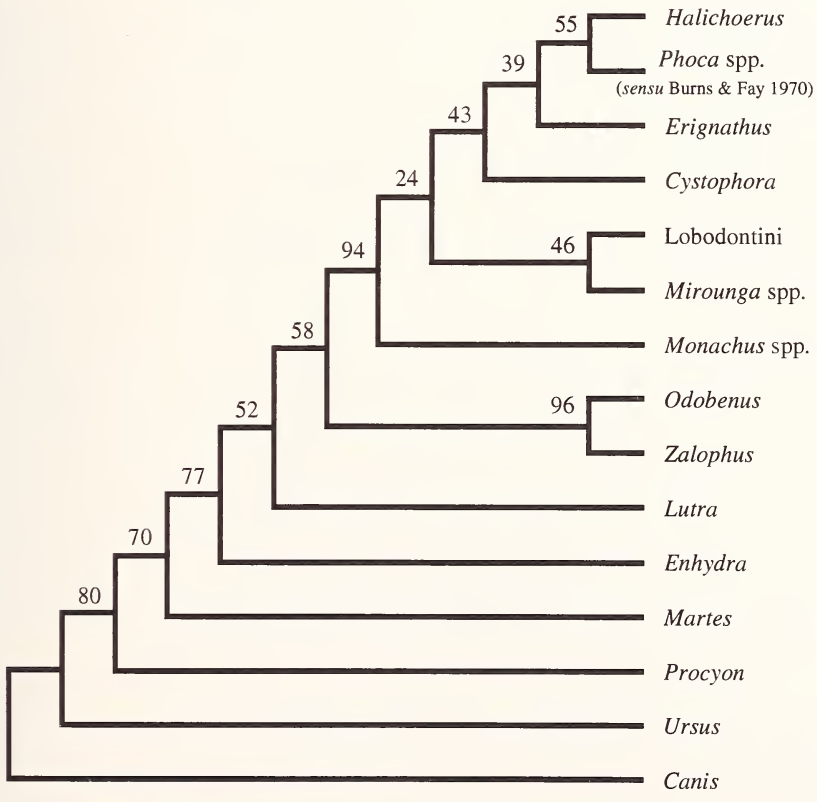

Fig.17: Cladogram resulting from a parsimony analysis of the inversely weighted data matrix with the taxa *Mirounga, Monachus, Phoca* (sensu Burns & Fay 1970), and Lobodontini collapsed so as to be monophyletic (length = 49,058 steps, CI = 0.518, HI = 0.709, RI = 0.634, RC = 0.483). Numbers represent bootstrap frequencies supporting each node (1,000 replications).

Contrary to most other analyses, the changes were the most severe in the monachines where paraphyly is indicated for the subfamily. This is likely attributable to the improper presumption of a monophyletic Lobodontini, forcing *Monachus* to become the sister taxon to the remaining phocids. This latter scenario has been postulated to be conducive towards obtaining a paraphyletic Monachinae (Berta & Wyss 1994). Moreover, under these conditions of imposed monophyly, the lobodontines and *Mirounga* do form a clade, as suggested by Hendey (1972) and King (1983) (but see Sarich 1976). Within the phocines, the only alteration was the exclusion of *Erignathus* from the Phocini, where it was normally firmly entrenched. *Cystophora*, however, maintains its position as the most basal of the phocines. Overall, the internal phylogeny of the phocids in the condensed solution strongly resembles the solution of Wyss (1988a), which, in effect, included some constrained monophyletic higher taxa. The more traditional appearance of the ingroup relationships (see below also) hints that previous studies into phocid phylogeny probably assumed the monophyly of some higher level taxa to varying degrees as well.

The visualization of the internal phylogeny of the condensed higher level taxa by a constraint analysis of the inversely weighted data matrix (Fig.14P and Tab.4) revealed branching patterns that largely agree with those of the overall solution. Despite their altered placement within the monachines, the internal topology of both *Monachus* and the lobodontines were identical with those of the overall solution. Within *Phoca* (sensu Burns & Fay 1970), a polytomy was again found, indicating uncertainty regarding the relationships in this region. However, *Pusa hispida* and *Pusa sibirica* do continue to form a clade in most solutions. As well, the enforced removal of *Erignathus* again resulted in a more basal shift of the clade of *Histriophoca* plus *Pagophilus* relative to *Phoca* spp. and *Pusa* spp.

The condensed solution is also typified by an increased amount of homoplasy (relative to the overall solution) presumably to account for the constrained monophyly of the otherwise normally paraphyletic higher taxa. This is most clearly indicated by the ensemble CI for the condensed solution (0.518), which although higher than the analogous value of the overall solution, actually falls below the value expected for a study of 15 taxa [0.618; Sanderson & Donoghue (1989)], while that of the overall solution was about on a par with its expected value (see **Overall Parsimony Analysis**). The increased levels of homoplasy present in the condensed solution were also indicated by the constraint analysis, where the constraint of the inversely weighted data matrix to the basic pattern of the condensed solution (see Fig.4P) resulted in one of the larger increases in length of all the constraint analyses, 619 extra steps (nine extra corrected steps) (Tab.4).

The increase in homoplasy for the condensed solution is argued against by several factors, however. Firstly, the ensemble HI is slightly lower (which might arise from the effective removal of nine taxa), while both the ensemble RI and RC are higher than their equivalent values in the overall solution. Another line of evidence originates from the somewhat surprising result that all the bootstrap frequencies for the condensed solution were roughly equivalent to those of the overall solution (compare Figs.8B and 17). While this could have been expected for the outgroup nodes (as their taxa, and thus hopefully their interrelationships, were unchanged), the failure of the bootstrap to reflect the presumably

more homoplasious ingroup topology of the condensed solution is puzzling. Beyond the major limitation that the bootstrap can only indicate signal strength within a data matrix (see **Statistical Tests**), it may also be connected with the reduced number of taxa present in the condensed solution, resulting in fewer reasonable alternative groupings. For instance, one would expect the members of each subfamily to associate with one another whether the subfamily is paraphyletic or not. Thus, the collapsing of the Monachinae to only three taxa in the condensed analysis dramatically reduces the number of alternative pairings, possibly artificially inflating the apparent support for those possibilities that remain.

Finally, it should be stressed that the differences in topology that were obtained in this analysis arose solely from improper assumptions of monophyly, and not because of large scale differences between the data matrices. The consensus character states for each higher level taxon are directly based on the same set of observations that led to the overall solution. Therefore, essentially the same matrix was used in both cases. As well, the altered findings are not dependent on either solution being the correct estimate of the actual (phocid) phylogeny. However, by improperly assuming the monophyly of higher taxa, we may actually be hindering our efforts in systematic biology to uncover the true phylogeny of a group of organisms.

CHARACTER ANALYSIS

The previous two sections dealt largely with the various methods devised to assess the degree of confidence one may have in a specific cladogram (cladistic hypothesis) versus other rival hypotheses. Together with the general misinterpretation of these tests (see **Statistical Tests**), what continually appears to be lost in all this is the realization that any cladistic hypothesis is only as good as the set of characters it is based upon and the underlying hierarchical pattern they indicate. In this regard, this section presents an in-depth analysis of all the characters examined in this study (also listed in Appendix B), with an emphasis on the 168 that were included in the cladistic analysis (excluded characters are marked with an asterisk). Historical notes and descriptions are initially provided for each character, followed by a prose equivalent to the information found in the apomorphy list (Appendix E). This latter feature is limited to the included characters, but reconstructions for the excluded characters may be derived from Appendix E. All reconstructions (including those of the excluded characters) are based on the topology displayed in the overall solution (Fig.5B). Goodness-of-fit statistics (but now based on the consensus and not the optimal solutions) for all individual characters are presented in Appendix F.

In the following, the citation(s) following each character refer(s) to our source for that character. In many cases, they may not correspond to the initial mention of the feature in the literature, but to the first use of the character in a systematic fashion. Descriptions of characters or character states were often modified from their indicated sources. This was typically done to accommodate the larger range of variation we observed in applying characters initially used to distinguish between a limited distribution of taxa over the fuller set examined here. In other cases, characters were derived from those in the literature

(e.g., character #24 is a derivation of character #23). Typically, this amounted to detailing the various manifestations of a "present" feature that was initially offered in present/absent form only. Finally, although some character states were not represented at the species level (e.g., state 2 for character #51), they did characterize individual specimens and so were retained.

Unfortunately, in attempting to assess the relative size of several characters, an admittedly arbitrary scheme often had to be employed (e.g., small, medium, large, or something equivalent). In such cases, size was determined in relation to the size of the surrounding bone (e.g., the skull as a whole for cranial characters, or the bone in question for post-cranial material), bearing the range of variation observed over the phocids in general in mind.

The use of tendencies for traits (e.g., tendency towards single-rooted postcanines; characters #143 and 144) has occasionally been criticized in cladistic analysis on the basis that characters should be more discretely discernible. However, characters examining tendencies were still employed here as they may be the only way to summarize highly variable morphologies or taxa that show differences between the two optimization criteria used here (accelerated transformation, ACCTRAN; and delayed transformation, DELTRAN).

Unless otherwise noted, anatomical terminology is standardized according to Miller (1962) and/or Davis (1964). Synonyms are given wherever possible. Finally, no polarity is implied by the sequence of character state coding (e.g., zero does not necessarily indicate the plesiomorphic state). In all cases, the polarity of each included character is explicitly stated in the text detailing its phylogenetic reconstruction.

Snout (21 characters)

Clearly the most important feature of the snout deals with the nasal processes of the premaxilla. The morphology of these processes and their relationships to neighbouring elements contain a good deal of useful, and largely untapped, systematic information, as is generally true for the remaining characters as well.

*1) relative position of external nares on snout: 0 = relatively dorsal ("high"); 1 = relatively ventral ("low") (Ridgway 1972).

The dorsal situation of the external nares on the snout has been proposed as a synapomorphy of the Monachinae (Ridgway 1972). However, the examination of both study skins and photographs revealed no appreciable distinction in the placement of the external nares between monachines and phocines. Due to this lack of variation, the character was deleted from the analysis.

*2) relative orientation of external nares on snout: 0 = vertical; 1 = horizontal (Ridgway 1972).

Ridgway (1972) described states 0 and 1 as being synapomorphic for the subfamilies Cystophorinae and Monachinae respectively. However, with the accepted paraphyly of the Cystophorinae (see King 1966), vertically oriented external nares would be better classified as another convergent feature between *Cystophora* and *Mirounga*. Or, as tentatively suggested herein, they might be another feature retained from the primitive phocid ancestor

(see **Overall Parsimony Analysis**). In any case, the distinction between the two states appears to be minor and somewhat arbitrary, with the "horizontal" condition really representing only a slight horizontal shift to a roughly diagonal position. As no unambiguous data for any species could be determined, either from study skins or from photographs, this character was subsequently deleted.

3) shape of anterior margin of premaxilla in dorsal view: 0 = flat, square, or bi-lobed; 1 = tapered and/or rounded (Burns & Fay 1970).

Burns & Fay (1970) used this feature to aid in establishing the systematic relationships of the phocines, and of the genera *Histriophoca, Pagophilus, Phoca* (all state 0), and *Pusa* (state 1) in particular. During our observations, we noted that some specimens displayed an intermediate morphology that could not be unequivocally assigned to either of the two extreme states. These specimens were coded as being polymorphic for this character.

A tapered or rounded premaxillary margin is primitive within the Caniformia, being found in virtually all outgroup taxa (*Lutra* displays the intermediate condition). The apomorphic state 0 occurs only within the phocids, but with independent origins in each subfamily. In the phocines, this state characterizes the subfamily ancestrally and is retained by all members, including *Pusa* spp. For the monachines, this state is limited to the clade composed of *Lobodon, Monachus* spp., and *Ommatophoca*, with *Lobodon* and *Monachus monachus* independently deriving the intermediate condition.

4) triangular lateral extensions of premaxilla into maxilla in dorsal view: 0 = absent; 1 = rudimentary or present (pers. obs.) (Fig.18).

In recording data for the previous character, we noted an unusual morphology for the premaxilla in a number of specimens. In most cases, the premaxilla is bounded laterally for most of its length by the maxilla when viewed dorsally, with the two bones meeting along a smooth curve. However, the anteromost portion of the premaxilla occasionally extends laterally as a small right triangle. This extension is not bounded laterally by the maxilla and its roughly right-angled posterior edge disrupts the smooth curve mentioned above. Although occurring sporadically in a wide range of species, this apomorphic condition only appears consistently in *Monachus schauinslandi* and *Monachus tropicalis*, with the polymorphic taxa *Enhydra* and *Ursus* apparently being in the process of independently acquiring this trait.

5) visibility of ventral portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible (Wyss 1988a).

As employed by Wyss (1988a), this character was used in conjunction with the next two (characters #6 and 7) to describe the visibility of the nasal processes as a whole. The condition in which the nasal processes were not always visible was felt to be a potential synapomorphy of the monachines among the carnivores, if not most mammals (de Muizon & Hendey 1980; de Muizon 1982a; Wyss 1988a). However, numerous exceptions to this have been noted, with *Histriophoca* and *Pagophilus* approaching, and *Monachus tropicalis* not displaying, this apparent monachine condition (de Muizon & Hendey 1980; de Muizon 1982a; Wyss 1988a)

We felt that the above coding was overly restrictive, with the possibility of creating a fair degree of homoplasy as those species sharing the general condition "nasal processes not

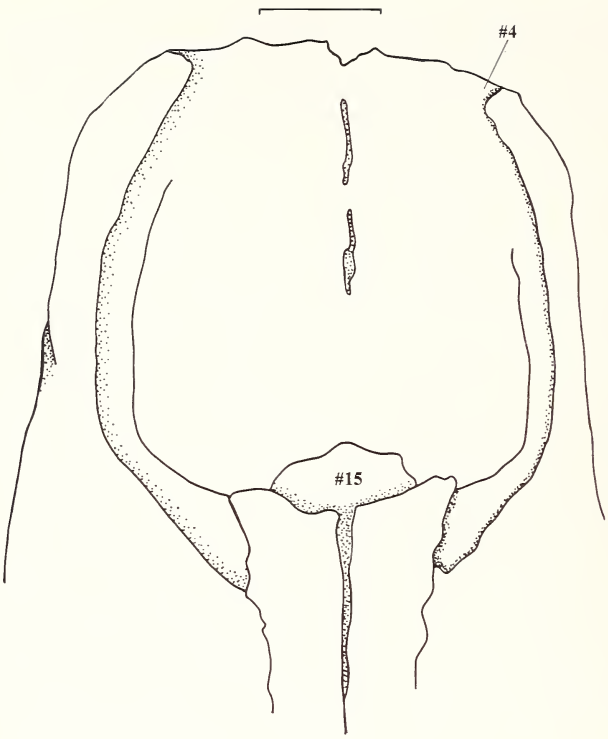

Fig.18: Dorsal view of the snout of *Monachus tropicalis* (USNM 102536) illustrating selected characters (indicated by their number; see **Character Analysis**) of this region. Anterior is towards the top of the page. Scale bar equals 1 cm.

always visible" did not always share the same location for that portion of the process that slips into the nasal aperture. As well, the all-encompassing character is inapplicable for genera such as *Cystophora, Mirounga*, and *Omnatophoca*, where the nasal processes are absent dorsally. Therefore, in order to minimize potential homoplasy and to maximize the applicability of this character for all species, we split the nasal processes into three equal portions (dorsal, middle, and ventral) and viewed each separately.

For the ventral portion of the nasal processes, the derived condition (state 1) is limited to only those monachines internal to *Hydrurga*. Within this clade, the polymorphic taxa *Monachus schauinslandi* and *Monachus tropicalis* show partial reversals to the plesiomorphic condition. This likely represents another synapomorphy of these two taxa, although this is not indicated here due to the manner in which PAUP handles polymorphic data (Swofford 1993; see **Methods and Materials**).

6) visibility of middle portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible; 9 = n/a – middle portion not present (de Muizon 1982a; Wyss 1988a).

For the suite of characters involving the visibility of the nasal processes of the premaxilla, the middle portion is probably the most important systematically. This middle portion is the one most often identified as defining the monachine condition, whereby the nasal processes are not always visible (Hendey & Repenning 1972; de Muizon & Hendey 1980;

de Muizon 1982a; Wyss 1988a). This is reflected here, with most monachines (with the exception of *Mirounga leonina, Monachus tropicalis*, and *Ommatophoca*) sharing the derived condition (state 1). In *Mirounga leonina*, the middle portion of the nasal processes is absent, rendering this character inapplicable (state 9), while *Monachus tropicalis* and *Ommatophoca* independently revert to the primitive condition (state 0). This previously undocumented occurrence in *Ommatophoca* may derive from the failure of the nasal processes to extend fully to the nasals (see character #12). Independent origins of a polymorphic condition occur in *Odobenus, Enhydra*, and *Histriophoca*. The presence of the derived state in this last genus (as a synapomorphy with *Pagophilus*) has been noted by de Muizon (1982a) and Wyss (1988a).

7) visibility of dorsal portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible; 9 = n/a – dorsal portion not present (Wyss 1988a).

This character apparently contains less systematic information than the other two characters dealing with the visibility of the nasal processes. Most species in this study display the primitive condition (state 0); only *Odobenus* derives the condition whereby the dorsal portion is not visible. Of those taxa where the dorsal portion is not visible due to its absence (*Cystophora, Mirounga* spp, and *Ommatophoca*), this condition can only be considered a synapomorphy of the two elephant seals. However, this last state is really more of an unavoidable consequence of character #12.

8) shape of ventral portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex (Burns & Fay 1970).

The derivation of characters #8 to 10, dealing with the shape of the nasal processes of the premaxilla, in many ways parallels that of the previous suite of characters which examined their visibility from a lateral view. In their more restricted focus on the Phocini, Burns & Fay (1970) initially coded the present suite of characters as "nasal processes concave ventrally and convex dorsally" (for *Phoca* and *Pusa*), or "wholly concave" (for *Histriophoca* and *Pagophilus*). During our observations, we noted that these two states were not sufficient to account for the range of variation observed over the larger set of taxa employed here. As well, such a coding would again exclude those previously mentioned genera that lack the dorsal portion of the nasal processes. Thus, the original character was again subdivided into three sections, which were examined individually.

In the ventral regions, most species retain the primitive condition of a concave shape of the nasal processes. Independent derivations of a straight morphology occur only in *Odobenus, Enhydra*, and *Halichoerus*. The convex morphology was never consistently present at the species level.

9) shape of middle portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – middle portion not present (Burns & Fay 1970).

Again, most species display the primitive condition of a concave shape of the middle portion of the nasal processes. The apomorphic straight morphology occurs intermittently throughout the Caniformia, either by itself (*Enhydra, Odobenus, Erignathus, Halichoerus*, and *Pusa caspica*), or as a polymorphism with state 0 (*Martes, Lutra, Procyon, Lobodon*, and *Pusa sibirica*). This distribution is explained either entirely through independent

origins (DELTRAN optimization), or as a complex series of reversals (ACCTRAN optimization). In this latter case, the straight morphology is a synapomorphy linking *Procyon* through to the lutrines which is lost ancestrally in the pinnipeds, before being regained several times therein. Again, the convex morphology was never consistently present at the species level. State 9 was unique to *Mirounga leonina*.

10) shape of dorsal portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – dorsal portion not present (Burns & Fay 1970).

Burns & Fay's (1970) initial coding for this group of characters (see character #8) points to the dorsal portion of the nasal processes as perhaps being the key region of variance. However, there does not appear to be a distinct pattern for the distribution of the various states present. The plesiomorphic condition of a convex shape of the dorsal portion of the nasal processes is generally retained throughout the Caniformia (and especially within the monachines), with numerous independent derivations of the remaining apomorphic states. (Again, the distribution of state 9 is more of a consequence of character #12.) Even within the phocines, there does not appear to be a readily discernible pattern of shared derived states; however, the distribution for the more generalized character used by Burns & Fay (1970) is tentatively supported here (but only tentatively; many of the taxa in question are polymorphic for this character and are differentially affected by the optimization criterion used).

11) contact between nasal processes of premaxilla and nasals: 0 = none; 1 = little (less than width of nasal processes); 2 = broad (greater than or equal to width of nasal processes) (Ridgway 1972; Wozencraft 1989).

The plesiomorphic condition among carnivores is for a broad contact between the premaxillary nasal processes and the nasals, with a reduction occurring in the phocids (de Muizon & Hendey 1980; Wozencraft 1989; Wyss & Flynn 1993). Wozencraft (1989) also indicates a reduced contact in lutrines, but Wyss & Flynn (1993) report that this is only true of *Enhydra*. Among phocids, this reduction is generally partial, if any, for the phocines, and full (or virtually so) for the monachines, but with *Monachus* spp. re-obtaining the primitive condition (Mivart 1885; Hendey & Repenning 1972; Ridgway 1972; de Muizon & Hendey 1980). A total lack of contact has been held to be diagnostic for the lobodontines (de Muizon & Hendey 1980). Additionally, *Phoca vitulina* may be naturally dimorphic for this character, with state 0 characterizing Atlantic forms, and state 1 or 2 being typical of Pacific individuals (Allen 1902; Doutt 1942; Chapskii 1955a, 1967).

Here, reduced contact is diagnostic of the phocids alone, with the family primitively characterized by state 0. This extreme situation for the hypothetical phocid ancestor could be an artifact associated with character #12, as two of the genera lacking the dorsal portion of the nasal processes (*Cystophora* and *Mirounga*) hold the basal positions within each phocid subfamily. However, it is likely an accurate portrayal, as the monachines generally retain a state of no contact between the nasals and the premaxillary nasal processes. The distribution reported above is generally upheld here. Among the monachines, the lobodontines, exclusive of *Leptonychotes* (state 2), are characterized by state 0, with *Monachus* spp. reverting to re-obtain a broad contact (although *M. monachus* only does so under ACCTRAN optimization). The phocines internal to *Halichoerus* likewise revert

to a broad contact, with *Phoca vitulina* being uniquely characterized among this group by a polymorphic reduced contact (states 0 or 1).

12) length of nasal processes of premaxilla along maxilla: 0 = extend only part way to nasals; 1 = extend fully or virtually fully to nasals (pers. obs.).

The over-reaching effects of this character on all others dealing with the nasal processes of the premaxilla have already been outlined. In association with the previous character, any reduction in contact between the nasal processes and the nasals is held to be apomorphic (de Muizon & Hendey 1980; Wozencraft 1989). However, the important factor here is not the degree of contact between the two, but the degree of extension of the nasal processes. Thus, we consider the situation where the nasal processes do extend to the nasals but fail to contact them (e.g., due to a thin interposing sliver of the maxilla as in *Halichoerus* or *Phoca vitulina*) as a trivial variation of full extension. Therefore, the apomorphic condition is obtained only in the genera *Cystophora, Mirounga*, and *Ommatophoca*. It is synapomorphic only for the two elephant seals.

For *Cystophora* and *Mirounga*, the apomorphic condition is likely associated with the convergent morphological changes occurring around the nasal region to allow expansion of the narial opening for extrusion of the inflatable nasal sac (King 1972; Reeves & Ling 1981; Kovacs & Lavigne 1986). Its parallel appearance in *Ommatophoca* is problematic. Although this species is comparatively poorly described, no inflatable nasal appendage has ever been reported for it. However, it should be noted that the nasal processes of *Ommatophoca* do extend much further than they do in either *Cystophora* or *Mirounga*. The apomorphic condition might be expected more for *Halichoerus*, a species with a nasal region very similar in morphology to *Cystophora* and *Mirounga* (King 1972; Reeves & Ling 1981). The similarity is so great that it is often felt that *Halichoerus* should possess a nasal appendage to account for it (King 1972).

13) shape of anterior margin of nasals (ignoring contribution of nasal suture): 0 = flat or broadly indented; 1 = lobular (uni-, bi-, or tri- lobed) (pers. obs.).

Although many authors have commented on various aspects of the morphology of the nasal bones, including their general shape at the anterior end (e.g., Chapskii 1955a; King 1972; Reeves & Ling 1981; Kovacs & Lavigne 1986), very few have examined the potential systematic usefulness of the nasal bones. Our observations revealed two major groups with respect to the shape of the anterior end of the nasals: those with a simple, roughly flat outline, and those with a more complicated lobular appearance. Of these two nasal types, the plesiomorphic lobular condition is distributed throughout the Caniformia, with the apomorphic flattened state represented only among the otarioids.

Unfortunately, this may be a consequence of the oversimplification of the coding scheme we adopted. As is immediately obvious, the lobular condition encompasses three distinct morphologies [see Fig.7 in King (1956:230)] and numerous derivations thereof. As we found no easy way to homologize these derivations with the major types, we were forced to condense all these forms into the lobular morphology. However, it should be noted that the caniforms nearly universally share a trident-like morphology, consisting of two lateral prongs and a broader medial one. We suggest that this is, in fact, the plesiomorphic condition, with the remaining lobular morphologies being derivations thereof (see the following character).

14) relative lengths of anterior prongs of nasal bones with a trident-shaped (= tri-lobular) morphology: 0 = lateral prongs greater than medial prong; 1 = lateral prongs subequal with medial prong; 2 = lateral prongs less than medial prong; 9 = n/a – nasal bones not trident-shaped (pers. obs.).

One mechanism to account for the numerous derivations of the hypothesized plesiomorphic trident-shaped nasal bones is through the differential expression of the lateral versus medial prongs. In particular, an extreme reduction of the medial prongs could lead to a bi-lobular morphology, that of the lateral prongs to a uni-lobular morphology, and that of both sets of prongs to the flattened morphology of the otarioids (see previous character).

Most of the Caniformia retain the plesiomorphic condition, whereby the lateral prongs are longer than the medial one. The remaining apomorphic states display limited distributions, primarily among the pinnipeds. The condition in which the nasal bones do not possess a trident-shaped morphology occurs only among the otarioids, *Mirounga* spp., and possibly *Cystophora* and *Monachus monachus* (both of which are polymorphic with other states), and may diagnose the pinnipeds ancestrally (ACCTRAN optimization). State 2 occurs unequivocally only in *Ursus* and *Lobodon*, while state 1 is found in *Halichoerus, Pagophilus*, and polymorphically with state 0 in *Histriophoca*.

15) visibility of nasal septum in dorsal view: 0 = does not extend beyond nasals (not visible); 1 = extends beyond nasals (visible) (King 1956; pers. obs.) (Fig.18).

Our observations for the previous nasal characters revealed that the nasal septum, which typically lies beneath and is covered by the nasals, was occasionally visible in dorsal view. Typically, when this situation occurred, the septum extended anteriorly to be visible between the prongs of the trident-shaped nasals, although it did extend completely beyond the nasals on some occasions. King (1956) lists these morphologies as a general tendency of *Monachus* spp., occurring to the greatest extent in *M. tropicalis* and the least in *M. schauinslandi*. Its appearance in *M. monachus* seems to be limited to old individuals (King 1956). This condition has also been noted in the fossil lobodontine *Homiphoca capensis* (de Muizon & Hendey 1980). Although we observed this derived condition (state 1) in numerous isolated phocid specimens, it was only consistently present in *Monachus tropicalis*, suggesting that its absence may be an artifact of preparation in some taxa. In any case, the systematic value of this apparently autapomorphic character is limited here.

16) shape of posterior edge of nasals, I: 0 = v-shaped (convergent); 1 = w-shaped (divergent) (Wozencraft 1989).

This character essentially amounts to the relationship between the nasals and the frontals. The divergent morphology is obtained when the frontal bones project between the nasals, while the convergent morphology is obtained by the reverse situation (King 1983). Despite noting the differences between the two taxa for this feature, Wozencraft (1989) proposed the divergent morphology as a synapomorphy of the otarioids. However, this has been criticized by Wyss & Flynn (1993), who note that *Odobenus* really possesses more of a flat termination to the nasals. Under the definition employed above, this would appear to be a modification of the convergent condition. However, despite recognizing the flattened termination, King (1983) still scored *Odobenus* as possessing the divergent morphology.

As well, our observations reveal that *Odobenus* does possess a very subtle divergent morphology, partially disguised by a rounding of the posterior edge of the nasals (see character #17). In any case, the convergent morphology has been repeatedly noted for phocids (Burns & Fay 1970; King 1983; Wozencraft 1989; Wyss & Flynn 1993).

The divergent morphology is present only in a number of the outgroup taxa: *Ursus*, the otarioids, and polymorphically in *Lutra*. Although the phocids share the plesiomorphic convergent morphology with *Canis*, they differ subtly in that the nasals intrude far more deeply between the frontals than in *Canis*, extending posteriorly past the anterior orbital rim. This represents yet another phocid synapomorphy (Wyss & Flynn 1993).

17) shape of posterior edge of nasals, II: 0 = pointed; 1 = rounded (Wozencraft 1989; pers. obs.).

Inclusion of this character follows from observations of the previous character dealing with the nasofrontal suture. Seemingly independent from the nature of the nasofrontal suture was the observation that the nasals either terminated in sharp points or were rounded. A rounded termination is plesiomorphic, characterizing most outgroup taxa except *Martes* and *Zalophus*. Most phocids display the apomorphic pointed morphology, but this condition arises independently within each subfamily: internal to *Cystophora* in the phocines, and in *Mirounga leonina* and internal to *Hydrurga* in the monachines. Among these more terminal taxa, only *Erignathus* and *Monachus schauinslandi* deviate from the typical pattern of their respective subfamilies.

*18) shape of posterior edge of nasals, III: 0 = pointed v-shape; 1 = rounded v-shape; 2 = rounded w-shape; 3 = pointed w-shape (Wozencraft 1989; pers. obs.).

This character is a combination of the previous two characters dealing with the shape of the nasals. However, it is inferior to the previous two in that it is too particular and thus reduces the number of potential synapomorphies in favour of autapomorphies (e.g., only *Zalophus* obtains state 3). It was, therefore, abandoned.

19) distinct caninus fossa: 0 = absent; 1 = present (de Muizon 1982a) (Fig.19).

A well-marked fossa running anteriorly along the alveolar edge of the maxilla from below the infraorbital foramen has been described as a synapomorphy of the phocines, with a convergent appearance in *Mirounga* spp. (de Muizon 1982a). However, there appears to be some confusion centred around the muscle this caninus fossa receives. De Muizon [pers. comm., citing Howell (1928)] states that the caninus muscle is lacking in phocids, so that the fossa serves instead as the origin for the maxillo-naso-labialis. However, such an interpretation is not at all clear from Howell (1928), which, together with other sources (e.g., Miller 1962; Crouch 1969; Bryden 1971), would seem to indicate that the two muscles are merely synonyms for one another. Only Piérard (1971) indicates the two muscles to be distinct entities, thereby voicing an opinion in agreement with de Muizon. Although de Muizon (pers. comm.) indicates that maxillo-naso-labialis fossa would be a more appropriate name for this structure in phocids, we will continue to use the term caninus fossa.

Among outgroup taxa, a distinct fossa was only present for *Canis* rendering the polarity of this character equivocal at the level of the Caniformia. Although the distribution of this character closely matches that of de Muizon (1982a) (we additionally noted the presence

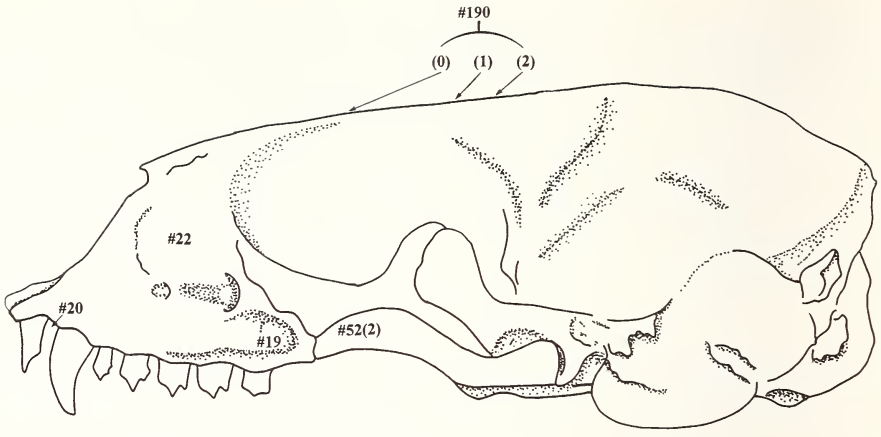

Fig.19: Lateral view of the right side of a phocid skull (*Phoca* sp.) illustrating selected characters (indicated by their number, with specific states presented in parentheses; see **Character Analysis**). Anterior is towards the left of the page. Adapted from Lawlor (1979).

of the fossa in *Hydrurga*), the caninus fossa is indicated here to be a synapomorphy of the whole of the phocids, with a single loss occurring in the ancestor of those monachines internal to *Hydrurga*.

20) depth of unnamed fossa on ventrolateral side of premaxilla: 0 = shallow; 1 = medium; 2 = deep; 9 = absent (pers. obs.) (Fig.19).

Our observations of the snout region revealed a distinct depression located between the last upper incisor and the upper canine in many specimens. This apparently unnamed fossa of the premaxilla provides room for the lower canine when the mouth is closed, and thus essentially relates to the size of the lower canine to some degree.

The general evolutionary trend for this character is for it to decrease in size from its primitive medium depth, often to the point of being entirely absent, in moving towards the pinnipeds. A shallow fossa is a synapomorphy retained from *Procyon* into each phocid subfamily. From there, several independent losses of the fossa occur, most notably in the clade of *Erignathus, Histriophoca*, and *Pagophilus*, and in those monachines internal to *Hydrurga*, with *Monachus* spp. showing a tendency to re-develop a shallow fossa. *Mirounga* spp. uniquely derives a deep fossa. Overall, this distribution likely reflects the trend towards homodonty in the pinnipeds, with large canines being secondarily reacquired in the sexually dimorphic *Mirounga* spp. (see also King 1983).

21) anterior opening of infraorbital canal relative to nasolacrimal foramen: 0 = anterior; 1 = ventral (or posterior) (Wozencraft 1989).

Although we are using the character as suggested by Wozencraft (1989), he goes on to suggest that this character may be more accurately recoded as referring to the relative length of the rostrum, noting that those taxa with long rostra also possess an anterior placement of the anterior canal opening. Several phocids are noted for their long rostra [e.g., *Cystophora, Hydrurga, Lobodon*, and *Mirounga*; King (1972)], but this may only be

in relation to other phocids and not to the Canifornia as a whole. As Wozencraft (1989) gave no criteria for distinguishing long versus short rostra, our observations deal strictly with the placement of the canal opening. These observations and the resulting polarity assessment do coincide with those of Wozencraft (1989). An anterior placement is shared primitively only by *Canis* and *Ursus*, while all remaining taxa are united by the apomorphic ventral (or posterior) placement.

Orbit and zygomatic arch (35 characters)

The orbital region in the pinnipeds, and especially in the phocids, yields a number of diagnostic features. Many of these are correlated with the proportionately narrow interorbital region of the pinnipeds. Although the distribution for most of the characters is well known and well referred to in the literature, very few of these traits have been examined in a systematic context for the phocids.

22) swelling of maxilla anterior to zygomatic arch: 0 = absent; 1 = present (Burns & Fay 1970; King 1972) (Fig.19).

Initially, this character dealt with the formation of a "shoulder" by a dorsolateral projection of the maxilla and jugal in the anterior wall of the orbit. King (1972: her Fig.18) described such a shoulder in *Cystophora* (also Reeves & Ling 1981; Kovacs & Lavigne 1986) and *Mirounga* as a mechanism to displace the eyes laterally to see around the (independently derived) nasal appendages. However, this shoulder was not readily apparent during any of our observations and instead, a swelling of the maxilla anterior to the zygomatic arch was noted for many species. This swelling is noted to be typical of the phocines (Burns & Fay 1970; King 1972), although it is expressed by all phocids to some degree (Burns & Fay 1970). It has been attributed to a lateral expansion of the maxilloturbinals, designed to counteract their constriction by the reduced interorbital region (King 1972) and/or as an adaptation to efficiently warm inspired air in response to the cooling environment of the late Tertiary and current high altitude habitats (de Muizon & Hendey 1980; Mills & Christmas 1990). The lack of a swelling in the lobodontines apparently arises from their accommodation of the expanded maxilloturbinals within a dorsoventrally expanded nasal cavity (de Muizon & Hendey 1980). This likely represents a secondary solution to the problem (the swelling being the first), as certain populations of the fossil lobodontine *Homiphoca capensis* are noted to possess a phocine-like swelling (de Muizon & Hendey 1980).

Here, a truly distinctive swelling (the apomorphic condition) was present only for *Phoca vitulina* and *Pusa* spp., although most phocines are polymorphic for this trait. It also appears in the lutrines, either independently in each (DELTRAN optimization), or as a synapomorphy which is later lost in the pinniped ancestor (ACCTRAN optimization).

*23) distinct preorbital process of maxilla: 0 = absent; 1 = present (Burns & Fay 1970) (Fig.20).

With recoding, this character was included in character #24.

24) size of preorbital process of maxilla: 0 = small; 1 = medium; 2 = large; 9 = absent (Burns & Fay 1970; pers. obs.) (Fig.20).

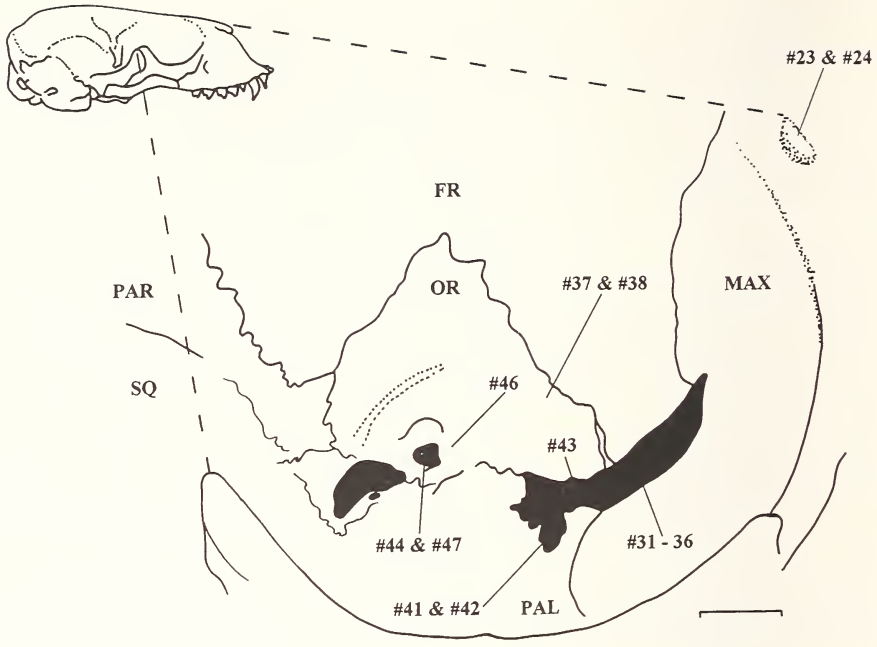

Fig.20: Dorsolateral view of the left interorbital region (see inset) of *Cystophora cristata* (USNM 188914) illustrating selected characters (indicated by their number; see **Character Analysis**) of this region. Anterior is towards the right of the page and dorsal to the top, with the zygomatic arch framing the bottom of the illustration. Abbreviations are as follows: FR = frontal; MAX = maxilla; OR = orbitosphenoid; PAL = palatine; PAR = parietal; and SQ = squamosal. Scale bar equals 1 cm. Inset adapted from Lawlor (1979).

Among pinnipeds, the general distribution of this feature is for it to be present in the otarioids, but only rarely so in the phocids (Mivart 1885), a difference Howell (1928) attributed to details of the orbicularis oculi and possibly the frontalis muscles. Turner (1848) questioned the value of this character for discriminating between the pinnipeds as it was present both throughout the otariids and in representative phocids (e.g., *Hydrurga*). A variable distribution in the pinnipeds is echoed by Hendey & Repenning (1972). Except for *Hydrurga* and *Lobodon*, the preorbital process is generally small in monachines, if not altogether absent, as in *Leptonychotes, Monachus schauinslandi*, and *Monachus tropicalis* (Mivart 1885; Hendey & Repenning 1972; de Muizon & Hendey 1980). Among phocines, Burns & Fay (1970) used the size of the preorbital process as one means of distinguishing between the closely related genera *Pagophilus, Pusa, Histriophoca*, and *Phoca* (listed in descending order of process size). In fissiped carnivores, the process is lacking in all but *Lutra* and *Ursus*, where it is rudimentary (Mivart 1885).

In contrast to the observations of Mivart (1885), we found a distinct preorbital process in all fissiped taxa expect *Procyon*. The plesiomorphic condition is for a small process, with an increase to medium size denoting a synapomorphy of the lutrines and the pinnipeds.

This condition is retained for the otarioids (but see character #26 for *Odobenus*) and largely throughout the monachines. *Mirounga* spp. show a tendency to develop a large process, while the process is lost entirely in the clade of *Monachus schauinslandi* and *Monachus tropicalis*. A distinct process is largely lost in the phocines, although many taxa are characterized by a slight ridge or roughening of the maxilla in its former location. Only *Cystophora* (state 1), *Erignathus*, and *Histriophoca* (both state 0) possess distinct preorbital processes.

*25) distinct postorbital process of maxilla: 0 = absent; 1 = present (pers. obs.).

With recoding, this character was included in character #26.

26) size of postorbital process of maxilla: 0 = small; 1 = medium; 2 = large; 9 = absent (pers. obs.).

To date, this feature has been used primarily to elucidate the higher level relationships within the Caniformia. Among the pinnipeds, the presence of the postorbital process has been used to distinguish the otariids from *Odobenus* and the phocids, where it is absent, or, at best, rudimentary (Mivart 1885; Ridgway 1972; King 1983; Wyss 1987). Howell (1928) attributes this absence in the phocids to the lack of an interorbital extension of the temporalis, combined with the larger, more dorsally positioned eyes of this group. However, it may develop with age in phocids as Allen (1887) mentions a distinct frontal (= postorbital?) process in very old individuals of *Monachus tropicalis*. Wozencraft (1989) lists a large postorbital process as being unique for the otariids among caniforms, although Wyss (1987) indicates that it is also present in ursids.

Although *Odobenus* is typically listed as lacking a postorbital process [only Mivart (1885: 497) indicates the presence of one, but he earlier (page 493) contradicts himself], there is cause to doubt these reports. Wozencraft (1989) notes that the strong facial compression characteristic of this taxon has resulted in the confluence of the postorbital process with the lacrimal flange (= preorbital process?) into a single process of questionable homology. Our observations support this finding, although the preorbital process is implicated in the place of the lacrimal flange. However, both the pre- and postorbital processes can be individually differentiated (primarily due to their different bones of origin), and we have chosen to recognize each as being medium in size (state 1).

The general trend within the Caniformia is for a reduction in the size of the postorbital process to its eventual loss ancestrally in the phocids. However, the primitive state for this character is uncertain due to both *Canis* and *Ursus* being polymorphic for this trait (both states 1 and 2). Beyond this, ACCTRAN optimization indicates an initial derivation of a small process for *Procyon, Martes*, and *Enhydra*, followed by a medium process uniting *Lutra* and the pinnipeds ancestrally. In contrast, DELTRAN optimization holds for state 1 being a synapomorphy extending from *Martes* to the pinnipeds ancestrally, with *Procyon* and *Enhydra* independently evolving state 0. *Zalophus* always uniquely obtains a large process. The postorbital process is lost ancestrally in the phocids and is never regained within this group. At best, various species possessed a slight ridge, or a roughening of the frontal bone, but nothing that we would term a distinct process.

*27) nasolacrimal (= lacrimal) foramen: 0 = absent; 1 = present (Wozencraft 1989).

With recoding, this character was included in character #28.

28) size of nasolacrimal foramen: 0 = small; 1 = medium or greater; 9 = absent (Wozencraft 1989; pers. obs.).

Among carnivores, the tendency towards the loss of the nasolacrimal foramen may be a synapomorphy of a monophyletic Pinnipedia. The foramen is truly lacking only among phocids, being vestigial in the otariids and often absent in old individuals (King 1983; Wyss 1987; Wozencraft 1989). A gradual loss of the nasolacrimal foramen is indicated here. Primitively, the Caniformia are characterized by a medium-sized foramen (*Canis* and *Ursus*). The foramen either becomes reduced in size for most of the remaining fissiped outgroups (ACCTRAN optimization), or is retained at medium size with some independent derivations of a small foramen (DELTRAN optimization), before becoming lost in the hypothetical pinniped ancestor. The vestigial nature of the foramen noted above by Wozencraft (1989) is not seen in our representative otariid; however, the outright lack of the foramen we observed in *Zalophus* might be artifactual, reflecting the fact that only adult specimens were examined in this study, or that *Zalophus* might not be a typical otariid in this respect. A vestigial foramen is indicated more in *Odobenus*, which is polymorphic for this character (states 1 and 9).

29) location of inferior oblique muscle origin relative to nasolacrimal foramen: 0 = widely separate; 1 = closely adjacent (Wozencraft 1989).

The inferior oblique muscle originates on the skull in the region of the lacrimal bone. The potential fossa denoting this origin, the fossa muscularis, is well developed only in ursids and the pandas, *Ailuropoda* and *Ailurus*, and is completely absent in procyonids and canids (Davis 1964). Our observations indicate that the fossa is also apparently lacking in the pinnipeds, mustelines, and lutrines. Thus, with no reliable indicator for the site of origin, we relied on the data in Wozencraft (1989) for this character. Unfortunately, this character is of limited use here as the closely adjacent morphology is autapomorphic for ursids. Examining for the presence of the fossa muscularis may not be any more informative, as our observations indicate that the presence of the fossa is again autapomorphic for ursids.

30) lacrimal: 0 = absent / not visible; 1 = visible (King 1971; pers. obs.).

The apparent loss of the lacrimal bone has been described for the pinnipeds on a number of occasions (Howell 1928; King 1971, 1983). This loss has been ascribed either to its outright loss, to a posterior displacement and a failure to ossify (Howell 1928), or, more likely, to its fusion with the maxilla during development (King 1971, 1983). In the otarioids, this fusion is age-dependent, with younger animals often displaying a lacrimal (King 1971). No separate lacrimal bone has ever been conclusively reported on a phocid skull of any age (King 1983). The only suspected case involves a tentative assessment for a small unidentified bone fused to the maxilla in a *Mirounga leonina* fetus [Kummer & Neiss 1957 (as cited in Wyss 1987)]. [At one point in our observations, we thought that we had observed the lacrimal in a *Leptonychotes* skull; however, further examination revealed that it was more likely a portion of the maxilloturbinal underlying the widened maxillo-frontal suture (see Howell 1928; character #31).] An age-dependent fusion of the lacrimal to the maxilla has also been noted for mustelines and lutrines (Wozencraft 1989). The disappearance of the lacrimal is limited here to *Martes, Enhydra* (which is polymorphic for this trait), and the pinnipeds. This apomorphic loss either arises

independently in *Martes* and the pinnipeds (DELTRAN optimization), or jointly for the mustelids and the pinnipeds, with *Lutra* reversing to the plesiomorphic condition (ACCTRAN optimization).

31) amount of bone reduction along maxillo-frontal suture in interorbital region: 0 = none / irregular perforations; 1 = little – small foramen or narrow fissure; 2 = great – large foramen and/or greatly widened suture (Burns & Fay 1970; pers. obs.) (state 1 – Fig.20).

So-called "defects" in the ossification of phocid skulls are reasonably common and have repeatedly been mentioned (Mivart 1885; Howell 1928; Burns & Fay 1970; King 1972), but have rarely been utilized in a systematic context. Perhaps the largest and most consistently present defect occurs in the interorbital region and corresponds to a widening of the maxillo-frontal suture. This defect (frequently referred to as the orbital vacuity) is irregularly shaped, but roughly crescentic in shape and often confluent with the sphenopalatine foramen of the palate (Burns & Fay 1970; see also character #43). The size of the widened maxillo-frontal suture is quite variable in the phocids, generally large in the otariids, and small or absent in the fissiped carnivores (Howell 1928; Burns & Fay 1970). One potential complicating factor is the report that the size of the suture apparently decreases with age in the lobodontines (de Muizon & Hendey 1980).

A widened suture is generally absent outside of the phocids, being found only for *Ursus* (state 1 – small foramen located at lacrimo-maxillo-palatine suture) and *Zalophus* (state 2 – large irregularly shaped foramen occupying most of anterior orbital wall together with the broadly confluent sphenopalatine foramen). The two phocid subfamilies are clearly differentiated by this feature, with virtually all phocines (*Pagophilus* being the notable exception) possessing a slightly widened suture (state 1), and virtually all monachines sharing a greatly expanded suture (although the lobodontines are generally polymorphic between states 1 and 2). Together with *Zalophus*, a large amount of bone loss along the maxillo-frontal suture may be a synapomorphy of the pinnipeds as a whole (ACCTRAN optimization), or it may have arisen independently in the otariids and the monachines (DELTRAN optimization).

*32) morphology of bone reduction along maxillo-frontal suture in interorbital region: 0 = none; 1 = irregular perforations; 2 = round / ovoid; 3 = inverse teardrop-shaped; 4 = roughly rectangular; 5 = crescent-shaped (Burns & Fay 1970; pers. obs.) (Fig.20).

Although reasonably reflective of the major shapes for the widened maxillo-frontal sutures of phocids, this character is too particular and was recoded as the more general #31 in an attempt to generate more synapomorphies.

*33) shape of maxillary (anteroventral) edge of widened maxillo-frontal suture: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – maxilla and frontal in contact (pers. obs.) (Fig.20).

This character was abandoned in favour of #31 in an attempt to generate a succinct summary of the widening of the maxillo-frontal suture in phocids.

*34) shape of frontal (posterodorsal) edge of widened maxillo-frontal suture: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – maxilla and frontal in contact (pers. obs.) (Fig.20).

This character was abandoned in favour of #31 in an attempt to generate a succinct summary of the widening of the maxillo-frontal suture in phocids.

*35) degree of invagination of maxillary (anteroventral) edge of widened maxillo-frontal suture: 0 = none to slight; 1 = medium or greater; 9 = n/a – maxilla and frontal in contact (pers. obs.) (Fig.20).

With recoding, this character was included in character #31.

*36) degree of invagination of frontal (posterodorsal) edge of widened maxillo-frontal suture: 0 = none to slight; 1 = medium or greater; 9 = n/a – maxilla and frontal in contact (pers. obs.) (Fig.20).

With recoding, this character was included in character #31.

*37) anterior process of orbitosphenoid: 0 = absent / barely extends onto palatine; 1 = present (pers. obs.) (Fig.20).

With recoding, this character was included in character #38.

38) degree of anterior extension of orbitosphenoid: 0 = extends to distinctly less than one-half length of palatine; 1 = extends to about one-half length of palatine; 2 = extends to distinctly greater than one-half length of palatine; 9 = absent / barely extends onto palatine (Wozencraft 1989; pers. obs.) (Fig.20).

In attempting to determine the relative position and size of the sphenopalatine foramen, we noticed that the length of the orbitosphenoid (with respect to the palatine) varied among, but was more or less constant within the different phocid species. To our knowledge, this has only been reported briefly for the otarioids (Wozencraft 1989), but never fully examined in a systematic context. The primitive condition is one in which the orbitosphenoid extends into the anterior half of the palatine, a condition found in most of the outgroups. (This assessment of state 1 for *Odobenus* is somewhat tentative due to the tremendous compression of the interorbital region that characterizes this genus, obscuring and modifying the exact relationships between the orbitosphenoid and palatine bones.) This plesiomorphic condition is retained primitively in the phocids and characterizes nearly all phocines. In contrast, the monachines derive state 1 ancestrally. The terminal branches of this subfamily (*Lobodon* plus *Monachus* spp.) display a tendency to reduce the orbitosphenoid further, but only *Monachus tropicalis* (and independently in *Erignathus*) essentially lack any anterior extension (state 9).

The above distribution of this character could be related to the length of the interorbital region. A relatively short orbitosphenoid could arise through either a truly shortened orbitosphenoid, a lengthened interorbital region filled in dorsally by the frontal, or a combination of these two factors. The relatively shorter orbitosphenoid of the phocids is due at least in part to their proportionately larger orbits as compared to the remaining caniforms (King 1972). Although this may explain the relatively reduced phocid orbitosphenoid, it does not appear to apply specifically within the phocids, as the phocids with the largest orbits – *Cystophora, Leptonychotes, Mirounga* spp., and *Ommatophoca* (King 1972) – do not possess the shortest orbitosphenoids. Likewise, *Lobodon*, which possesses a relatively small orbit (King 1972), does not have the predicted relatively long orbitosphenoid.

39) ethmoid / turbinal bones in wall of interorbital region: 0 = absent; 1 = present (pers. obs.).

One manifestation of the numerous defects in ossification mentioned previously for phocid skulls (see character #31) apparently allows for the normally covered ethmoid to form a part of the wall of the interorbital region. Howell (1928) suggests that the visibility of the ethmoturbinals in *Pusa hispida* is due to their crowding by the extremely narrow interorbital region, causing them to force their way through the overlying frontal bones. In any case, this derived condition seems to be independent of the other major defect in the interorbital region, the widened maxillo-frontal suture (character #31), and only occurs consistently for *Zalophus* and *Mirounga angustirostris*. *Lobodon* is polymorphic for this trait, and *Erignathus*, although unrecognized here, also shows a strong tendency towards this trait.

40) approach of palatine to lacrimal region: 0 = does not reach lacrimal region; 1 = reaches or almost reaches lacrimal region (Wozencraft 1989).

In most mammals (but, significantly, excluding the lutrines), the maxilla is restricted to the facial region, causing the anterior orbital wall to be formed by some combination of the lacrimal, frontal, palatine, and jugal (Wyss 1987). However, the unique condition of a reduced lacrimal in pinnipeds allows the maxilla to expand posteriorly to contribute to the medial surface of the anterior orbital wall (Wyss 1987). Together, these two features reduce the contact between the lacrimal (or lacrimal region for those taxa lacking a distinct lacrimal) and either the palatine or jugal (see character #54). Both states of reduced contact have been described as a synapomorphies for a monophyletic Pinnipedia only (Wyss 1987; Wyss & Flynn 1993), although the latter case may characterize the lutrines as well (see character #54).

The above scenario is generally echoed here, with most outgroups displaying the primitive condition, in which the palatine closely approaches or reaches the lacrimal region. The converse of this condition is a synapomorphy of either *Martes*, the lutrines, and the pinnipeds, with a reversal in *Enhydra* (ACCTRAN optimization), or of *Lutra* and the pinnipeds alone, with a parallel appearance in *Martes* (DELTRAN optimization).

41) location of sphenopalatine vacuity: 0 = enclosed in palatine; 1 = not enclosed in palatine (Wozencraft 1989) (Fig.20).

As originally coded by Wozencraft (1989), the derived condition, shared only by the otarioids, was one where the sphenopalatine vacuity was enlarged and eclipsing the orbitosphenoid dorsally. This condition, he further noted, was a function of both the enlargement of the orbital vacuity, including the sphenopalatine foramen (see character #42), and the length of the orbitosphenoid. As we have previously dealt with the relative length of the orbitosphenoid (character #38), we have employed a more generalized coding, asking merely if the sphenopalatine vacuity is limited to the palatine or not.

Even under our modified coding, this character is still a potential synapomorphy of the otarioids. Most of the taxa in this study possess the primitive morphology of an enclosed sphenopalatine vacuity. The derived condition is found only in the otarioids and in most of the monachines. However, there is some uncertainty as to whether this represents convergence between the two groups (DELTRAN optimization), or a synapomorphy, with the phocines reversing to the plesiomorphic condition (ACCTRAN optimization). It seems more likely that the former situation is true. Although the sphenopalatine vacuity in all

pinnipeds (including the phocines) is enlarged as compared to fissiped carnivores (a potential synapomorphy), this expansion is not as great in the phocids. In the otarioids, the expansion is very great and the vacuity eclipses the bone situated dorsal to it (either the frontal or the orbitosphenoid). The monachines secondarily approach the otarioid condition, with the sphenopalatine vacuity generally contacting the margin of the dorsally neighbouring bone, and, in a few isolated cases, eclipsing it, but never to the degree found in the otarioids.

42) relationship of sphenopalatine foramen and pterygopalatine canal: 0 = totally confluent, only single foramen visible; 1 = confluent, but individually distinguishable; 2 = separate (Wozencraft 1989; pers. obs.) (Fig.20).

The enlarged sphenopalatine vacuity of the pinnipeds makes exact identification of foramina in this area difficult. Burns & Fay (1970) state that the vacuity in this region is either homologous with, or includes only a part of, the sphenopalatine foramen. Our observations of an apparent intermediate state (state 1), whereby a single sphenopalatine vacuity is obviously composed of two broadly confluent foramina, hints at the latter. As no one to our knowledge has examined this region in detail for the pinnipeds, the identification of the second foramen cannot be absolute; however, it is likely the pterygopalatine canal. This conjecture is not without precedence, as Davis (1964) describes the confluence of these two cavities into a single foramen in *Ailuropoda* (albeit not enlarged into a vacuity as in the pinnipeds). As well, these two cavities are irregularly confluent throughout the carnivores (Story 1951).

Having the sphenopalatine foramen separate from the pterygopalatine canal is indeed plesiomorphic among the Caniformia, with their total confluence to a single foramen being a synapomorphy of the lutrines plus the pinnipeds. (It should be noted that there is no objective way to discriminate between the confluence of the cavities and merely the loss of one of them.) This state is retained throughout most of the pinnipeds except for the phocines, which display both the primitive pinniped (state 0) and "intermediate" (state 1) states. The intermediate condition unites at least some (DELTRAN optimization), or all (ACCTRAN optimization) of the phocines, with a variable number of reversals accounting for state 0. It should be noted that many phocids were polymorphic for this character, and that these polymorphisms included various combinations of all states, including the plesiomorphic state 2.

43) continuity of sphenopalatine vacuity and widened maxillo-frontal suture: 0 = separate; 1 = confluent; 9 = n/a – widened maxillo-frontal suture absent (Burns & Fay 1970; pers. obs.) (Fig.20).

The expansion of both the maxillo-frontal suture and the sphenopalatine vacuity in the pinnipeds leads to the possibility of their confluence. Burns & Fay (1970) indicate that this is a relatively frequent occurrence among the phocines. The distribution of this character follows the major trends of either of its constituent characters (#31 or 41). The lack of a widened maxillo-frontal suture in most outgroup taxa renders the "inapplicable" condition (state 9) as symplesiomorphic. In phocids, a widened maxillo-frontal suture is almost universally present (missing only in *Pagophilus*), so the distribution of the current character relies more on the morphology of the sphenopalatine vacuity. The more restricted

vacuity of phocines is generally separate from the maxillo-frontal suture, in contrast to the observations of Burns & Fay (1970). This state also defines the ancestral phocid condition. Correspondingly, the more expanded vacuity of monachines is generally confluent with the maxillo-frontal suture, especially in the clade composed of *Lobodon, Monachus* spp., and *Ommatophoca*. This condition also arises convergently in *Zalophus*.

44) relative vertical position of optic foramina: 0 = in lower third of interorbital region; 1 = between lower third and upper two-thirds of interorbital region; 2 = in upper two-thirds of interorbital region (pers. obs.) (Fig.20).

Observations for other characters related to the optic foramina (characters #45-47) revealed that the foramina are not at a constant relative height in the skull. The most common condition was for the foramina to be situated about one-third of the way up the interorbital region (state 1), with displacements to varying degrees occurring both above (state 2) and below (state 0) this apparent demarcation point.

In fact, a ventral displacement of the optic foramina (state 0) is primitive among caniforms, being found in all fissipeds except *Lutra*. *Lutra* instead groups with the pinnipeds in possessing state 1. Three major groups roughly fall out within the pinnipeds. The otarioids are clearly defined by dorsally displaced foramina (state 2), while the phocines (excepting *Cystophora* and *Halichoerus*) revert to the primitive condition. The monachines generally retain the ancestral pinniped morphology (state 1), although *Hydrurga* and *Mirounga leonina* independently obtain the otarioid condition.

45) intracranial openings of optic foramina of orbitosphenoid: 0 = separate; 1 = converging / intermediate; 2 = confluent (Mivart 1885) (Fig.21).

Mivart (1885) initially used a simpler form of this character to distinguish the otarioids (state 2) from the phocids (state 0). Only *Hydrurga*, and possibly *Lobodon*, were noted to deviate from this pattern (Mivart 1885). However, our observations revealed an apparent intermediate condition (state 1) in addition to these two more extreme morphologies. This intermediate state closely resembles state 2, except that each opening is still individually distinguishable despite being reasonably confluent with the other.

Within the Caniformia, any tendency towards confluence of the intracranial openings of the optic foramina is apomorphic. Parallel appearances of the totally confluent morphology (state 2) occur in the otarioids and generally in the monachines internal to *Mirounga* spp. The apparent intermediate condition does not intervene between the two extreme morphologies, but instead occurs independently several times within the Caniformia.

46) interorbital septum anterior to optic foramina: 0 = absent; 1 = present (Wozencraft 1989) (Fig.20).

To some degree, the interorbital septum reflects the narrowness of the interorbital region. This septum is present in those taxa in which the optic foramina possess a common rostral border (Wozencraft 1989), and is formed by the adpression and fusion of the paired wings of the orbitosphenoid anterior to the optic foramina. The septum is typically identified only with the otariids (Turner 1848; Wozencraft 1989). However, the phocids might also be expected to possess an interorbital septum as the pinnipeds as a whole possess a narrower interorbital region than do other carnivores (Howell 1928; see also character

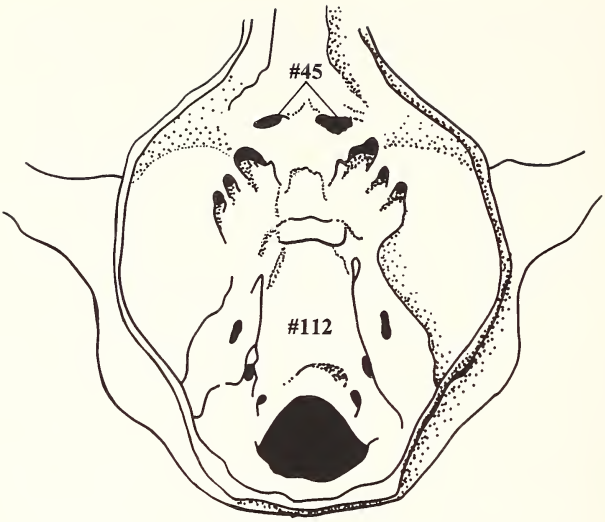

Fig.21: Dorsal view of a frontally-sectioned felid *(Felis domestica)* cranium illustrating selected characters (indicated by their number; see **Character Analysis**) of this region. Anterior is towards the top of the page. Adapted from Gilbert (1968).

#49). This might be especially true for the monachines, as the least interorbital width in this subfamily occurs in the middle or posterior portion of the interorbital region (King 1972; Wyss 1988a), or, in other words, around the region of the orbitosphenoid.

Our observations, however, do not substantiate this line of reasoning. Instead, the apomorphic interorbital septum is an uncommon occurrence, being found in only *Zalophus, Monachus monachus*, and *Monachus tropicalis* (the latter of which also possesses an anteriorly located least interorbital width; see character #49). The presence of the septum in the two monk seals might indicate a synapomorphy of the genus as a whole, with a reversal in *Monachus schauinslandi* (ACCTRAN optimization), or simply parallel evolution in each species (DELTRAN optimization).

47) continuity of bilateral optic foramina (interorbital foramen) in interorbital region: 0 = not continuous, no common passage; 1 = continuous, form passage through interorbital region (Mitchell 1975) (Fig.20).

Mitchell (1975) noted that a patent interorbital foramen [i.e., where the left and right optic foramina are continuous medially (either in whole or in part), thereby creating a foramen that pierces the interorbital region] was diagnostic of otariids and of the primitive fossil pinniped *Allodesmus kernensis*. Although we observed that continuity of the foramina is aided by their sharing of a common rostral border, this is not an absolute requirement, as the distribution of this character differs slightly from that of the previous one. Again, the apomorphic continuity of the foramina is uncommon, occurring as expected in *Zalophus*, but also independently in *Martes* and *Monachus monachus*.

48) alisphenoid canal: 0 = absent; 1 = present (Wozencraft 1989).

The distribution of the alisphenoid canal is one of the key characters supporting the diphyletic hypothesis of pinniped ancestry. Along with other evidence, the occurrence of the canal in otarioids together with its lack in phocids has led some workers to ally the

otarioids with ursids and the phocids with mustelids (e.g., Mivart 1885; Tedford 1976; King 1983; Wozencraft 1989). Although suggestive, this character does not resolve the question of pinniped ancestry on its own. Howell (1928) has noted one otariid specimen in which the canal was not bilaterally present, which fuels the contention of other workers that the common absence of the canal in phocids and mustelids is due to convergence (Wyss 1987; Wyss & Flynn 1993).

Although our observations agree with those in the literature, the relationships advocated here indicate a somewhat novel suggestion for the evolution of the alisphenoid canal. The monophyly of the pinnipeds still necessitates homoplasy to explain the distribution of this character; however, the homoplasy now arises from a reversal by the otarioids to re-obtain the primitive condition of possessing the canal as found in *Canis* and *Ursus*.

49) location of least interorbital width: 0 = distinctly anterior to middle of interorbital region; 1 = approximately in the middle of interorbital region; 2 = distinctly posterior to middle of interorbital region (Wyss 1988a).

King (1972, 1983) has argued that the greater reliance of pinnipeds on sight rather than smell has resulted in the lateral compression of the interorbital region (and the underlying turbinal bones) to accommodate larger orbits. This has resulted in a proportionately narrower interorbital region in pinnipeds as compared to fissiped carnivores (Howell 1928), and is the most pronounced in the smaller species (King 1972). The exact nature of this compression is not constant within the pinnipeds, however, with the least interorbital width varying in its location: anterior for the phocines minus *Cystophora* and *Erignathus*, and posterior for all other pinnipeds (Burns & Fay 1970; King 1972; Wyss 1988a).

Unfortunately, the distribution of this character does not lend itself to a simple description. The general tendency is for the phocids to shift the least interorbital width anteriorly from the plesiomorphic posterior placement to the middle of the interorbital region. This also occurs in *Martes* and *Procyon*. The remaining outgroup taxa maintain the plesiomorphic condition. ACCTRAN optimization indicates that state 1 is synapomorphic for both the phocids and the clade of *Martes* and *Procyon*, with two intervening reversals accounting for the lutrines and otarioids. DELTRAN optimization holds for independent origins in *Martes, Procyon*, and in each phocid subfamily. However, both optimization schemes indicate that a posterior placement is primitive in the pinnipeds, as Wyss (1988a) suggested. Within the phocids, the distributions mentioned above are only generally supported, with most members retaining a middle placement. The diagnostic anterior and posterior placements only occur for scattered phocines (and also *Monachus tropicalis*) and monachines respectively.

50) location of greatest zygomatic width: 0 = anterior to glenoid fossa (i.e., within zygomatic arch proper); 1 = at level of glenoid fossa (i.e., at squamosal) (pers. obs.).

One mechanism to possibly accommodate the larger eyes and orbits of the phocids is for the zygomatic arches to be bowed outwards and generally broadened (Howell 1928; see character #51). However, we noted some variation in the location of the broadest point of the zygomatic arches. In some forms, the broadest point was located at about the level of

the glenoid fossa, causing the zygomatic arch to take on a roughly triangular form (tapering anteriorly) when viewed dorsally. In the remaining forms, the broadest point was situated anterior to the fossa, causing the arches to take on their typical arched morphology. Of these two forms, the apomorphic state 0 describes a synapomorphy of the mustelids (including the lutrines) and the pinnipeds, with only *Zalophus, Erignathus*, and *Lobodon* independently reversing to the primitive condition (state 1).

51) relative position of zygomatic arches: 0 = lower than tooth row; 1 = level with tooth row; 2 = higher than tooth row (Ridgway 1972).

The increase in orbit size noted for phocids (King 1972, 1983) has apparently been achieved with some unique changes involving the zygomatic arch (see the following character also). For instance, simply dropping the zygomatic arches will increase orbit diameter (Howell 1928). An extreme dropping of the zygomatic arches (state 0) has been described as peculiar to *Ommatophoca*, contributing to the proportionately huge (even for a phocid) orbit and eyeballs characteristic of this genus (Mivart 1885; King 1969, 1972, 1983; Ridgway 1972; Ray 1981). However, this extreme condition was never observed consistently in this study, even for *Ommatophoca*. Instead, parallel instances of the apomorphic intermediate condition (a slight dropping of the zygomatic arches – state 1) were found in *Odobenus* and in the monachines internal to *Mirounga* spp., except for *Monachus monachus* which reverted to the plesiomorphic condition (state 2).

52) direction of arch of anterior portion of jugal: 0 = downwards; 1 = flat, no distinct arch; 2 = upwards (Mivart 1885) (state 2 – Fig.19).

In noting the immense orbits of *Ommatophoca*, Mivart (1885) made mention of a distinctive downward arch to the zygomatic arches in this genus. Although most obvious in *Ommatophoca*, this latter feature is common among monachines, and appears to be related to a unique elongation of the maxillo-jugal suture associated with the dropping of the zygomatic arches in this group (see previous character). In most carnivores, the typical morphology of the jugal is of a rather compact bone, with the body being narrower than its articulating ends. Together with the relatively restricted, roughly vertical articulations of the jugal with the squamosal, and especially with the maxilla, this gives the ventral border of the jugal a distinctive upward arch. In those monachines with lowered zygomatic arches, and in *Ommatophoca* in particular, the maxillo-jugal suture is greatly elongated posteriorly, and the jugal tapers anteriorly. As well, the elongation of the suture results in its horizontal rotation, so that the ventral margin of the jugal is now primarily composed of that portion contributing to the suture, and the jugal now possesses a characteristic downward arch (or, at least, is flat, with no arch in either direction). The upward arch, which is associated with the narrower body, remains, but is no longer as obvious, having been shifted posteriorly and diminished in amplitude.

The possible connection between an elongated maxillo-jugal suture and the previous character is supported by their similar distributions. Flat or downward arching jugals (both of which are apomorphic) also diagnose the clade demonstrating the lowered zygomatic arches (lobodontines and *Monachus* spp.). A downwardly arching jugal is limited within this clade to *Lobodon, Monachus* spp., and *Ommatophoca*, but with reversals in *Monachus monachus* and *Monachus schauinslandi* to states 2 and 1 respectively. However, a flat

jugal has a wider distribution, characterizing the monachines as a whole (DELTRAN optimization), or possibly all phocids ancestrally (ACCTRAN optimization). This situation arises from the convergent possession of a flat jugal in *Cystophora, Erignathus*, and *Mirounga* spp. from the subset of monachines mentioned above. In these three genera, state 1 results from the increased robustness of the body of the jugal. In no case is the maxillo-jugal suture elongated, nor does the suture contribute to the ventral margin of the jugal.

53) degree of overlap of maxillary and squamosal processes of zygomatic arch on medial surface of zygomatic arch: 0 = little or none; 1 = approach closely – maxilla and squamosal almost or in contact (pers. obs.).

The phocids, and especially the monachines, seem to be characterized by modifications to the sutures in the zygomatic arch (see characters #52 and 56). Generally, these modifications take the form of an elongation of the sutures, and, in the case of the maxillo-jugal suture, a rotation to a more horizontal position. In some cases, this elongation and rotation is sufficient to bring the maxillary and squamosal processes of the zygomatic arch into contact with each other, or at least in very close proximity. Either situation is uncommon in the carnivores. This derived condition (state 1) is not widespread throughout the phocids either, and is found independently in only *Erignathus* and *Leptonychotes*.

54) approach of jugal to lacrimal region: 0 = does not approach lacrimal region; 1 = reaches lacrimal region / almost touches or does touch anterior wall of orbit (Wozencraft 1989; Wyss & Flynn 1993).

Wozencraft (1989) originally employed a more restrictive coding than that used here, examining whether the jugal contacted the lacrimal or not. This resulted in the derived condition ("does not contact lacrimal") occurring in a wide variety of carnivores, including ursids, mustelines, lutrines, and pinnipeds. However, as pointed out by Wyss & Flynn (1993), the separation between the two bones in many cases is merely due to the intervention of a thin sliver of the maxilla. Recognition of this as a trivial variation of the primitive condition ("jugal and lacrimal in contact") reduces the distribution of the derived condition (state 0 here) to the pinnipeds alone (and possibly the lutrines; see below). Such a coding also reflects the peculiar contribution of the maxilla to the anterior orbital wall in pinnipeds (Wyss 1987; Wyss & Flynn 1993; see character #40). Although Wyss (1987) indicates that lutrines also possess the derived condition, he discounts this as the configuration of the bones of the anterior orbital wall approximates that of the remaining mustelids more so than that of the pinnipeds. In any case, we too have opted for a less severe coding, partially reflecting our agreement with Wyss & Flynn (1993), and also reflecting the problems caused by the reduced nature of the lacrimal in the pinnipeds.

Yet, despite the failure of the jugal to contact the lacrimal region apparently being a pinniped synapomorphy, an obvious transition sequence for this character occurs within the monachines. In the supposedly primitive *Monachus* spp., the jugal terminates relatively medially [also Allen (1887) for *Monachus tropicalis*], above the centre of the infraorbital foramen. This termination point moves progressively laterally through the intermediate fossil taxon *Homiphoca capensis* to the more derived lobodontines, where it occurs lateral to the infraorbital foramen (Hendey & Repenning 1972; de Muizon & Hendey 1980).

As could be expected, the distribution of this character closely matches that of character #40, which deals with the approach of the palatine to the lacrimal region. Here, the lutrines plus the pinnipeds are united by the derived condition, in which the jugal does not approach the lacrimal. Together, both of these characters, which reflect the unusual contribution of the maxilla to the anterior orbital wall, not only support pinniped monophyly [as in Wyss (1987) and Wyss & Flynn (1993)], but also a lutrine affinity for the pinnipeds. The transition sequence mentioned above was not consistently borne out, although the jugal of *Monachus* spp. was observed to approach the lacrimal to a greater degree than in other phocids.

*55) dorsal process of squamosal process of zygomatic arch: 0 = absent; 1 = present (King 1983; Wozencraft 1989).

With recoding, this character was included in character #56.

56) degree of interlock between jugal and dorsal process of squamosal process of zygomatic arch: 0 = weak; 1 = medium; 2 = strong; 9 = dorsal process of squamosal absent (Wozencraft 1989).

This character stems from the oft-cited observation that the squamosal process of the zygomatic arch and the bifurcated distal end of the jugal form an unusual interlocking or mortised contact in phocids (Mivart 1885; King 1983; Wyss 1987; Wozencraft 1989) and the fossil pinniped genera *Allodesmus, Desmatophoca*, and *Pinnarctidion* (Mitchell 1975; Repenning 1975; Wyss 1987; Berta 1991). However, as a similar junction, but of slightly different morphology is also found in sirenians and desmostylians (Barnes 1989), we adopted Wozencraft's (1989) formulation of the character, which focuses on one particular aspect of the junction. The distinct dorsal process of the squamosal process he mentions is found only in phocids (Wozencraft 1989) and most species of *Allodesmus* [see photos and drawings in Mitchell (1975) and Barnes (1979)].

While we affirmed that the presence of the dorsal process is uniquely shared by all phocids among the taxa examined here (see character #55), we also noted that the "strength" of the resulting interlock varies. In some phocids, the jugal merely abuts the dorsal process of the squamosal process (state 0 – weak interlock), while in others, the jugal wraps up and around the dorsal process to varying degrees, thereby increasing the strength of the mortised contact (states 1 and 2). A medium strength interlock is the common morphology for the phocids and characterizes the family primitively. The remaining apomorphic states arise independently on a number of occasions: a weak interlock in *Halichoerus, Lobodon*, and *Pusa sibirica*, and a strong interlock in *Cystophora, Monachus tropicalis*, and *Pusa caspica*.

Palate and ventral side of snout (18 characters)

Although the palatal region appears to contain a good deal of phylogenetic information, a significant use of palatal characters is primarily limited to Chapskii (1955a) and Ridgway (1972). A primary source of characters is the contours of the hard palate. Chapskii (1955a) indicates this to be a useful source, although the high incidence of intraspecific polymorphism does tend to hinder easy descriptions for some species.

*57) incisive foramina (= palatine fissures / foramina): 0 = absent; 1 = present (pers. obs.).

With recoding, this character was included in characters #58 to 61.

58) size of incisive foramina: 0 = small; 1 = medium; 2 = large; 9 = absent (pers. obs.).

To our knowledge, the incisive foramina have never been used to help resolve phocid phylogeny, despite readily apparent differences in size, general location, and even in their presence or absence. Size, perhaps, is the most obvious character, although the functional significance of any size differences is unknown. We divided the foramina roughly into size classes based on the size of the foramina relative to the size of the anterior end of the hard palate. Increased emphasis for assigning foramina to their appropriate size class was given to their width (rather than their length; see the following character), due to its greater range of variation.

In moving towards the pinnipeds, the general trend is for a stepwise reduction in the size of the incisive foramina. *Canis* and *Ursus* possess the plesiomorphic condition of large foramina, with medium-sized and small foramina describing successive synapomorphies for the remaining fissipeds (excluding *Lutra*) and the pinnipeds respectively. Within the pinnipeds, the otarioids retain small foramina, as do the two phocid subfamilies ancestrally. The phocines are characterized by a reversal back to larger incisive foramina: large foramina for *Halichoerus* and *Phoca largha*, and medium-sized foramina in the remaining species, excluding *Cystophora*. The monachines largely retain small foramina. *Mirounga* spp. (although *M. leonina* is polymorphic for this character) and *Monachus schauinslandi* continue the trend to smaller foramina by losing them outright (see character #61). In contrast, the remaining monk seals show a tendency to revert to larger foramina, as does *Hydrurga*.

59) posterior extension of incisive foramina: 0 = enclosed within premaxilla; 1 = contact premaxillary-maxilla suture; 2 = extend into maxilla; 9 = incisive foramina absent (Chapskii 1955a).

In some ways, this character overlaps the previous one, as the posterior extension of the foramina is a function of their size. However, whereas the previous character was more a function of their width, this character deals more with their length. Our observations revealed two distinct morphologies (state 0 and 2), with a somewhat arbitrary intermediate (state 1). This latter state is likely not truly intermediary, but rather a modification of one of the two more extreme conditions.

The plesiomorphic state for the Caniformia is uncertain for this character. In most of the basal outgroups the incisive foramina are restricted to the premaxilla, but in *Canis*, the foramina extend well into the maxilla. In any case, the lutrines, otarioids, and the phocids are all united by the possession of foramina that extend into the maxilla to varying degrees. Both phocid subfamilies retain this condition primitively, before showing parallel derivations of foramina that only contact the premaxillary-maxilla suture, again hinting that state 1 is not a true intermediate condition. *Mirounga* spp. and *Monachus schauinslandi* convergently lack incisive foramina, while *Zalophus* and *Cystophora* independently re-obtain state 0.

60) number of incisive foramina: 0 = one; 1 = two; 9 = absent (pers. obs.).

Surprisingly, our observations revealed that the incisive foramina are not always paired (the plesiomorphic condition). Other than those forms that lack the foramina, or show

tendencies thereto (*Mirounga* spp. and *Monachus schauinslandi*), the foramina apparently coalesce in *Odobenus*, leading to the unique possession of a single midline foramen.

61) reduction of incisive foramina: 0 = absent; 1 = present (Allen 1887).

As noted in the previous characters dealing with the incisive foramina, three phocids, *Mirounga angustirostris, Mirounga leonina*, and *Monachus schauinslandi*, convergently share (between the two genera) the apomorphic tendency towards the absence of the incisive foramina. This loss appears to be the extreme outcome of another apomorphic tendency: the gradual closing over of the foramina by the bones of the hard palate. This latter tendency is convergently displayed to various degrees in four monachine genera *(Hydrurga, Leptonychotes, Mirounga*, and *Monachus). Hydrurga, Leptonychotes* (albeit both are polymorphic for this trait), and *Monachus monachus* display a very early stage in which the foramina are only partially covered over. Allen (1887) described a similar condition in *Monachus tropicalis*, but this was not observed here. In *Mirounga* spp., this process has advanced to the point so that the foramina are completely covered over, with only a pair of depressions laying evidence to their prior existence. Finally, *Monachus schauinslandi* displays the advanced condition where even the depressions are filled in and the foramina can be said to be truly absent. It should be noted that this is not a true developmental series, but isolated glimpses in three parallel ones, as these taxa are not each other's closest relatives.

62) position of major palatine foramen relative to maxillo-palatine suture: 0 = anterior; 1 = on; 2 = posterior (Ridgway 1972).

The plesiomorphic caniform condition for this character is generally agreed to be one where the anterior openings of the major palatine foramen open on, or very closely adjacent to, the maxillo-palatine suture (Wozencraft 1989; Bryant et al. 1993). This plesiomorphic placement is constant within the various carnivoran families, excluding the mustelids (Pocock 1921) and the pinnipeds (Wozencraft 1989). Many independent origins of an apomorphic anterior positioning have been postulated: various mustelines (Pocock 1921; Bryant et al. 1993), the lutrines (and within each of the genera *Lutra* and *Aonyx*) (van Zyll de Jong 1987; Bryant et al. 1993), all monachines except the fossil lobodontine *Homiphoca capensis* (de Muizon & Hendey 1980), and *Pagophilus* (Ridgway 1972). The only specific description of a posterior shift of the foramina is for *Histriophoca* (Ridgway 1972), although a tendency towards this has been noted for *Pusa* spp. in particular (Chapskii 1955a) and most phocines in general (Burns & Fay 1970).

Here, an apomorphic anterior shift of the foramina unites *Lutra* with the pinnipeds. This condition is retained by the hypothetical phocid ancestor and largely throughout the monachines, with only *Ommatophoca* showing a reversal to the primitive condition (state 1). The phocines primitively reverse to the plesiomorphic condition, with *Pagophilus* and *Phoca vitulina* separately redeveloping the anterior shift, and *Erignathus* uniquely deriving the posterior shift.

63) shape of maxillo-palatine suture: 0 = flat / square; 1 = rounded / triangular (Allen 1887).

This and the following two characters deal with the outline of the palatine bones on the palate. In addition to Allen's (1887) observation of a straight transverse suture in *Monachus*

tropicalis, our observations revealed that the anterior edge of the palatines displays other distinct morphologies. This plesiomorphic condition entails the maxillo-palatine suture having a rounded or triangular appearance. The flattening of this suture (manifested as a straight or square anterior edge to the palatines), as in *M. tropicalis*, is a synapomorphy of *Lutra* and the whole of the pinnipeds. Only *Mirounga leonina* and *Pusa sibirica* reverse to re-obtain the primitive condition, although a few other species are polymorphic between the two states.

64) outline of palatine bones in ventral view: 0 = square; 1 = "butterfly-shaped" (Ridgway 1972).

In essence, this character examines the entire ventral outline of the palatines and thus partially overlaps both the preceding and following characters. In contrast to the previous character, however, the different shapes here are determined more by the posterior half of the palatines, rather than the anterior edge. As well, all three characters appear to diagnose synapomorphies at different taxonomic levels. This character is apparently fairly specific, as Ridgway (1972) has used it to distinguish between the genera *Cystophora* (state 0) and *Mirounga* (state 1).

An apomorphic, butterfly-shaped outline to the palatine bones is a purely phocid condition, arising independently within this family on several occasions, and with numerous other species being polymorphic for the trait. It tends to characterize the phocines, existing as a synapomorphy of all members save *Cystophora* (ACCTRAN optimization), or merely for the clade internal to *Phoca largha*, with *Pagophilus* and *Phoca vitulina* independently reversing back to a square outline (DELTRAN optimization). Among monachines, butterfly-shaped palatine bones only exist unequivocally for *Lobodon, Mirounga angustirostris*, and *Monachus tropicalis*. The states observed here for *Cystophora* and *Mirounga* generally match those described by Ridgway (1972), except that *Mirounga leonina* obtains the plesiomorphic condition.

65) shape of posterior edge of palatine: 0 = (roughly) triangular; 1 = arched; 2 = straight (de Muizon 1982a).

The final character involving the ventral outline of the palatines deals exclusively with their posterior edge. King (1956) lists *Monachus monachus* as possessing a rounded posterior edge, while *Monachus tropicalis* possesses a pointed morphology (also Allen 1887). *Monachus schauinslandi* may be polymorphic for these two states [Kenyon & Rice 1959; also compare King (1956) and King & Harrison (1961)]. De Muizon (1982a) has pointed to a straight posterior border of the palatines as being a synapomorphy of his Cystophorini *(Cystophora, Histriophoca*, and *Pagophilus)*, but it may also occur independently in *Erignathus* (Chapskii 1955a). Ridgway (1972) confirms a straight posterior border for *Histriophoca*. However, these observations are partially contradicted by Doutt (1942), who described a rounded "Roman arch" (state 1) in *Histriophoca* and *Pagophilus*. This contradiction for *Histriophoca* may be due to it being polymorphic for this trait (between states 1 and 2), as hinted at by Burns & Fay (1970). Along with *Monachus schauinslandi* (see above), this may also be true for most species in general (Chapskii 1955a). Another complicating factor is our observation that states 1 and 2 lie along a continuum. A straight posterior edge may merely represent a very shallow double

arch. The triangular morphology appears to be independent of this continuum, but may also be an artifact created by a large notch in the posterior edge of the palate (see characters #67 and 68). Thus, the pointed "Gothic arch" described for *Phoca vitulina* and *Pusa hispida* by Doutt (1942) may actually be a combination of an arched posterior edge with a large triangular notch.

An arched posterior edge of the palate is both plesiomorphic and common throughout the Caniformia. This primitive condition is retained into both phocid subfamilies, and largely typifies most species. A triangular morphology occurs independently among a few species in both subfamilies: *Phoca* spp. among the phocines, and *Leptonychotes, Lobodon*, and *Monachus tropicalis* among the monachines. The other apomorphic state, a straight posterior edge, is found convergently in *Odobenus* and the clade of *Histriophoca* plus *Pagophilus*. In contrast to the observations of Chapskii (1955a), polymorphism was observed to be minimal for this character among the phocids.

66) presence of posteriorly directed process in midline of posterior edge of palatine: 0 = absent; 1 = present (Chapskii 1955a).

In contrast to the notching of the posterior palatal edge present in many phocines (see characters #67 and 68), Chapskii (1955a) noted a small, posteriorly directed process in *Histriophoca, Pagophilus*, and occasionally in *Phoca vitulina*. This condition is primitive among caniforms, with the loss of the process being a synapomorphy of *Lutra* and the pinnipeds. But, among this group, only *Mirounga leonina* consistently regained the posteriorly directed process.

67) morphology of notching in posterior edge of palatine: 0 = rounded; 1 = triangular; 2 = incision; 9 = none (Ridgway 1972).

The notching or incision of the posterior edge of the palate has been variously noted for *Phoca* spp. and *Pusa* spp. (Doutt 1942; Chapskii 1955a; Burns & Fay 1970; Ridgway 1972). Such a condition does not seem to be typical among the remaining phocines (Doutt 1942; Chapskii 1955a; Ridgway 1972; de Muizon 1982a), although Burns & Fay (1970) hint that *Histriophoca* may be polymorphic for this character. King (1956) describes a small incision for *Monachus monachus*, which we would reclassify here as a small triangular notch based on her Fig.7 (page 230).

The primitive condition for the Caniformia as a whole is the lack of any notching. This agrees with the previous character, where a posteriorly directed process is postulated as being plesiomorphic. Notching of any form is reasonably rare and largely restricted to the phocids. The most common form is a triangular shape, occurring consistently in *Mirounga angustirostris* and the clade of *Lobodon* plus *Monachus* spp., but appearing polymorphically (with state 9) in a number of other pinnipeds. *Monachus tropicalis* uniquely derives the incision, while a rounded notch was obtained only for *Histriophoca*, and then only as a species polymorphism with a triangular notch.

68) size of notching in posterior edge of palatine: 0 = small; 1 = medium; 2 = large; 9 = absent (Chapskii 1955a).

The notching present in the posterior edge of the palate of many phocids can have an adverse effect on the determination of the shape of the posterior edge of the palate as a

whole (character #65). Doutt (1942) apparently describes a moderate case for *Phoca vitulina* and *Pusa hispida*, where a large triangular notch changed the shape of the posterior edge of the palate from a rounded Roman arch to a pointed Gothic arch. In such cases, there is usually a slight inflection point between the arch and the notch to indicate the two separate morphologies. However, in some specimens, the confluence was so complete that there was no objective way to decide between a triangular posterior edge and a combination of an arched posterior edge with a very large triangular notch. But, despite Chapskii's (1955a) assertion that the palatal contours are generally subject to a fairly high level of intraspecific variation, he still holds this character to be a useful feature for subdividing the phocines.

In keeping with the previous character, the lack of a notch is primitive among the caniforms and is retained into the basal forms of both phocid subfamilies. A small notch is convergently obtained in *Histriophoca* and the clade of *Lobodon* plus *Monachus* spp. Two monk seals go on to derive larger notches – *M. monachus* (state 1) and *M. schauinslandi* (state 2) – as does *Mirounga angustirostris* (state 2). Many species were polymorphic, with the notch being equally present (i.e., one or more of the states 0, 1, or 2) and absent. Yet, somewhat curiously, the "present" state was not necessarily for a small notch, as one would expect if the notch was in the process of being gained, but often for a medium-sized or greater one (as in *Zalophus, Hydrurga*, and *Phoca vitulina*).

69) relationship of bony nasal septum to posterior edge of palate: 0 = does not reach posterior edge of palate; 1 = closely approaches / reaches posterior edge of palate (Chapskii 1955a; Ridgway 1972).

Ridgway (1972) used this character to distinguish between the closely related genera *Histriophoca* (state 1 – closely approaches) and *Pagophilus* [state 1 – reaches posterior edge; also Burns & Fay (1970)]. Although useful at the level employed by Ridgway (1972), the distinction between "closely approaching" and "actually reaching" seemed to be fairly minor at the level employed in this study. As well, under such a coding scheme, Burns & Fay (1970) observed that both *Histriophoca* and *Phoca* spp. would be polymorphic for this character. One solution would be to code this character even more finely using the sutures of the hard palate, especially the maxillo-palatine suture (Chapskii 1955a). However, this is often difficult to accurately determine in intact skulls, so we instead propose a more stringent coding of Ridgway's (1972) character: either the bony nasal septum extended posteriorly to approach the posterior edge of the palate, or it distinctly did not.

One exception to this dichotomy was observed fairly consistently in *Mirounga angustirostris*. Here, state 1 was achieved through a combination of a slight posterior extension of the bony nasal septum, a strong notching of the posterior end of the palate (see character #67), and a dorsal arching of the palate in the midline to meet the nasal septum. Together, these factors create a functionally shorter palate, allowing the otherwise slightly elongated nasal septum to reach its posterior end.

The primitive condition, where the bony nasal septum fails to reach the posterior end of the palate, is shared by all the outgroups except *Procyon*. The apomorphic trait is typically associated with the Monachinae (although two parallel reversals occur within the

subfamily), but also appears in two phocines, *Cystophora* and *Pagophilus*. This comes about either as a synapomorphy of the monachines alone, with convergent appearances in the two phocines (DELTRAN optimization), or as a synapomorphy of the phocids as a whole, with an early reversal in the phocines, followed by a re-derivation in *Pagophilus* (ACCTRAN optimization).

70) orientation of pterygoid hamuli: 0 = directed laterally; 1 = in midline; 2 = directed medially (Mivart 1885; Allen 1887; Chapskii 1955a).

The orientation of the pterygoid hamuli appears to be directed by one, and possibly, two factors. The function of the hamuli is to suspend the soft palate over the internal nares. Therefore, the width of the soft palate will directly influence the direction of the hamuli. A second possible influence involves the origin of the pterygoideus externus (= medialis) from the adjacent pterygoid fossa (Davis 1964). Changes in the robustness of this muscle might indirectly affect the hamuli. An increase in robustness (e.g., in those taxa employing a more grinding masticatory motion) may serve to direct the hamuli inwards, whereas a decrease in robustness would cause the orientation to be determined more by the hamuli's primary function. Descriptions of hamular orientation are rare, but laterally directed hamuli have been noted in *Leptonychotes* (Mivart 1885), *Monachus tropicalis* (Allen 1887), and isolated phocines (Chapskii 1955a, 1967). Chapskii (1967) hints at an apparent shift from medially to laterally directed hamuli during the ontogeny of *Phoca largha*. Otherwise, only *Erignathus* has been noted to possess medially directed hamuli (Chapskii 1955a).

All fissiped caniforms are characterized by hamuli situated in the midline, with apomorphic deviations from this occurring only in the pinnipeds. Medially directed hamuli occur convergently in *Mirounga* spp., and either in *Odobenus* alone (DELTRAN optimization), or in the otarioids as a whole (ACCTRAN optimization). However, like all other pinnipeds, none of these taxa are known to employ a grinding style of mastication. Laterally directed hamuli are peculiar to the phocids, appearing independently in *Halichoerus* and the clade of monachines internal to *Hydrurga* (with *Monachus monachus* reversing to the plesiomorphic condition). A relative reduction of the pterygoideus externus has not been described in phocids (see Howell 1928; Bryden 1971; Piérard 1971), and it is not known if these taxa possess a proportionately wider soft palate.

*71) relationship of ethmoid to pterygoid process of basisphenoid on ventral surface of skull: 0 = does not contact pterygoid; 1 = contacts pterygoid (pers. obs.).

With recoding, this character was included in character #72.

72) degree of contact between ethmoid and pterygoid process of basisphenoid: 0 = narrow; 1 = greater than or equal to medium breadth; 9 = none (pers. obs.).

Among the Caniformia, the pterygoid process of the basisphenoid extends to different degrees both anteriorly and posteriorly (see character #73 for the latter). In the anterior direction, we observed two major mechanisms for preventing (or minimizing) contact between the ethmoid and the pterygoid process. Either the two elements did not approach each other closely, or if they did, then contact was prevented by the presence of the pterygoid canal (sensu Burns & Fay 1970). In some cases, the canal was too small to prevent contact absolutely and merely minimized the amount of contact (e.g., changing a potentially broad contact to a narrow one).

The apomorphic condition where the ethmoid and pterygoid process contact one another is generally restricted to the Pinnipedia, being found only in *Procyon* (state 1) and *Martes* (polymorphic between all states) among fissipeds. The early evolution of this character in the pinnipeds is difficult to ascertain due to the polymorphism present in the otarioids. However, the likely scenario is for a narrow contact ancestrally, with the otariids showing a tendency to lose this contact while the phocids and *Odobenus* independently continue to increase its width (as under ACCTRAN optimization). Parallel trends to reducing the contact between the ethmoid and pterygoid are also found in the phocids. A narrow contact is regained in *Phoca largha* and *Pusa* spp., while contact is lost outright in *Phoca vitulina* and the clade of *Lobodon* plus *Monachus* spp.

73) relationship between pterygoid process of basisphenoid and auditory bulla: 0 = does not extend to auditory bulla; 1 = extends to auditory bulla (Burns & Fay 1970).

The posterior extent of the pterygoid process is fairly restricted in most carnivores. Only among *Odobenus* and the phocids does it extend posteriorly to reach the auditory bulla (Burns & Fay 1970). Surprisingly, despite supporting his contention of an *Odobenus*-phocid pairing, this character was not mentioned by Wyss (1987). Our analysis indicates that only the phocids, in parallel with *Lutra* (DELTRAN optimization), unequivocally display the apomorphic condition (state 1); *Odobenus* is polymorphic for this trait. However, the additional polymorphic appearance of this trait in *Enhydra* suggests that this character might be a putative synapomorphy of the lutrines plus the pinnipeds, with the otarioids at least partially reversing to the primitive condition (ACCTRAN optimization).

74) bony constituents of wall of foramen ovale with respect to alisphenoid and squamosal: 0 = alisphenoid only; 1 = both alisphenoid and squamosal; 2 = squamosal only (pers. obs.).

Most anatomical atlases of representative carnivores indicate that the foramen ovale runs solely through the alisphenoid (e.g., Miller 1962; Davis 1964; Crouch 1969). This morphology appears to be fairly consistent throughout the carnivores (see Flower 1869). However, our observations reveal that the squamosal occasionally makes a contribution to the walls of the foramen ovale, and, in some cases, contains the foramen entirely. [A ventral contribution is also occasionally made by the pterygoid in some phocids (pers. obs.), but this is not examined here.]

Any contribution by the squamosal to the foramen ovale represents a derived condition. This is largely diagnostic of, and restricted to, the monachines, with the subfamily characterized ancestrally by a partial squamosal contribution (state 1). This state, which arises independently in *Martes* and *Pusa caspica*, is retained throughout the monachines, with a purely squamosal contribution being found in *Monachus* spp. and convergently in *Cystophora*.

Basicranial region (43 characters)

The conservative nature of the basicranial region has rendered it very important historically for elucidating the phylogenetic relationships of various caniform taxa (e.g., Turner 1848; Flower 1869; Pocock 1921; Segall 1943; McLaren 1960b; Hunt 1974). It may be particularly valuable with respect to the phocids, as this region of the skull apparently

shows a lower degree of intergeneric and intraspecific variation than other regions of the skull (King 1966). However, despite its apparent stability, there is still the potential for some homoplasy within this region (see Hunt & Barnes 1994). Important basicranial characters involve such landmarks as the carotid canal [the distinguishing feature of arctoid carnivores (Wyss 1988a)], the auditory bulla, and various other processes and foramina of the region.

75) visibility of the mastoid process in dorsal view: 0 = not visible; 1 = visible (Wyss 1988a).

The condition whereby the mastoid process is visible in dorsal view is unusual among mammals, being restricted primarily to the phocines, with some convergent appearances in the monachines (King 1966; Burns & Fay 1970; Ray 1976b; de Muizon 1982a, Wyss 1988a). Typically, *Monachus* spp. and/or *Ommatophoca* are implicated (King 1966; Ray 1976b; de Muizon 1982a), although Burns & Fay (1970) indicated that it occurred in about half of all the monachine specimens they examined. These convergent appearances can apparently be eliminated if the character is recoded to examine for the presence or absence of a medially curving mastoid crest (de Muizon 1982a), or, equivalently, of a distinct oblique ridge formed by the mastoid process (Burns & Fay 1970). The presence of either of these synonymous features is apparently exclusive to the phocines (Burns & Fay 1970; de Muizon 1982a). We retained the less precise coding in an effort to determine the exact distribution of this character among the Monachinae.

As indicated above, the apomorphic morphology (state 1) is primarily restricted to, and universal among, the phocines. *Pusa caspica* and *Pusa sibirica* appear to be independently losing this trait, primarily due to a reduction in the size of the mastoid process. Convergent appearances of this trait were consistently observed in only two monachines, *Monachus monachus* and *Ommatophoca*, as well as in the fissiped *Procyon*.

76) relative shape of basioccipital-basisphenoid region: 0 = concave; 1 = flat; 2 = convex (Wyss 1988a).

Burns & Fay (1970) noted that all phocines share a relatively flat to convex basioccipital-basisphenoid region, as opposed to the strongly concave form in monachines. Wyss (1988a) extended this last observation to include the otarioids, adding that he believed the concave morphology to be primitive (presumably for the pinnipeds), and therefore not synapomorphic for the monachines. We have modified the coding of this character somewhat by dividing the state "flat to convex" into its two constituent morphologies.

In contrast to Wyss (1988a), our analysis indicates that a flat morphology is primitive for the arctoids (the plesiomorphic state for the caniforms is equivocal), as well as for the pinnipeds. Instead, a concave basioccipital-basisphenoid region is a derived trait, possibly characterizing the monachines ancestrally (ACCTRAN optimization). However, it is only manifested in *Mirounga* spp. among extant species; the remaining monachines largely emulate the supposed phocine condition, displaying either the flat (*Ommatophoca*) or convex morphologies (*Hydrurga, Lobodon, Monachus* spp.), or both *(Leptonychotes)*. The phocines tend towards retention of the flat morphology, with only *Halichoerus* and *Phoca vitulina* developing the convex condition. This latter state also appears convergently in *Canis* and *Enhydra*.

*77) postglenoid (= glenoid) foramen in squamosal: 0 = absent; 1 = present (Wozencraft 1989).

With recoding, this character was included in character #78.

78) size of postglenoid (= glenoid) foramen in squamosal: 0 = small; 1 = medium; 2 = large; 9 = absent (Wozencraft 1989).

The pinnipeds are supposedly unique among the Caniformia in their lack of a postglenoid foramen (Wozencraft 1989), a structure that is present and generally quite conspicuous in all other members of this group (Flower 1869). However, Mivart (1885) has noted the presence of a small postglenoid foramen throughout the pinnipeds, while Berta (1991) considers it to be either vestigial or absent within this group. The form of the foramen appears to be quite variable in *Histriophoca*, from not being universally present to occasionally being shifted laterally so as to be just anterior to the external auditory meatus (Burns & Fay 1970). Our observations corroborate these last two findings, revealing that the postglenoid foramen is not universally absent in pinnipeds, but instead very much reduced and slightly displaced in position. In the phocids, the inflation of the auditory bulla (see characters #80-82), often in combination with an enlargement of the mandibular fossa, virtually eliminates the area between these structures and, as such, the foramen is generally shifted onto the posterior lip of the fossa. Occasionally, we also observed a lateral displacement of the postglenoid foramen equivalent to that noted by Burns & Fay (1970).

Although the postglenoid foramen is common throughout the caniforms (including the pinnipeds), the high degree of polymorphism displayed by this character makes for an uncertain evolutionary pathway, primarily among the outgroup taxa. The plesiomorphic condition is of a large foramen, a state which may persist through to the hypothetical ancestral monachine (DELTRAN optimization). Another scenario holds for a small foramen being a synapomorphy linking *Procyon* through to the phocids (ACCTRAN optimization). Beyond this disparity, there are features in common to the two evolutionary scenarios. A medium-sized foramen is synapomorphic for the phocines (with an independent appearance in *Procyon*), with *Histriophoca* and *Pagophilus* reverting to the plesiomorphic condition. The monachines generally possess a small foramen, as does *Pusa caspica*. Although a number of species were polymorphic for lacking the foramen, only two were consistent for this trait: *Martes* and *Hydrurga*.

79) shape of anterior edge of auditory bulla: 0 = concave; 1 = flat; 2 = convex (Ridgway 1972).

This was another character employed by Ridgway (1972) to distinguish between the genera *Cystophora* (state 1 to 2) and *Mirounga* (state 0). The plesiomorphic state is uncertain due to the autapomorphic appearance of the convex morphology in *Canis*; however, a flat morphology is both primitive and ubiquitous for the arctoids. This state is retained ancestrally in the phocids, with *Lutra, Halichoerus*, and the monachines convergently deriving a concave anterior edge. In the monachines, this morphology is often associated with an unusually robust mandibular symphysis which encroaches upon the auditory bulla. *Lobodon* plus *Monachus* spp. revert to the primitive arctoid state.

80) inflation of ectotympanic: 0 = not inflated; 1 = slightly / moderately inflated: 2 = inflated (Wozencraft 1989) (Fig.22).

As with most other carnivores, an inflated auditory bulla is common to all phocids, albeit to varying degrees (Howell 1928; Segall 1943; Hunt 1974). It ranges in size from "large" in *Leptonychotes* to "small" in *Monachus tropicalis* (King 1972). The inflated bulla of

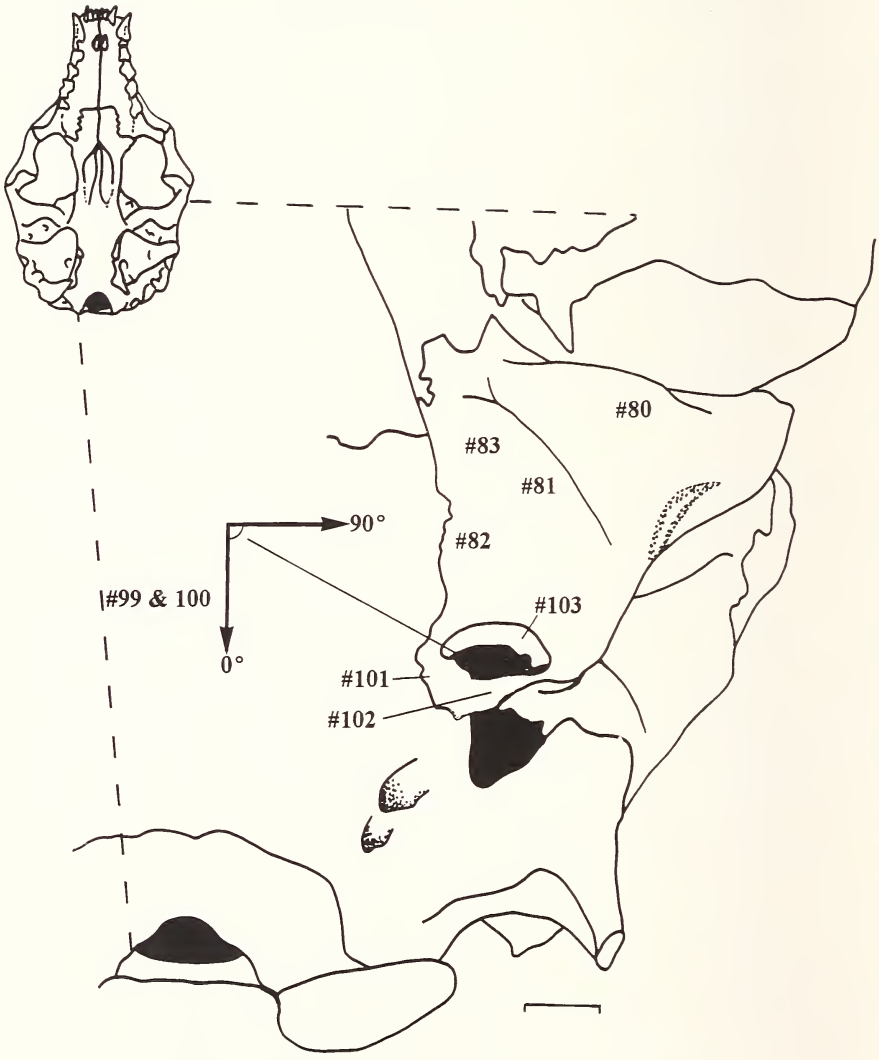

Fig.22: Ventral view of the idealized phocid left basicranial region [but based largely on *Monachus tropicalis* (USNM 102536)] (see inset) illustrating selected characters (indicated by their number; see **Character Analysis**) of this region. Anterior is towards the top of the page and lateral to the right. Scale bar equals 1 cm. Inset adapted from Lawlor (1979).

phocids clearly separates them from the non-inflated bulla of the otarioids (Howell 1928; Repenning 1972; Wyss 1987), a difference that is manifested even during fetal development (Howell 1928). We attempted to elucidate the pattern of bulla inflation using three characters from Wozencraft (1989) that identify different bullar elements. Unfortunately, differentiation between the ectotympanic and entotympanic portions of the auditory bulla is difficult among carnivores due to their high degree of fusion in the adult bulla (Repenning 1972; Hunt 1974). Differentiating between the two regions is aided in some phocids by the presence of a distinct sulcus between them (van der Klaauw 1931; Burns & Fay 1970; see character #83); however, the distinction between this character and the following two remains somewhat arbitrary. Instead, we will use these three characters to represent inflation of respective regions of the bulla (lateral, middle, and medial respectively) rather than of the elements themselves. A further problem is that the inflation of the auditory bulla is best judged internally (see Repenning 1972), but we were limited to an external examination of the bulla in almost all cases.

Despite noting that the ectotympanic forms a large percentage of the bulla in otarioids, Repenning (1972) singles phocids out from the pinnipeds for their enlarged ectotympanic portion. This is corroborated by Wozencraft (1989), who indicates that only the ursids and the otarioids lack an inflated ectotympanic among the carnivores. Again, the plesiomorphic condition for the Caniformia is uncertain; however, it is likely an ectotympanic that is not inflated, as this is the condition shared by all the outgroups except *Canis* and *Martes* (both state 1). These observations are largely in conflict with those of Wozencraft (1989). As expected, an inflated ectotympanic (state 2) is reasonably common among phocids, but more so among phocines where it is ancestral and retained by all members except *Pagophilus* (state 0), and possibly *Histriophoca* (states 0, 1, and 2) and *Phoca vitulina* (states 0 and 1). Among monachines, state 2 characterizes only *Hydrurga* and the clade of *Lobodon* plus *Monachus* spp. In this last clade, a slightly inflated ectotympanic is a synapomorphy of *Monachus schauinslandi* and *Monachus tropicalis*.

81) inflation of caudal entotympanic along anteroposterior axis: 0 = not inflated; 1 = slight / moderate inflation; 2 = inflated (Wozencraft 1989) (Fig.22).

Hunt (1974) indicates that inflation of the caudal entotympanic is primarily responsible for the overall inflation of the carnivoran bulla. Yet, the contribution of the entotympanic to the auditory bulla among the arctoids is quite variable. It is the greatest in some phocines, comprising two-thirds to three-quarters of the bulla (Burns & Fay 1970), but generally comprises about two-thirds of the bulla in most phocids (Repenning 1972). Mustelids display an intermediate ratio, usually comprising more than one-third of the bulla (King 1983), while the entotympanic contributes little more than the formation of the carotid canal in otarioids (Repenning 1972). Among the carnivores, Wozencraft (1989) lists canids, procyonids, mustelids (excluding lutrines and mephitines), and phocids as possessing a caudal entotympanic inflated along the anteroposterior axis. Our observations agree with this distribution, although the polarity is reversed for the caniforms. Here, an inflated entotympanic is plesiomorphic, and its presence in the phocids (except for *Hydrurga* and *Monachus schauinslandi*, which independently obtain state 1) represents a reversal.

82) inflation of medial portion of caudal entotympanic: 0 = not inflated; 1 = slight / moderate inflation; 2 = inflated (Wozencraft 1989) (Fig.22).

According to Wozencraft (1989), the inflation of the medial portion of the entotympanic possesses the same distribution as the previous character: canids, procyonids, mustelids (excluding lutrines and mephitines), and phocids. However, in this case, our observations disagree slightly with those of Wozencraft (1989). Again, the polarity is reversed for the caniforms, with the inflated morphology being primitive. As well, this condition is largely retained throughout the caniforms, with only *Ursus* (state 1), the otarioids (state 0), and the monachines *Hydrurga, Monachus* spp., and *Ommatophoca* (states 0 or 1, or both) showing a reduction in the inflation of this portion of the entotympanic.

83) distinct sulcus dividing ectotympanic and entotympanic portions of auditory bulla: 0 = absent; 1 = present (Burns & Fay 1970) (Fig.22).

In discussing the auditory bulla of *Histriophoca*, Burns & Fay (1970) noted the presence of a distinct sulcus dividing the ectotympanic and entotympanic regions in a number of specimens. This sulcus is also very distinct in *Cystophora*, and is apparently present, although less distinct, in other phocids as well (van der Klaauw 1931). Although we observed this sulcus to varying degrees in many phocids (primarily the monachines), these seem to be the sole descriptions of this feature, except for a quick note by Howell (1928) concerning the virtual obliteration of the suture in a fetal *Phoca vitulina*. However, the apomorphic expression of a distinct sulcus is uncommon, being found only in *Martes* and the clade of *Monachus schauinslandi* and *Monachus tropicalis*. Although numerous isolated pinniped specimens possessed rudimentary sulci (coded here as a polymorphism), this morphology was only manifested at the species level for *Odobenus, Hydrurga*, and *Leptonychotes*.

84) relationship between auditory bulla and petrosal: 0 = does not cover petrosal; 1 = covers petrosal (King 1966; Wyss 1988a).

King (1966) initially noted the condition whereby the petrosal projects into the posterior lacerate foramen of phocines and *Monachus* spp. (also de Muizon 1982a). As this condition also obtains in *Odobenus* and certain fossil pinnipeds, Wyss (1988a) regarded this morphology as likely being primitive at some level higher than the phocids. As exposure of the petrosal is a mechanism to improve hearing underwater (Repenning 1972; de Muizon 1982a), this condition is, at best, primitive at the level of the lutrines, but more likely the pinnipeds as a whole. De Muizon & Hendey (1980) regarded the converse state (state 1) as diagnostic of the lobodontines. However, Ray (1976b) urged caution in employing both this character and related ones, as the complexity of the general region does not lend itself to being reduced to simple characters. As well, the polymorphic nature of *Leptonychotes* and *Ommatophoca* for this character, and the difficulties in distinguishing between the petrosal and mastoid in this region create additional problems (Ray 1976b).

Our analysis indicates an opposite polarity for this character to that of Wyss (1988a). Here, state 1 is primitive among the Caniformia and the derived condition is found convergently between the lutrines, all phocines, and *Monachus* spp. The occurrence of the derived condition in both *Enhydra* and *Lutra* may represent either convergent evolution

(DELTRAN optimization), or a synapomorphy necessitating a reversal to the plesiomorphic condition ancestrally for the pinnipeds (ACCTRAN optimization).

85) relationship between auditory bulla and paroccipital process: 0 = does not reach process; 1 = reaches (or very closely approaches) process (Wyss 1988a).

In acknowledgement of the limitations of the previous character mentioned by Ray (1976b), Wyss (1988a) proposed this related feature. Wyss (1988a) noted that the condition where the auditory bulla covers the petrosal is coincidental with the bulla extending posteriorly to nearly contact the exoccipital. Through our observations, we have modified this character still further, asking if the bulla contacts (or at least closely approaches) the major process of the exoccipital, the paroccipital process. Naturally, contact with the paroccipital process, or lack thereof, is tied in with inflation of the auditory bulla, particularly the posterior region (Flower 1869). Most fissipeds are noted for a relatively inflated bulla (Segall 1943; Repenning 1972; Hunt 1974), and this is sufficient in *Canis* and *Procyon* to cause contact between it and the paroccipital process (Davis 1964). This condition is also obtained in feloids (Turner 1848; Wozencraft 1989), but not in ursids, where the bulla is relatively flat (Turner 1848; Segall 1943; Davis 1964). However, contact is maintained in the ursids by a bony ridge running between the bulla and the paroccipital process (Segall 1943). In contrast, Flower (1869) holds that the paroccipital process is generally separate from the auditory bulla in most arctoids.

The plesiomorphic state for the Caniformia is inferred to be one where the auditory bulla and paroccipital process are in contact. Together with its occurrence in felids, this suggests that this state is primitive at the level of the carnivores. The derived condition, where contact is lost, describes a synapomorphy linking the lutrines with the pinnipeds. However, this distribution is contingent on our equating of the bony ridge possessed by ursids with the primitive condition, where the auditory bulla and the paroccipital process are directly in contact.

86) groove separating mastoid bulla and petrosal: 0 = absent; 1 = present (King 1972; de Muizon 1982a).

There is some uncertainty on our part as to what feature de Muizon (1982a) was attempting to diagnose with this character. The region around the posterolateral edge of the auditory bulla is punctuated by a number of grooves, pits, and foramina in phocids [see characters #87, 88, 108, and 109; Figs.6 and 7 in de Muizon (1982a)], and de Muizon's description makes it unclear as to which exact feature he is referring. As de Muizon (1982a) describes the transition of a pit unique to *Histriophoca* and *Pagophilus* into a groove in *Cystophora*, the likely candidate is the "digastric pit" of Burns & Fay (1970: 374). However, as we were unable to find any evidence of either the pit or the groove in the above taxa, we settled instead for a definition synonymous with the stylomastoid groove of King (1972). In other words, the definition we employed is the literal one: is there a groove running between the posterolateral edge of the auditory bulla and the petrosal?

The groove, as we have defined it, is an apomorphic trait found only in *Odobenus* and all phocids. [However, this is dependent upon the assessment of state 0 by PAUP for non-lutrine fissipeds. In these taxa, the plesiomorphic contact between the auditory bulla and the paroccipital process (see previous character) made it impossible to determine the

condition of this character and they were coded as "unknown".] Although this distribution appears to support Wyss's (1987) contention of an *Odobenus*-phocid clade (also Wyss & Flynn 1993), the interpretation of this distribution here is for either parallel origins in each of the two taxa (DELTRAN optimization), or for a synapomorphy of the pinnipeds as a whole, with *Zalophus* reversing to re-obtain the primitive condition (ACCTRAN optimization).

*87) hypomastoid fossa (found along posteroventral edge of the auditory bulla and containing the stylomastoid groove): 0 = absent; 1 = present (Wozencraft 1989).

With recoding, this character was included in character #88.

88) depth of hypomastoid fossa: 0 = shallow; 1 = medium; 2 = deep; 9 = absent (Wozencraft 1989).

The presence of a hypomastoid fossa was employed by Wozencraft (1989) to unite the otarioids with the ursids. Perhaps the key to this outcome is the defining of the fossa so as to be dependent on the presence of a petromastoid ridge running between the paroccipital and mastoid processes (see character #89). However, our observations revealed that these two features are not always coincidental, with many phocids possessing an apparent hypomastoid fossa while lacking the petromastoid ridge. Thus, we modified Wozencraft's (1989) coding of the character so that the two features now appear as separate characters here (see character #89).

The presence of a hypomastoid fossa is primitive among the Caniformia; however, it is difficult to be more specific due to the high incidence of polymorphism in the basal arctoids. *Canis* is characterized by a shallow fossa, while *Procyon* and *Ursus* may share a deep fossa (ACCTRAN optimization only). The apomorphic loss of the fossa unites *Martes*, the lutrines, and the pinnipeds. Several reversals towards a redevelopment of the fossa occur in the pinnipeds, primarily among the otarioids (states 0 or 2) and the monachines. For the monachines, a shallow fossa is regained internal to *Mirounga* spp., and is increased to a deep fossa in *Monachus* spp. Only scattered phocines regain the hypomastoid fossa: *Cystophora* (states 1 and 2), *Erignathus* (states 0 and 1), and possibly *Pagophilus* and *Phoca vitulina* (both states 0 and 9)

89) distinct petromastoid ridge connecting paroccipital and mastoid processes: 0 = absent; 1 = present (Wozencraft 1989).

As mentioned above, this feature rather than the hypomastoid fossa (see character #88) was perhaps the key to Wozencraft (1989) uniting the otarioids (also Mivart 1885; Howell 1928) with the ursids (also Davis 1964). In contrast, de Muizon (1982b) (as cited in Wyss 1987) has used the reduction or outright loss of the petromastoid ridge as an apomorphic trait uniting the mustelids (exclusive of leptarctines and melines, but including lutrines) with the phocids. Wyss (1987) discounts this assessment, noting that the mastoid region in phocids is highly modified, thus rendering the comparison with the mustelid region somewhat dubious. As well, apparent petromastoid ridges have been described for *Leptonychotes, Monachus* spp., and *Ommatophoca* (Mivart 1885; Wyss 1987). Complicating all this is the often highly variable form of the petromastoid ridge. We observed that it rarely takes the form of a distinct ridge, but is instead usually fairly low and rounded. As well, in taxa such as *Canis* and *Procyon*, what might be called the

petromastoid ridge is, like the paroccipital processes (see character #85), pressed against the auditory bulla. For our purposes, we required the petromastoid ridge to be separate from the auditory bulla, although not necessarily a prominent, obvious structure.

Our analysis supports Wozencraft (1989), with an apomorphic petromastoid ridge occurring only in *Ursus* and the otarioids, although this is due here to parallel evolution rather than uniting the two groups as a synapomorphy. However, it should be noted that the acceptance of the analogous structure in *Canis* and *Procyon* as a proper petromastoid ridge supports a scenario in keeping with that of de Muizon (1982b), with the loss of the ridge being a synapomorphy linking the mustelines, lutrines, and the pinnipeds as a whole, with the otarioids reversing to re-obtain the plesiomorphic condition.

*90) source of "paroccipital" process: 0 = occipital; 1 = occipital and mastoid; 2 = mastoid (Burns & Fay 1970).

This character reflects the confusion created by having numerous synonyms for a given structure present in the literature. Burns & Fay (1970:375) are entirely correct in saying that the paroccipital processes of phocids should more properly be referred to as the paramastoid processes, as they are "of the occipital and near the mastoid." However, this is also true for all caniforms we have so far examined. It would appear that this process has been historically misnamed (e.g., Turner 1848; Flower 1869; Mivart 1885; Howell 1928; Davis 1964; DeBlase & Martin 1981). Perhaps the least confusing alternative would be to use the non-origin specific synonym "jugular process" (e.g., Miller 1962; Crouch 1969). However, Burns & Fay (1970) suggest that the use of this term be restricted to those instances when the paroccipital and paramastoid processes are confluent or connected by a petromastoid ridge (see character #89). Other than being an unnecessary restriction, this suggestion confuses matters further as it is unclear exactly what the term "paroccipital process" refers to in such a definition (but likely the mastoid process). An overriding complicating factor in all this is that the processes in this general region appear to be distinguished on the basis of which muscles originate from them, rather than on their specific bone of origin. As the paroccipital process serves at least as a partial origin for the digastric muscle (Howell 1928; Miller 1962; Davis 1964; Crouch 1969; Bryden 1971; King 1972), perhaps in one of the early descriptions of this muscle, its process of origin did, in fact, originate on the mastoid, but near the occipital. This character was excluded because of all of this confusion.

91) morphology of paroccipital processes: 0 = absent; 1 = elongated ridges; 2 = bumps / pillars (pers. obs.).

Flower (1869) comments that the general form of the arctoid paroccipital process is one of a roughly triangular bony prominence projecting posterolaterally from the skull which is generally separate from the auditory bulla (but see character #85). Yet, the morphology of the paroccipital process, and its relationships with other structures of the basicranial region, does appear to possess phylogenetically useful variation within the arctoids. Some of this variation is summarized in this and the following three characters.

One immediate observation of the general form of the paroccipital processes (other than simply their presence versus absence) is that they are laterally compressed in some taxa to take on the form of elongated ridges. Among the fissiped caniforms, Turner (1848)

indicates this to be the case solely for the canids. In the phocids, the general pattern is for the paroccipital processes to be poorly developed, if not virtually absent, in the phocines and well developed in the monachines. The exceptions are *Erignathus* and *Mirounga* spp., which take on the characteristics of the opposite subfamily (Bryden 1971; King 1972). The paroccipital processes of the otarioids are well developed, and are confluent with the mastoid process via the petromastoid ridge (Howell 1928; Wozencraft 1989; see character #87).

The lateral compression of the paroccipital processes is a synapomorphy linking the lutrines and the pinnipeds. Several independent reversals to the primitive caniform morphology of rounded processes occur within the pinnipeds: *Zalophus, Mirounga angustirostris*, and the phocines internal to *Cystophora* (with *Erignathus* reversing again to re-obtain the primitive pinniped condition). Paroccipital processes were entirely absent only for *Pusa caspica*, although *Pusa sibirica* was polymorphic for this condition.

92) size of paroccipital processes: 0 = small / not prominent; 1 = intermediate; 2 = large / prominent; 9 = processes absent (pers. obs.).

A reduction in the size of the paroccipital processes has only been indicated for the phocines (exclusive of *Erignathus*), *Mirounga* spp., and various mustelids (including the lutrines) among the caniforms (Turner 1848; Flower 1869; Bryden 1971; King 1972). The observation that the paroccipital processes are apparently lost during ontogeny in *Phoca largha* (Chapskii 1967) hints at their former presence in ancestral forms. Our observations largely bear this out. Large processes are plesiomorphic for the Caniformia, before being drastically reduced to state 0 in *Martes*, the lutrines, and the pinnipeds. The monachines, exclusive of *Mirounga* spp., are generally characterized by medium-sized processes. This occurs either as a synapomorphy of the lobodontines plus *Monachus* spp. (ACCTRAN optimization), or only of *Lobodon* plus *Monachus* spp. (DELTRAN optimization). The phocines largely retain small processes except for *Cystophora* and the clade of *Erignathus, Histriophoca*, and *Pagophilus*, which independently derive medium-sized processes. Reversals to large processes occurred only in *Zalophus, Monachus schauinslandi* plus *Monachus tropicalis*, and possibly *Hydrurga*. Again, paroccipital processes were consistently absent in *Pusa caspica*, and polymorphically so in *Pusa sibirica*.

93) relationship between paroccipital processes and mastoid bone: 0 = separate; 1 = adjacent / continuous; 9 = n/a – paroccipital processes absent (pers. obs.).

In many taxa, we noted that the paroccipital processes were not distinct, isolated structures. Other than contacting the auditory bulla (see character #85), the paroccipital processes often graded into either the mastoid bone anteriorly (more common in forms with small processes such as the Phocini), or the nuchal crest posterodorsally (see the following character). With respect to the mastoid bone, the general distribution is for it to be continuous with the paroccipital processes in *Ursus, Martes*, the otarioids, and the phocines internal to *Cystophora* (except *Pusa caspica* which obtains state 9). This could arise through parallel evolution in each of these taxa (DELTRAN optimization). However, the polymorphism of *Procyon* and *Lutra* also allows for the situation whereby state 1 is plesiomorphic for the arctoids (the condition for the caniforms being equivocal), which the otarioids and phocines (minus *Cystophora*) reverse back to after state 0 arises as a synapomorphy of the lutrines plus the pinnipeds (ACCTRAN optimization).

94) relationship between paroccipital processes and nuchal (= lambdoidal) crest: 0 = separate; 1 = adjacent / continuous; 9 = n/a – paroccipital processes absent (Hendey & Repenning 1972).

Hendey & Repenning (1972) note the tendency of the nuchal crest to become confluent with the enlarged paroccipital processes in *Monachus schauinslandi* and *Monachus tropicalis*. However, at best, this apomorphic feature only arose independently as polymorphisms for *Monachus monachus* and *M. tropicalis*, although we noted it in isolated specimens of *Lobodon, Mirounga leonina*, and *Monachus schauinslandi*. Again, processes were consistently absent in *Pusa caspica*, and polymorphically so in *Pusa sibirica*.

95) relative size and shape of posterior lacerate foramen: 0 = not confluent with petrobasilar fissure; 1 = confluent with petrobasilar fissure; 9 = petrobasilar fissure absent (Wyss 1988a).

In most mammals, the posterior lacerate foramen is roughly circular and restricted to an area posteromedial to the auditory bulla. As well, in carnivores, the fissure between the auditory bulla and both the basioccipital and basisphenoid, the petrobasilar fissure, typically disappears during development (Wyss 1988a). However, the phocines, exclusive of *Erignathus*, are peculiar in that the posterior lacerate foramen expands anteromedially to become confluent with the patent petrobasilar fissure (King 1966; Wyss 1988a). We observed that most of the taxa examined here possess at least a crack between the basioccipital and basisphenoid bones and the bulla (see also character #96). Although not a true fissure, we have equated this crack with a reduced petrobasilar fissure. Thus, the state identified by King (1966) and Wyss (1988a) for the phocines is due to the confluence of both an expanded posterior lacerate foramen and an expanded (rather than patent) petrobasilar fissure.

This slight difference in interpretation accounts for state 1 being the most common state here, and primitive at the level of the Arctoidea (the case for the caniforms being equivocal). [The analogous state as defined by King (1966) and Wyss (1988a) was restricted to the phocines minus *Erignathus*.] The converse situation, where the posterior lacerate foramen and petrobasilar fissure are not confluent, is a synapomorphy of the monachines. State 9 was independently obtained for *Martes* and *Erignathus*, due to their parallel outright loss of the petrobasilar fissure [as described by Burns & Fay (1970) for *Erignathus*].

96) relationship between petrobasilar fissure and basioccipital-basisphenoid suture: 0 = in contact, suture unexpanded; 1 = in contact, suture greatly expanded and confluent with fissure; 9 = petrobasilar fissure absent (pers. obs.).

As in the previous character, this character attempts to summarize some of the bone loss occurring in the ventral basicranial region of phocids. In the phocines, numerous perforations are present in this region, most of which display high intraspecific variability (Burns & Fay 1970; King 1972). One of the few features that we observed consistently at the species level is of a medial expansion of the basioccipital-basisphenoid suture away from the auditory bulla. In most cases, this expanded suture was confluent with the expanded petrobasilar fissure, resulting in a great deal of bone loss in the basicranial area. As hinted at by King (1966), this apomorphic condition (state 1) is found only in *Pusa*

spp. However, acceptance of this as a synapomorphy of its members *(P. caspica* and the clade of *P. hispida* and *P. sibirica)* depends on the resolution of the polytomy in this region. Again, state 9 was independently obtained for *Martes* and *Erignathus*.

97) visibility of posterior opening of carotid canal in ventral view: 0 = not visible; 1 = visible; 9 = carotid canal absent (Wyss 1988a).

In concert with character #101, Wyss (1988a) viewed this feature as a synapomorphy of the phocines minus *Erignathus*. Wyss (1988a) tied the apomorphic conditions of both features (state 0 in both) to the characteristic inflated bulla of phocines. However, it is unclear to us why these same conditions would not also occur in most arctoids, which also generally possess inflated bullae (Segall 1943; Repenning 1972; Hunt 1974; see also characters #80-82). Our observations also revealed that the two features (i.e., characters #97 and 101) were not necessarily coincident with one another; thus, they appear separately in this analysis. As well, we were uncertain as to whether the phrase "visibility of the carotid canal" referred to the canal in general, or to the foramen of the canal. Thus, we draw a distinction between these two meanings here, and each appears as a separate character. Visibility of the carotid canal here refers to whether evidence of a carotid canal could be glimpsed in ventral view. Wyss (1988a) implies that the carotid canal is visible in most arctoid carnivores except for the clade mentioned above.

In most taxa, including virtually all phocines, a carotid canal could be ascertained in ventral view; only *Ursus, Martes, Zalophus*, and *Pusa hispida* failed to demonstrate evidence of the canal in ventral view. [As the carotid canal is diagnostic of arctoid carnivores only (Wyss 1988a), the characters dealing with this feature (#97-104) do not apply to *Canis*.] Unfortunately, the polarity of this character cannot be determined due the occurrence of both states in the basal arctoids, so Wyss's (1988a) assessment of state 0 as the apomorphic trait cannot be verified.

98) visibility of foramen of posterior opening of carotid canal in ventral view: 0 = not visible; 1 = visible; 9 = carotid canal absent (Wyss 1988a).

This variation on the previous character probably provides a more definitive test of Wyss's (1988a) original character. Any inflation of the auditory bulla will tend to overhang and thus obscure the foramen of the carotid canal. The previous character merely examined for any evidence of the carotid canal, which could be as little as a small divot in the posteroventral edge of the bulla.

Unlike the previous character, a polarity assessment is possible here and indicates that state 0 is plesiomorphic among arctoids [in contrast to Wyss (1988a)]. The apomorphic condition, whereby the foramen is visible in ventral view, is limited in distribution to *Enhydra* and *Hydrurga*, although *Procyon, Lutra, Odobenus*, and *Mirounga angustirostris* are polymorphic for this character.

99) direction of posterior opening of carotid canal, I: 0 = distinctly greater than 45° medially (i.e., roughly medially); 1 = roughly 45° medially; 2 = distinctly less than 45° medially (i.e., roughly posteriorly); 9 = absent (King 1972) (Fig.22).

The direction of the posterior opening of the carotid canal appears to be related to an interaction between the auditory bulla and both the basioccipital and basisphenoid bones. King (1972) notes that there is a tendency in monachines for the basioccipital and

basisphenoid to extend ventrally along the medial edge of the bulla, forcing the opening of the carotid canal posteriorly. In the phocines, this tendency is apparently absent and the carotid canal faces more medially (King 1972). If the lack of this tendency of the basioccipital and basisphenoid bones in the phocines is due to their uniquely expanded petrobasilar fissure (see character #95), then one might predict that the remaining caniforms will approximate the monachine condition.

Among the arctoid carnivores, the primitive condition is for a posteriorly facing carotid canal (the monachine condition) as postulated above. An apomorphic medial shift of the opening of the carotid canal is found universally in the phocines [although it may not characterize them ancestrally (DELTRAN optimization)], and convergently in *Martes* (state 0) and *Lobodon* (state 1). Most phocines (including *Erignathus*, which lacks an expanded petrobasilar fissure) display a medially directed canal. An intermediate shift (state 1) is only found convergently in *Cystophora* and the clade of *Histriophoca* plus *Pagophilus*.

*100) direction of posterior opening of carotid canal, II: 0 = roughly 90° (i.e., medially); 1 = distinctly greater than 45° medially but distinctly less than 90°; 2 = roughly 45° medially; 3 = distinctly less than 45° medially but distinctly greater than 0°; 4 = roughly 0° (i.e., posteriorly); 9 = carotid canal absent (pers. obs.) (Fig.22).

This character represents an inferior coding (with respect to character #99) of the direction of the posterior opening of the carotid canal, as it is too particular and thus limits the number of potential synapomorphies. Therefore, it was abandoned in favour of the previous character.

101) posteromedial bony shelf of auditory bulla extending from aperture of carotid canal to posterior lacerate foramen: 0 = absent; 1 = rudimentary or present; 9 = carotid canal absent (Wyss 1988a) (Fig.22).

As with character #97, Wyss (1988a) described the absence of the bony shelf in phocines, exclusive of *Erignathus* [a distribution echoed by Burns & Fay (1970)], as being an apomorphic trait attributable to the inflated auditory bulla of this group. However, if this is the case, the similar possession of an inflated bulla in most other arctoid carnivores should cause the shelf to be absent in these forms as well, rendering this feature a symplesiomorphy of the group. Our analysis indicates this to be the case, with the apomorphic possession of the shelf being limited to *Erignathus* and the clade of the lobodontines plus *Monachus* spp. Of this latter group, *Monachus monachus* re-obtains the primitive morphology. The shelf may be developing in the polymorphic *Enhydra*.

102) dorsal wall of carotid canal: 0 = open; 1 = closed; 9 = carotid canal absent (pers. obs.) (Fig.22).

Our observations of the basicranial region of the otarioids revealed a peculiar morphology involving the carotid canal and the posterior lacerate foramen. In all the phocids and most other arctoids we examined, the carotid canal is completely encircled by the caudal entotympanic of the auditory bulla, so that its opening is separate from the posterior lacerate foramen. However, in the otarioids, the dorsal wall (which is rotated more medially in *Odobenus* and the phocids *Mirounga* spp. and *Ommatophoca*) of the carotid canal is incomplete, and its foramen is confluent posterodorsally (or posteromedially for

Odobenus) with the posterior lacerate foramen. As this condition also occurs in some basal arctoids *(Martes* and *Ursus)*, the primitive state for the arctoids becomes equivocal. However, all reconstructions favour independent origins of this trait between the otarioids (where it is synapomorphic), *Martes*, and *Ursus*.

103) unidentified bone encircling posterior opening of carotid canal: 0 = absent; 1 = present; 9 = carotid canal absent (pers. obs.) (Fig.22).

This character describes a feature peculiar to, and apparently universal among, *Monachus schauinslandi*. In this species, the posterior opening is at least partially encircled (but usually completely so) by a bone distinct from the remainder of the auditory bulla. The identity of this bone is uncertain. It may represent a second caudal entotympanic element, as found in, or postulated for, most of the close phocid relatives advocated here: ursids, otarioids, lutrines, and mephitine mustelids (see Hunt 1974). It has been suggested that a second element may arise during the ontogeny of the Type B bulla possessed by phocids (Wincza 1896; as cited in Hunt 1974). Or, it may merely represent an unfused portion of the single caudal entotympanic. To our knowledge, despite being apparent in some photographs of the basicranial region of *M. schauinslandi* (e.g., King and Kenyon 1961), this feature has never been described before.

104) opening of carotid canal in auditory bulla: 0 = anterior or anteroventral to posterior lacerate foramen; 1 = adjacent to posterior lacerate foramen; 9 = carotid canal absent (Wozencraft 1989).

An anterior opening of the carotid canal relative to the posterior lacerate foramen diagnoses all arctoids except ursids, which uniquely possess an adjacent placement within this group (Wozencraft 1989). This distribution was observed here; however, the basal location of *Ursus* (which possesses state 1 as an autapomorphy) within the arctoids renders the plesiomorphic state of this character equivocal for this group. As well, *Mirounga leonina* and *Ommatophoca* were polymorphic for this character.

*105) median lacerate foramen in auditory bulla: 0 = absent; 1 = present (pers. obs.).

With recoding, this character was included in character #106.

106) size of median lacerate foramen: 0 = small; 1 = medium; 2 = large; 9 = absent (pers. obs.).

The median lacerate foramen (= anterior lacerate foramen, external carotid foramen) appears to be present in most caniforms except *Ailuropoda*, which is polymorphic for this feature (Segall 1943; Story 1951; Davis 1964). Our observations indicate that its apomorphic loss (or perhaps just its lack of distinctiveness from the musculotubular canal lying immediately lateral to it) occurs in *Mirounga* spp. (see character #105). In the remaining caniforms, the foramen is of a variable size. The plesiomorphic condition is for an intermediate size (state 1), as found in *Canis* and *Ursus*, but a small foramen is quickly derived after this. DELTRAN optimization holds that this latter condition is largely retained, with independent derivations of a medium-sized *(Monachus schauinslandi)* or large foramen (otarioids, *Cystophora*, and *Ommatophoca*), and of its outright loss (*Mirounga* spp.). In contrast, ACCTRAN optimization indicates that a large foramen is synapomorphic for the pinnipeds and retained ancestrally for each phocid subfamily.

Beyond this, independent reversals to state 0 occur within each subfamily (and twice within the monachines), with *Mirounga* spp. again uniquely deriving state 9.

107) mastoid lip in region of external cochlear foramen: 0 = absent; 1 = rudimentary or present (Wyss 1988a).

The presence of a mastoid lip that partially obscures the posterior wall of the auditory bulla and the external cochlear foramen (see the following character) has been noted as being diagnostic of the lobodontines (Repenning & Ray 1977; de Muizon & Hendey 1980; de Muizon 1982a; Wyss 1988a). However, while the mastoid lip is a derived feature, it is not unique to, or indeed universal among, the lobodontines. Instead, it appears convergently in *Leptonychotes, Lobodon*, and the clade of *Pusa sibirica* plus *Pusa hispida*, with polymorphic appearances in *Enhydra, Lutra, Halichoerus*, and *Pusa caspica*.

108) external cochlear foramen: 0 = open; 1 = closed; 9 = absent (de Muizon 1982a).

The external cochlear foramen, first identified and named by Burns & Fay (1970), is unique to phocids, linking the round window to the external surface of the skull to facilitate underwater hearing (Repenning 1972; de Muizon 1982a). Although Repenning (1972) states that the foramen is present in all phocids to various degrees, there is a tendency towards the closure of the foramen in each subfamily to provide the resistance to increased water pressure needed for deep diving (de Muizon 1982a). In the Monachinae, the external cochlear foramen is covered by a mastoid lip in the lobodontines (de Muizon 1982a; Wyss 1988a; but see previous character). In the Phocinae, the closure is accomplished in *Halichoerus, Phoca* spp., and *Pusa* spp. by an expansion of the auditory bulla (de Muizon 1982a). However, this closure is less absolute than that of the lobodontines (de Muizon 1982a), so that Burns & Fay (1970) merely note the presence of a reduced foramen in these same phocines.

The external cochlear foramen first arises as a synapomorphy of the phocids. (The assessment of it being missing in the remaining caniforms is a posteriori, as there is no objective way to distinguish between the states "absent" and "closed" based on gross examination of the skull.) The parallel trends towards the closure of the foramen in each phocid subfamily were observed, although the distributions are modified somewhat. In the monachines, it is generally closed in the lobodontines and *Monachus tropicalis*. This latter observation requires either *Monachus monachus* and *Monachus schauinslandi* to convergently re-open the foramen (DELTRAN optimization), or *Monachus tropicalis* to reverse from a state 0 synapomorphy of *Monachus* spp. (ACCTRAN optimization). In the phocines, parallel closure occurs in *Erignathus* and *Pusa sibirica*, the latter possibly as a synapomorphy with *Pusa hispida* (ACCTRAN optimization).

109) relationship between stylomastoid and auricular foramina: 0 = confluent / common; 1 = intermediate; 2 = separate; 9 = auricular foramen absent (de Muizon 1982a).

In noting the "dumbbell-shaped" morphology of the stylomastoid foramen of most phocines, Burns & Fay (1970) realized that this condition actually represents a confluence between the anterior stylomastoid foramen and the posterior auricular foramen, the latter of which is apparently unique to the phocids. These two foramina share a wide range of morphologies, from completely separate to partially confluent, as in the phocines (Burns & Fay 1970), to completely confluent as an auriculostylomastoid foramen in *Mirounga* spp.

(de Muizon 1982a). Our analysis indicates that the auricular foramen first appears ancestrally in the phocids (again, assuming that it is absent in the remaining caniforms), and is separate from the stylomastoid foramen. This condition is retained throughout both subfamilies, with their confluence into a single auriculostylomastoid foramen (state 0) arising in parallel in *Mirounga* spp. and *Pusa sibirica*. This latter observation is another a posteriori assessment, based on the assumption that these phocids still possess the auricular foramen and have not reverted to the primitive condition for the caniforms, in which it is absent.

110) relationship of tympanohyal and stylomastoid foramen: 0 = separated; 1 = closely associated (Wozencraft 1989).

This and the following character deal with the relationship of the tympanohyal to the stylomastoid foramen. As the hyoid apparatus is rarely referred to in the literature, and even more rarely preserved in museum collections (due, in part, to the tympanohyal being cartilaginous), we were forced to rely on the observations of Wozencraft (1989) for both this and the following character. Among the caniforms, a close association between the tympanohyal and the stylomastoid foramen is plesiomorphic. The apomorphic condition, where the two are separated, is a lutrine-pinniped synapomorphy, with an independent origin in the ursids. Observations by Burns & Fay (1970) may contradict this for the phocids; however, the degree of the contradiction depends on the definitions of "closely associated" versus "separated" employed by Wozencraft (1989).

111) location of tympanohyal relative to stylomastoid foramen: 0 = anterior; 1 = posterior (Wozencraft 1989).

An anterior placement of the tympanohyal relative to the stylomastoid foramen is a synapomorphy of the phocids (Wozencraft 1989). This morphology has been corroborated in the phocids by Burns & Fay (1970).

112) position of petrosal relative to intracranial ridges of basioccipital continuous anteriorly with the dorsum sellae: 0 = widely separate; 1 = intermediate; 2 = closely adjacent (Wozencraft 1989) (Fig.21).

As originally coded by Wozencraft (1989), this character dealt with the nature of the petrosal-basioccipital suture, with a note that it was usually not visible from the ventral side of the skull. A wide separation was held to define the clade of the ursids plus the otarioids (Wozencraft 1989). However, the exact nature of this character is elusive, as this character is not apparent from an examination of Wozencraft's (1989) citation for it (van der Klaauw 1931), which appears to refer to either the petrobasilar fissure (see characters #95 and 96), or something analogous to character #84. In any case, in keeping with Wozencraft's (1989) apparent intention (i.e., determining the intracranial approach of the petrosal to the basioccipital), we modified the character slightly to how it now appears above.

The condition where the petrosal and intracranial basioccipital ridges are closely adjacent is plesiomorphic among the caniforms, with any apomorphic separation of the two structures generally characterizing the pinnipeds only (*Ursus* is polymorphic between all three states). This is largely manifested by a wide separation (the ancestral pinniped

condition), with only *Pusa sibirica* obtaining an intermediate separation. Reversals to the plesiomorphic condition occur in both subfamilies: *Pagophilus* and *Phoca vitulina* among phocines, and *Hydrurga* and *Lobodon* among monachines. For the two monachines, this occurs either due to convergence (DELTRAN optimization), or as a synapomorphy followed by a reversal for the remaining, more terminal taxa (ACCTRAN optimization). Thus, with the addition of the phocids, the distribution of our coding largely matches that of Wozencraft (1989). This is due to either the two codings being synonymous (i.e., our coding matches the intent of his original definition) or correlated in some manner.

113) relative size of dorsal region of petrosal: 0 = unexpanded; 1 = intermediate; 2 = expanded (Wyss 1988a).

Several mechanisms allow for the pinnipeds to improve their underwater hearing: creating an external cochlear foramen (see characters #107 and 108), exposing the petrosal externally (see character #84), increasing the size of the promontorium, and/or generally increasing the size of the petrosal (Repenning 1972; Repenning & Ray 1977; de Muizon 1982a). This character and the following one each deal with mechanisms employed by the phocids to increase the size of the petrosal. As defined by Repenning & Ray (1977), the dorsal part of the petrosal is that region above the line extending from the vestibular aqueduct across the top of the cochlear aqueduct to the anterodorsal surface of the petrosal apex. This region is clearly expanded in virtually all known phocids (fossil and Recent), except *Monachus schauinslandi*. The largely unexpanded dorsal region in this phocid (to the exclusion of the other members of *Monachus*) has been used as evidence to support its status as the most primitive of all phocids (Repenning & Ray 1977; Wyss 1988a).

An unexpanded dorsal region of the petrosal is indeed plesiomorphic among the Caniformia. However, our observations reveal that the apomorphic, expanded morphologies (states 1 and 2) have a wider distribution than previously stated, characterizing such non-phocids as *Martes, Ursus*, and *Odobenus* [for *Odobenus*, at least, this morphology may be associated with a greatly expanded petrosal apex (Repenning 1975; see following character)]. All three represent convergent evolution (together with the phocids), although ACCTRAN optimization indicates that the expanded condition may be a synapomorphy of the pinnipeds, with *Zalophus* reversing to re-obtain the primitive condition. Among the phocids, an expanded dorsal petrosal is universal except for several monachines: *Ommatophoca, Monachus schauinslandi, Monachus tropicalis* (all state 0), and *Monachus monachus* (state 1). This may represent a synapomorphy of the group, with a reversal in *Lobodon* and further derivation in *Monachus monachus* (ACCTRAN optimization), or independent evolution in the various clades (DELTRAN optimization).

114) relative size and shape of petrosal apex: 0 = absent / unexpanded and pointed; 1 = intermediate; 2 = dorsoventrally thickened and bulbous (Wyss 1988a).

Overlapping the previous character somewhat, this character specifically examines the very apex of the dorsal region of the petrosal. Wyss (1988a) notes that the phocids exclusive of *Monachus* spp. are united by a massive expansion of the apex, causing it to present a dorsoventrally thickened, bulbous morphology. This morphology has been held to provide a greater sensitivity to sound underwater (Hendey & Repenning 1972), and is in contrast to the condition in most other carnivores and the otarioids, where the apex is unexpanded

and pointed. In *Monachus* spp., the petrosal apex is intermediate between these two extremes (de Muizon 1982a; Wyss 1988a). Wyss (1988a) only employed the two extreme states (homologizing the condition in *Monachus* spp. with the non-phocid condition); however, there is cause to recognize the intermediate state. Only the phocines and *Mirounga* spp. are accurately described as possessing a globular apex. In the lobodontines, the enlarged apex is more of a lower and broader structure (Hendey & Repenning 1972; Ray 1976b).

The distinction between the phocid subfamilies seems to be minimal, however. Despite claims by Repenning (1975), *Odobenus* was not held to possess an expanded apex (but was noted to have an expanded dorsal petrosal region in general; see previous character), and an expanded apex was synapomorphic for the phocids only and generally retained throughout the family. Only *Lobodon* (state 1) and *Monachus* spp. (state 0) showed predispositions towards returning to a plesiomorphic, unexpanded petrosal apex.

115) roof of internal auditory meatus: 0 = reduced; 1 = full internal auditory meatus (Wyss 1988a).

The phocids are distinguished from the remaining pinnipeds (and most other mammals) by the complete reduction of the internal auditory meatus, resulting in separate entrances for the facial and auditory nerves (Gray 1905; Wyss 1988a). Wyss (1988a) further noted that in conjunction with this reduction, the petrosal lip forming the roof of the internal auditory meatus is absent, or, in the case of *Monachus* spp., reduced to a bony spur. We have chosen to separate these two features dealing with the status of the internal auditory meatus and the condition of its former roof (see the following character), as they apparently diagnose synapomorphies of different sets of taxa. For this character, the reduction of the internal auditory meatus is indeed a synapomorphy uniting all phocids.

116) bony spur of roof of internal auditory meatus: 0 = absent; 1 = present (Wyss 1988a).

As indicated under the previous character, the reduction of the internal auditory meatus in phocids typically results in the complete loss of the petrosal lip forming its roof. However, in *Monachus* spp., a bony spur remains and projects medially above the canals of the facial and auditory nerves (Wyss 1988a). Given the typical basal placement of this genus in the phocids, Wyss (1988a) has implicated this morphology as an intermediate stage leading to the complete loss of the petrosal roof. Instead, the possession of a bony spur (or more properly, the incomplete reduction of the petrosal roof) appears to be a synapomorphy linking *Monachus schauinslandi* and *Monachus tropicalis*, although we also noted it in isolated specimens of *Halichoerus, Leptonychotes, Mirounga leonina, Monachus monachus, Pusa caspica*, and *Pusa hispida*. The plesiomorphic condition, where the spur is absent, is really a combination of two distinct morphologies. In the remaining phocids, the spur is truly absent and the petrosal lip is typically quite broad, but with virtually no medial expansion. In some taxa (e.g., *Mirounga leonina*), even the lip is lacking entirely. Meanwhile, in non-phocids, the spur is "present", but not visible, as it is subsumed within the complete petrosal roof of the internal auditory meatus.

117) inflation of bullar chamber: 0 = not inflated; 1 = inflated (Wozencraft 1989).

As implied by Repenning (1972), this character provides a truer measure of the inflation of the auditory bulla (see characters #80-82). However, as we were limited in most cases

to a gross external examination of the bulla, we have again relied upon the data in Wozencraft (1989) for this character. Numerous authors have noted the inflated bulla of caniforms (Howell 1928; Repenning 1972; Hunt 1974), and this condition is indicated here to be plesiomorphic and prevalent for the group; only the lutrines and *Zalophus* lack an inflated bullar chamber. This latter situation occurs either convergently in each species (DELTRAN optimization), or as a synapomorphy of the lutrines followed by a reversal to the primitive condition for the pinnipeds, with *Zalophus* independently obtaining state 0 (ACCTRAN optimization).

Bony tentorium and bony falx (5 characters)

Although the bony tentorium and the bony falx are found throughout the carnivores, their potential systematic value has generally been ignored. Using characters from both features, Nojima (1990) argued for a diphyletic origin of the pinnipeds, grouping the otarioids with the ursids and the phocids with the mustelids. However, the common possession of an "A Type II" bony tentorium between ursids, otarioids, and probably all mustelids, to the exclusion of all phocids except *Histriophoca* and *Pagophilus* (Nojima 1990), renders this conclusion somewhat doubtful. As well, Wyss (1987) discounts a phocid-mustelid pairing based on tentorial characters due to the high variability of the bony tentorium throughout the arctoids.

118) contribution of parietal to bony tentorium: 0 = none / processus tentoricus absent; 1 = contributes (Nojima 1990).

The bony tentorium is composed of two main elements projecting from the occipital and from the parietal (processus tentoricus) (Nojima 1990). Among the caniforms, only phocids, possibly exclusive of *Histriophoca* and *Pagophilus*, lack a processus tentoricus, and hence lack a parietal contribution to the bony tentorium (Nojima 1990). Here, the apomorphic lack of a parietal contribution to the bony tentorium is a synapomorphy of the phocids. Furthermore, this condition is universal for the group, including *Histriophoca* and *Pagophilus*.

119) contribution of parietal to bony falx: 0 = none; 1 = contributes; 9 = bony falx absent (Nojima 1990).

As with the bony tentorium, the parietal also occasionally contributes to the bony falx. Of those taxa where the bony falx is present (see character #121), Nojima (1990) indicates a parietal contribution only in the otarioids and the ursids. In phocids, the bony falx is derived exclusively from the occipital (Nojima 1990). This is largely borne out here. A parietal contribution to the bony falx is plesiomorphic in caniforms, characterizing both *Canis* and *Ursus*. Beyond this, the bony falx is initially absent before reappearing, albeit with no contribution from the parietal, as a synapomorphy linking *Lutra* with the pinnipeds. Within this group, a parietal contribution occurs independently in *Zalophus* (possibly the otarioids as a whole; ACCTRAN optimization), *Histriophoca*, and *Mirounga angustirostris* (possibly *Mirounga* spp. as a whole; ACCTRAN optimization).

120) ventral extension of bony tentorium: 0 = does not approach floor of braincase; 1 = approaches dorsal region of petrosal; 2 = approaches or contacts floor of braincase (Nojima 1990).

The morphologies of the bony tentorium and bony falx (see the following character) appear to largely depend on the parietal contribution to each (see characters #118 and 119). In those forms lacking such a contribution (i.e., the phocids generally), both structures are reduced. The bony tentorium, in particular, is reasonably compact in such cases, and fails to reach the floor of the braincase (Nojima 1990). In contrast, the bony tentorium is much expanded in those species with a processus tentoricus, frequently extending to the petrosal apex, or, more commonly, to the floor of the braincase (Wyss 1987; Nojima 1990). However, this relationship is not absolute, as canids obtain state 0 despite possessing a processus tentoricus (Nojima 1990). As well, we noted that a ventral extension to the petrosal apex was only found in the phocids, and not in any forms with a distinct processus tentoricus [although the presence of this structure in *Histriophoca* and *Pagophilus* is unclear (see Nojima 1990)].

The somewhat aberrant morphology of the canids causes the primitive state for the caniforms to be equivocal. However, as Nojima (1990) indicates that all feloids possess state 2, this state is likely plesiomorphic for the caniforms, if not the carnivores as a whole. This condition is retained throughout the caniforms, before the phocids derive state 0 ancestrally. This very much reduced bony tentorium is common to all phocids, with the phocines *Halichoerus* and *Histriophoca* (possibly as a synapomorphy with *Erignathus* and *Pagophilus*; ACCTRAN optimization) independently deriving a tentorium that approaches the petrosal apex.

121) morphology of bony falx proper: 0 = absent; 1 = sail-shaped; 2 = vertical; 3 = inverse sail (Nojima 1990; pers. obs.).

In carnivores, the bony falx is not nearly so ubiquitous as the bony tentorium, being found only in *Ursus* spp. and the pinnipeds (Nojima 1990). Despite this limited distribution, the bony falx does possess several distinct morphologies that our observations reveal are generally dependent on the contribution of the parietal (see character #119). A sail-shaped bony falx, in which the falx arcs posterodorsally from the anterior junction of the two halves of the bony tentorium, is generally restricted to the phocids, which generally lack a parietal contribution to the falx. The contribution of the parietal in the otarioids fills out the bony falx, causing it to extend directly dorsally (state 2) or to arc anterodorsally (state 3). However, these trends are again not absolute, with most phocid specimens obtaining state 2. As well, although the parietal frequently contributes to states 2 and 3, this was not necessarily always the case. In *Ursus*, the bony falx is only partial, despite a parietal contribution, and fails to reach the dorsal wall of the skull (Nojima 1990). We have chosen to distinguish this partial bony falx (see the following character) from the bony falx proper examined here. So, together with the complete lack of a bony falx in the remaining ursids (Nojima 1990), *Ursus* has been scored as lacking the bony falx.

The possession of a bony falx is a derived characteristic within the Caniformia, and is a synapomorphy of *Lutra* and the pinnipeds. For this group, a vertical bony falx is primitive and largely retained throughout. A further derivation to the reduced sail-shaped morphology occurs a number of times within the phocids: *Cystophora, Halichoerus, Monachus schauinslandi, Pusa caspica*, and *Pusa sibirica*. DELTRAN optimization holds these all to be independent derivations, whereas ACCTRAN optimization indicates this

state to be a synapomorphy of the phocines, before a reversal back to the vertical morphology occurs internal to *Halichoerus*. Independent origins of the sail shape in *Monachus schauinslandi* and in each of the two pusids account for the remaining appearances of this state under this latter scenario. The inverse sail morphology never appeared consistently at the species level, being observed only as a polymorphism with state 2 in *Histriophoca* and *Ommatophoca*.

122) partial bony falx: 0 = absent; 1 = present (Nojima 1990; pers. obs.).

The partial bony falx is a small projection originating from the anterodorsal junction of the two halves of the bony tentorium. Although it and the bony falx proper are apparently mutually exclusive (Nojima 1990), we have occasionally noted the simultaneous presence of these two structures. It may be that the partial bony falx indicates the former or future presence of an inverse sail-shaped bony falx, a morphology that was never consistently observed for any species (see previous character). The two structures possess similar orientations and were never observed coincidentally. In any case, we list the partial bony falx as a character separate from the morphology of the bony falx proper. As noted before, Nojima (1990) lists this feature as occurring only in *Ursus*.

Our analysis indicates that the partial bony falx is actually a primitive feature within the Caniformia. It is found in *Canis* and *Ursus* (both of which lack a bony falx proper), before becoming lost in the remaining caniforms (although *Enhydra* and *Erignathus* are polymorphic for this trait).

Dorsal braincase (4 characters)

In carnivores, this region is largely devoid of phylogenetically informative features due to it being almost completely covered by the enlarged temporalis muscle (Davis 1964). Understandably then, most of the few useful characters are associated with this muscle in some manner.

123) shape of fronto-parietal suture: 0 = flat; 1 = unilobe; 2 = bilobed; 3 = trilobed or greater (Burns & Fay 1970).

The fronto-parietal suture is often more than just a simple flat suture. In *Histriophoca* and *Pagophilus*, the suture is usually trilobed, while in *Phoca* and *Pusa* it is bilobed (Burns & Fay 1970). We also noted an additional, unilobular morphology in many species. However, this character is not as straightforward as it would first appear, as the suture rarely appears as a clear-cut example of one of the states listed above. Very often, the lobes are compacted together, and an arbitrary judgment must be made as to what constitutes a main lobe as opposed to an accessory lobe of the main one. As well, individual specimens of *Hydrurga* and *Ommatophoca* confounded this problem still further by having an open anterior fontanelle, something that is apparently quite common in adult *Ommatophoca* (King 1969, 1972, 1983; Ray 1976b). The systematic value of this character is limited still further by the high amount of intraspecific polymorphism.

Despite these numerous problems, a reasonably clear pattern emerged from this character. A flat suture is plesiomorphic, with a unilobular suture diagnosing the mustelids (including the lutrines) plus the pinnipeds. *Zalophus* reverses to the plesiomorphic condition. A multilobed suture is peculiar to the phocids, which are united ancestrally and generally

throughout by a bilobed morphology (albeit polymorphically with states 0 and/or 1 in many species). A unilobular suture is independently regained in *Pusa hispida* (possibly as a synapomorphy with *Pusa sibirica*; ACCTRAN optimization) and the clade of *Monachus schauinslandi* plus *Monachus tropicalis*. The trilobed condition occurs uniquely for the clade of *Histriophoca* plus *Pagophilus*.

*124) separate temporal ridges: 0 = widely spaced; 1 = approximately in midline; 9 = absent (pers. obs.).

During our observations, we noted that in place of a sagittal crest, many specimens possessed distinct paired ridges on either side of the midline. However, this character more properly belongs with characters of the sagittal crest, as separate temporal ridges merely represent incipient crests (Doutt 1942; King 1972). As well, the distance between the ridges appears to be an age-dependent feature (and therefore of questionable systematic value), with the ridges converging on the dorsal midline with increasing age (Doutt 1942). Thus, with recoding, this character was included in character #126.

*125) sagittal crest: 0 = absent; 1 = present (Ridgway 1972).

With recoding, this character was included in character #126.

126) size of sagittal crest: 0 = absent, but separate temporal ridges present; 1 = small; 2 = medium; 3 = large; 9 = absent (Ridgway 1972; pers. obs.).

The sagittal crest is a notoriously labile feature, being subject to both age variation and sexual dimorphism. We tried to minimize the latter problem by scoring a species as possessing a sagittal crest if a crest was consistently present in either sex. The development of sagittal crests in very old individuals from the convergence of the separate temporal ridges has been noted by both Doutt (1942) and King (1972). This potential problem was minimized by examining only adult individuals.

Although reasonably common throughout most of the Carnivora, there are conflicting reports of the manifestation of sagittal crests among the phocids. Ridgway (1972) only mentions distinct crests for *Hydrurga* and *Leptonychotes*, to which Ray (1976b) would apparently add *Mirounga* spp. and *Phoca vitulina* (also Chapskii 1955a). However, de Muizon & Hendey (1980) indicate reduced crests in *Leptonychotes* and *Lobodon*. King (1972) claims crests of various sizes (but typically small) for all phocids except the three smallest genera *(Histriophoca, Pagophilus*, and *Pusa)* which possess widely spaced temporal ridges. *Halichoerus* apparently develops a strong crest with old age (Chapskii 1955a), as does *Monachus tropicalis* (Allen 1887).

This study indicates that sagittal crests are possessed primitively within the Caniformia, before being reduced to separate temporal ridges in going to the pinnipeds. *Canis* is unusual in possessing a large sagittal crest (only found elsewhere in *Zalophus*), with the sagittal crests typically being small in fissiped caniforms. Separate temporal ridges arise as a synapomorphy of the pinnipeds (and possibly *Lutra* as well; ACCTRAN optimization), with a convergent appearance in *Procyon*. Within the phocids, the trend is towards the loss of even this feature. This is limited in the phocines (*Erignathus* and *Pusa sibirica* only), but more widespread in the monachines, diagnosing *Mirounga angustirostris* and the clade of *Lobodon, Monachus* spp., and *Ommatophoca*. However, small sagittal crests

are regained in *Monachus monachus*, and as a synapomorphy of *Hydrurga* and *Leptonychotes*, before both the sagittal crests and temporal ridges are lost outright. *Halichoerus* and *Monachus tropicalis* also possessed sagittal crests, albeit as a polymorphism with other states.

Teeth (23 characters)

Despite the great importance attached to teeth by mammalian systematists, they are only infrequently used as a systematic tool within the phocids. Much of this arises from the trend toward homodonty in the pinnipeds, which largely eliminates many potential morphological characters, combined with a high intraspecific variability in the phocids at least (King 1966, 1983; Hillson 1986). Indeed, many studies tend to concentrate on attributes of the dentition as a whole (e.g., tooth formulae), rather than on the morphology of individual teeth (e.g., Burns & Fay 1970; de Muizon 1982a). Additionally, as Chapskii (1955a) has noted for the phocines, the systematic value of phocid teeth may be limited by the high functional demand placed upon them by food specialization within the group and the resultant rapid evolution arising from this (also Davies 1958b). However, teeth characteristics have played a major role in Chapskii's (1955a, 1967) attempts to sort out phocine phylogeny.

127) number of upper incisors in one-half of jaw: 0 = zero; 1 = one; 2 = two; 3 = three (King 1966).

Other than the possession of an inflatable nasal apparatus, the incisor formula was a key character used to support the Cystophorinae, with both *Cystophora* and *Mirounga* possessing a 2/1 pattern, as opposed to the 3/2 pattern of phocines or the 2/2 pattern of monachines (Scheffer 1958; King 1964, 1966; Ridgway 1972). However, beyond the convergent *Cystophora* and *Mirounga* (see King 1966), the incisor formula seems to describe synapomorphies of both phocid subfamilies, although the phocines may retain the ancestral phocid number (McLaren 1975). In an effort to generate synapomorphies with some of the outgroup taxa (which are generally 3/3), we have split the incisor formula into two characters, corresponding to the number of upper and lower incisors respectively.

Only *Odobenus, Cystophora*, and the monachines diverge from the plesiomorphic condition of three upper incisors. *Odobenus* uniquely derives one upper incisor (Mivart 1885; Cobb 1933), although it is commonly misidentified as a postcanine due to its position and the unusual pattern of dental succession in this animal (King 1983; see Cobb 1933). The condition of two upper incisors in *Cystophora* and the monachines represents either a case of convergence (DELTRAN optimization), or a synapomorphy of the phocids, with the remaining phocines reversing to re-obtain the primitive condition (ACCTRAN optimization).

128) number of lower incisors in one-half of jaw: 0 = zero; 1 = one; 2 = two; 3 = three (King 1966).

As with the upper incisors (see previous character), three lower incisors are plesiomorphic for the caniforms. However, the reduction to two incisors now occurs either as a synapomorphy of the lutrines plus the pinnipeds, with a reversal to the plesiomorphic

condition in *Lutra* (ACCTRAN optimization), or as a synapomorphy of the pinnipeds, with a parallel appearance in *Enhydra* (DELTRAN optimization). Two lower incisors are largely retained throughout the pinnipeds, with further reductions occurring only in *Cystophora, Mirounga* spp., and possibly *Leptonychotes* (all convergent origins of state 1), and *Odobenus* (state 0).

*129) morphology of incisors: 0 = peg-like; 1 = unicuspate; 2 = caniform; 3 = complex (pers. obs.).

This character was abandoned after numerous unsuccessful attempts to accurately summarize incisor shape in phocids. Any differences between the given states are highly subjective and, as implied by characters #131 and 132, overall incisor morphology is not constant within the series of a given species, causing additional coding difficulties.

130) shape of upper incisors in cross-section: 0 = round; 1 = intermediate; 2 = (strongly) laterally compressed (Wyss 1988a).

Among phocids, the phocines (excluding *Erignathus*) are distinguished by the lateral compression of their upper incisors (Burns & Fay 1970; Wyss 1988a). However, with the additional observations of rounded incisors in the monachines and strongly compressed incisors in the non-phocid carnivores, Wyss (1988a) interpreted the rounded condition as a synapomorphy of the phocids, with the phocines, exclusive of *Erignathus*, reversing to the primitive compressed morphology. *Histriophoca* may be polymorphic for this character (Burns & Fay 1970; but see Scheffer 1960).

Although the above distribution is largely supported for the pinnipeds, only *Martes* and *Enhydra* were observed to possess strongly compressed incisors among the fissipeds. In contrast to Wyss (1988a), this renders rounded incisors as plesiomorphic for the caniforms, and also makes the ancestral state for the phocids equivocal. Under DELTRAN optimization, the primitive rounded incisors are retained through to the phocids, with the laterally compressed incisors typical of the phocines becoming a synapomorphy of most of this group. Meanwhile, ACCTRAN optimization holds for sequential reversals between states 0 and 2, so that laterally compressed incisors become ancestral for the phocids, and the trend to rounded incisors describes a synapomorphy of most of the monachines. Other than *Erignathus*, only *Cystophora* (states 0, 1, and 2) and *Phoca vitulina* (state 1) depart from the typical phocine pattern. Among the monachines, truly rounded incisors are only typical of *Lobodon, Mirounga* spp. and *Monachus* spp. The remaining taxa possess either state 1 *(Leptonychotes* and *Ommatophoca)* or state 2 *(Hydrurga).*

131) relative size of upper incisors: 0 = outermost incisor about equal in size to remaining incisor(s); 1 = outermost incisor of much greater size than remaining incisor(s); 9 = n/a – only one upper incisor present per quadrant (de Muizon & Hendey 1980).

In the phocids, the outermost upper incisor is typically larger than the remaining one (King 1983). This is especially true of the lobodontines, where this enlarged tooth, together with the upper canine, aids in opening breathing holes in the sea ice (de Muizon & Hendey 1980). The lack of an enlarged outermost upper incisor in the fossil lobodontine *Homiphoca* led de Muizon & Hendey (1980) to postulate this condition as primitive for the monachines. However, our observations indicate that this morphology (i.e., state 0) is

actually apomorphic, and is found in only *Procyon* and *Pagophilus* among extant caniforms. With its single upper incisor, *Odobenus* uniquely obtained state 9.

132) relative size of lower incisors: 0 = outermost incisor about equal in size to remaining incisor(s); 1 = outermost incisor of much greater size than remaining incisor(s); 9 = n/a – one or fewer lower incisors present per quadrant (Scheffer 1960).

In contrast to the previous character, the condition whereby the lower incisors are all of about equal size possesses a much wider distribution and is, in fact, plesiomorphic for the caniforms. State 9 tends to be indicated as a synapomorphy of the pinnipeds due to its presence in *Odobenus, Cystophora*, and *Mirounga* spp. However, this is likely due to convergent evolution between the three taxa, as was indicated for the lower incisor formula (see character #128) upon which this character is indirectly based. Instead, in noting that most phocids obtain a larger outermost incisor [as noted in *Histriophoca* by Scheffer (1960) and *Homiphoca* by de Muizon & Hendey (1980)], we propose this state as a synapomorphy of the pinnipeds, with *Zalophus* reversing to the primitive caniform condition. Among phocids, only *Lobodon* and *Pusa sibirica* (possibly as a synapomorphy with *Pusa hispida*; ACCTRAN optimization) likewise reverse to state 0.

133) displacement of incisors (upper or lower): 0 = absent – all in line with one another; 1 = present – incisor series slanted; 9 = n/a – incisors absent or singular (Allen 1887; Hendey & Repenning 1972).

Typically, the incisors are positioned in line with the remaining teeth along the curvilinear tooth row. Presumably, this configuration aids in the efficient dissipation of biting forces. However, a slight posterior displacement of the lower medial incisor relative to the incisor row has been noted in most phocids, including the fossil lobodontine *Homiphoca* (Allen 1887; Hendey & Repenning 1972). Often, this displacement only applies to the roots, with the medial incisors tending to be oriented more horizontally so that their crowns line up with those of the other incisors (Allen 1887). We additionally noted that the equivalent condition can occur in the upper incisors as well, albeit extremely rarely. Although this apomorphic displacement of the incisors is present in individual specimens of most phocid species, it only manifests itself at the species level for a non-phocid, *Lutra*. However, together with *Enhydra*, both *Monachus monachus* and *Monachus schauinslandi* are polymorphic for this trait. This character was inapplicable for *Odobenus* only.

134) procumbency of incisors (upper or lower): 0 = absent; 1 = present; 9 = n/a – upper or lower incisors absent (de Muizon & Hendey 1980).

Several phocid taxa possess the morphology whereby the upper (and less frequently the lower) incisors are angled anteriorly (i.e., are procumbent). This feature is apomorphic and is associated with three of the four lobodontines – *Leptonychotes, Lobodon*, and *Ommatophoca* (de Muizon & Hendey 1980) – a distribution supported here. This represents a synapomorphy of these taxa together with *Monachus* spp., which reverts to the primitive condition.

In *Leptonychotes*, this feature together with the large caniform morphology of the incisors (see character #131) and canines function as an ice ream to keep breathing holes open in the winter (Bertram 1940; King 1972; de Muizon & Hendey 1980; Kooyman 1981c). The procumbent incisors of *Lobodon* and *Ommatophoca* are more likely associated with

feeding, as neither taxon is known to actively maintain breathing holes (Bertram 1940).

135) number of upper postcanines: 0 = three; 1 = four; 2 = five; 3 = six (pers. obs.).

The trend to homodonty in the cheek teeth (with the concomitant loss of the carnassial set) of the pinnipeds makes distinguishing within and between the premolars and molars difficult, if not functionally unnecessary. Thus, the cheek teeth are usually collectively referred to as the postcanines. However, differentiating between the postcanines is possible, as four premolars and one molar per quadrant (for a total of five postcanines) have been noted for most phocines, as well as for the monachines *Homiphoca, Leptonychotes*, and *Mirounga leonina* (Chapskii 1955a; de Muizon & Hendey 1980; Burns 1981; Ling & Bryden 1981; Stewart & Stewart 1987). This condition is likely constant (and ancestral) throughout the phocids at least, although Bertram (1940) indicates that the pattern in *Leptonychotes* and *Lobodon* may be one of three premolars and two molars per quadrant. Despite the ease of differentiating between the cheek teeth in fissiped caniforms, we likewise refer to them collectively as postcanines in an effort to identify synapomorphies with the pinnipeds.

The most common condition in the caniforms is for five upper postcanines. *Canis* and *Procyon* obtain state 3, which may be symplesiomorphic (DELTRAN optimization), or independently obtained from an equivocal root for the caniforms (ACCTRAN optimization). *Odobenus* and *Enhydra* are autapomorphic for states 0 and 1 respectively. As noted by King (1983), *Zalophus* is polymorphic between states 2 and 3, a condition which is reflective of the otariids when viewed at the family level (King 1983). A sixth upper postcanine (which was interpreted as M^2) occurs frequently in *Halichoerus* (Burns & Fay 1970), but this was not supported here.

136) number of lower postcanines: 0 = three; 1 = four; 2 = five; 3 = six; 4 = seven (pers. obs.).

As with the upper postcanines, the assessment of the plesiomorphic condition is again equivocal, being either six *(Martes, Procyon*, and possibly *Ursus)* or seven (*Canis* only) postcanines. However, the lutrines plus the pinnipeds are united by a synapomorphic reduction to five postcanines, with *Odobenus* uniquely reducing this further to three postcanines. Four postcanines were never consistently obtained at the species level.

137) morphology of postcanines: 0 = peg-like / unicuspate; 1 = triconodont; 2 = multicuspate (de Muizon & Hendey 1980).

The wide variety of postcanine morphologies occurring within the phocids ranges from the heavy, robust postcanines of *Monachus* spp. to the weak, often loosely rooted, ones of *Erignathus* and *Ommatophoca* (King 1983). *Lobodon* is frequently noted for its intricate, sieve-like multicuspate postcanines which are used to strain euphausiid shrimp (Bertram 1940; Kooyman 1981a). Yet, despite this range, the postcanines of most phocids can be traced to one form, that of the triconodont morphology, which is typified by a major middle cusp with smaller to subequal cusps flanking it anteriorly and posteriorly. This form is typical of the phocines (Ridgway 1972) and is postulated to be primitive for the phocids, being found in such putative ancestors as *Paragale* and *Potamotherium* (Hendey & Repenning 1972; de Muizon & Hendey 1980). The extant phocids are characterized by the modification of this basic triconodont form, either through the loss

of one or both of the accessory cusps, the formation of additional accessory cusps (typically posteriorly), or both (Doutt 1942; Ridgway 1972; de Muizon & Hendey 1972; see characters #138 and 139). In *Erignathus*, the diagnostic tooth wear is so extreme as to frequently obliterate the triconodont morphology of the postcanines (Chapskii 1955a; Burns 1981; King 1983). All these variations on the triconodont theme were still classified as triconodont, so long as such an origin could be reasonably established.

The plesiomorphic condition of multicuspate postcanines was found in all fissiped outgroups. This is reduced in the pinnipeds, but the ancestral form is equivocal between states 0 and 1. The otarioids largely obtain peg-like or unicuspate postcanines, although *Zalophus* is polymorphic between states 0 and 1. This latter observation accords with the assessment that accessory cusps represent a derived feature in the otariids (Repenning & Tedford 1977). Most phocids display triconodont postcanines, which develop either ancestrally for the family as a whole (ACCTRAN optimization), or convergently in each subfamily, with the phocids primitively retaining the equivocal pinniped ancestral state (DELTRAN optimization). Only *Lobodon* (state 2) and *Mirounga leonina* (state 0, possibly as a synapomorphy of *Mirounga* spp.; ACCTRAN optimization) fail to exhibit triconodont postcanines. The unicuspate teeth of *M. leonina* appear to develop from the fusion of the individual cusps of a triconodont precursor (pers. obs.).

138) tendency to form additional cusps in triconodont postcanines: 0 = absent; 1 = present; 9 = n/a – postcanines not triconodont (Chapskii 1955a).

As mentioned above, the triconodont morphology tends to show a high degree of variation from the basic (idealized) pattern. In most cases, the exact morphology of the postcanines is associated with prey type (Chapskii 1955a; Davies 1958b). This and the following two characters attempt to diagnose any systematic trends in this variation. The tendency to form additional accessory cusps in triconodont teeth is primarily manifested in the addition of small fourth cusp (and, occasionally, a very small fifth cusp) posteriorly, although an additional anterior cusp is possible. This multicuspate condition has been implicated in the retention of actively moving prey items (Chapskii 1955a). Additional accessory cusps have been variously noted for most of *Histriophoca, Pagophilus, Phoca* spp., and *Pusa* spp. (Doutt 1942; Chapskii 1955a). Chapskii (1955a) indicates that an additional cusp may also be formed, albeit very rarely, in *Erignathus*.

This character applies only to three distantly related clades within the phocids: the phocines (with and without the polymorphic *Cystophora*), *Hydrurga*, and *Monachus* spp. [Together with similar distributions in the following two characters, this could be interpreted to support independent origins of the triconodont morphology in each phocid subfamily (see previous character). As well, the indication that the plesiomorphic state 9 is ancestral for the polymorphic *Zalophus* hints at a convergent origin for triconodont postcanines in otariids (also Repenning & Tedford 1977).] The distribution of this character is complicated and shows no clear pattern under either optimization criterion. However, the tendency to gain additional accessory cusps was consistently present in two main groups: *Monachus schauinslandi* (possibly together with *Monachus tropicalis*; ACCTRAN optimization), and *Phoca* spp. plus *Pusa* spp. Likewise, the lack of the tendency was found in three clades: *Monachus monachus, Halichoerus*, and *Erignathus* plus *Histriophoca* plus *Pagophilus*.

139) tendency to lose accessory cusps in triconodont postcanines: 0 = absent; 1 = present; 9 = n/a – postcanines not triconodont (Chapskii 1955a).

The other variant on the triconodont morphology is to lose some or all of the accessory cusps, a tendency associated with a change in diet to softer foods (Chapskii 1955a). Occasionally, this loss is so extreme that the tooth appears to be unicuspate, as in *Halichoerus* or *Leptonychotes* (Mivart 1885; Chapskii 1955a; Ridgway 1972). Other taxa noted for the loss of the accessory cusps include *Phoca* spp. (Ridgway 1972) and, to varying degrees of severity, *Histriophoca* (Chapskii 1955a; Scheffer 1960). State 9 is plesiomorphic for this character. The trend toward losing the accessory cusps is a synapomorphy of the phocines (with and without *Cystophora*), and virtually universal, missing only in *Pusa sibirica* (possibly as a synapomorphy with *Pusa hispida*; ACCTRAN optimization). In those monachines where this character is applicable, the tendency appears only in *Monachus monachus*, and is lacking in *Hydrurga* and *Monachus schauinslandi* (possibly as a synapomorphy with *Monachus tropicalis*; ACCTRAN optimization).

140) size of accessory cusps in triconodont or multicuspate postcanines: 0 = small, continuous with major cusp; 1 = larger, distinct from major cusp; 9 = n/a – postcanines not triconodont or multicuspate (de Muizon 1982a; pers. obs.).

Triconodont postcanines may occur convergently in both the phocines and monachines (see character #137). This is somewhat corroborated by the different morphologies of the accessory cusps in applicable phocines (state 0), and in *Hydrurga* and *Lobodon* among the monachines (state 1) (de Muizon 1982a). A *Hydrurga-Lobodon* pairing among lobodontines has frequently been advocated on the basis of their distinctive postcanine morphology (Hendey 1972; de Muizon & Hendey 1980; de Muizon 1982a; King 1983). We have limited the distribution of this character to the pinnipeds (automatically rendering state 9 as plesiomorphic), and to those pinnipeds with triconodont or multicuspate teeth in particular. Apomorphic, small accessory cusps are universal among the phocines, with and without *Cystophora*. Both apomorphic states are found in the monachines: state 0 for *Monachus* spp. at least, possibly as a synapomorphy of the clade *Lobodon, Monachus* spp., plus *Ommatophoca* (ACCTRAN optimization); and state 1 for *Hydrurga* and *Lobodon* only. The convergent possession of state 1 in the latter two taxa speaks against their previous pairing within the lobodontines.

141) relative size of upper postcanines: 0 = all subequal; 1 = #1 (PM^1) noticeably smaller than rest, which are subequal; 2 = #5 (M^1) noticeably smaller than rest, which are subequal; 3 = #1 and #5 noticeably smaller than rest, which are subequal; 4 = #1 and/or #5 noticeably larger than rest, which are subequal; 9 = n/a – postcanine homology uncertain (Allen 1887; Scheffer 1960; de Muizon & Hendey 1980).

The relative sizes of both the upper and lower postcanines appear to contain a good deal of potential systematic information. Unfortunately, any such value is tempered by the problematic nature of both characters. In attempting to summarize the vast amount of variation present throughout the phocids, we concentrated on the first and last postcanine, which appeared to present the clearest and most consistent trends throughout the family (see also Allen 1887; Scheffer 1960). In particular, McLaren (1960a) apparently holds a small last molar to be diagnostic of *Pusa* spp.; however, this reduction of M^1 may be a

trend for all phocids except *Hydrurga* and *Lobodon* (de Muizon & Hendey 1980). Unfortunately, a coding based on the first and last postcanines is limited to the phocids only, due to the generally different homology between the postcanines of the phocids and the outgroups (very few of which possess a 4/1 postcanine formula). Thus, the inapplicability of this and the following character for the outgroups (including the otarioids, in order to avoid biasing the results in favour of a monophyletic Pinnipedia) results in their polarities being determined to some degree by the outgroup relations entailed by the remaining characters.

The primitive condition in phocids is for all upper postcanines to be subequal in size, a state maintained ancestrally in each subfamily. The phocines internal to *Cystophora* are largely characterized by a reduction of the first postcanine only; only *Histriophoca* (state 0) and *Pusa sibirica* (state 3) deviate from this. Among monachines, there exists a tendency to decrease both the first and last postcanines in those taxa internal to *Hydrurga* [as described for *Monachus tropicalis* by Allen (1887)]. *Ommatophoca*, and possibly *Monachus monachus*, retain primitive subequal postcanines. *Mirounga* spp. is uniquely diagnosed by state 4, with the last postcanine typically being the enlarged tooth. A reduction of only the last postcanine was never consistently present at the species level.

142) relative size of lower postcanines: 0 = all subequal; 1 = #1 (PM_1) noticeably smaller than rest, which are subequal; 2 = #5 (M_1) noticeably smaller than rest, which are subequal; 3 = #1 and #5 noticeably smaller than rest, which are subequal; 4 = #1 and/or #5 noticeably larger than rest, which are subequal; 9 = n/a – postcanine homology uncertain (Allen 1887; Scheffer 1960).

This character presents much the same distribution as the previous one [and as indicated by Allen (1887) and Scheffer (1960) for *Monachus tropicalis* and *Histriophoca* respectively]. As with the upper postcanines, subequal lower postcanines represent the ancestral state for the phocids and both subfamilies. The phocines, excluding *Cystophora*, now universally share a reduced first postcanine, as does the clade of *Lobodon* plus *Monachus* spp. among monachines. The reduction of both the first and last postcanines is here limited to *Leptonychotes, Mirounga angustirostris* (possibly as a synapomorphy of *Mirounga* spp.; ACCTRAN optimization) and *Monachus tropicalis*. States 2 and 4 never appeared consistently at the species level.

143) tendency to single-rooting of upper postcanines: 0 = absent; 1 = present (de Muizon 1982a).

A tendency towards having single-rooted postcanines was noted exclusively among phocids for *Halichoerus* by de Muizon (1982a). This tendency is also strongly present, and apparently developing, in otariids (Mivart 1885; King 1983). However, this character might have a larger distribution contingent on the definition of the term "tendency". In phocids, upper postcanine #1 is invariably single-rooted, #5 double-rooted, and #2 to #4 often transitional and variable, a pattern observed in *Histriophoca* by Scheffer (1960). When postcanine #5 is single-rooted, this is more often due to its reduced size (see characters #141 and 142), than to any trend towards single-rootedness of the postcanines. Therefore, if a true tendency to single-rootedness is present, it should affect the inner postcanines, and will be scored as being present if one or more of these postcanines is consistently single-rooted within a species.

The tendency to single-rootedness of the upper postcanines is an apomorphic condition uniting the pinnipeds ancestrally, with a parallel appearance in *Ursus*. This contrasts with the opinion that the otariids possess double-rooted postcanines (except for the first) ancestrally (Repenning & Tedford 1977). However, the single-rooted morphology is only retained in the otarioids, *Cystophora, Halichoerus*, and *Mirounga* spp., before reversals to the plesiomorphic morphology occur in each phocid subfamily. The case in which all the upper postcanines were single-rooted was slightly rarer, occurring only among *Zalophus* [although M^1 is double-rooted in a number of other otariids (Repenning & Tedford 1977; King 1983)] and *Mirounga* spp.

144) tendency to single-rooting of lower postcanines: 0 = absent; 1 = present (de Muizon 1982a).

Under ACCTRAN optimization, the distribution of the tendency to single-rooting of the lower postcanines is identical to that of the upper postcanines. However, the polymorphic nature of *Cystophora* leads to another possibility, that of convergent evolution in the otarioids [thereby possibly rescuing Repenning & Tedford's (1977) hypothesis of double-rooted postcanines ancestrally in the otariids], *Halichoerus*, and *Mirounga* spp. (DELTRAN optimization). Again, single-rooting of all lower postcanines was limited to *Zalophus* and *Mirounga* spp.

145) relative size of gap between upper postcanines 4 and 5: 0 = smaller than other gaps; 1 = subequal to other gaps; 2 = larger than other gaps; 9 = n/a – postcanine homology uncertain (Ridgway 1972; pers. obs.).

Ridgway (1972) used the relative size of the gaps between the postcanines (less than versus equal to a tooth width) as a means of distinguishing between the genera *Erignathus* and *Halichoerus*. However, during our observations, we noted that the gaps between the postcanines of a given individual were not of a consistent size. Typically, it was the gap between the last two postcanines that was the discrepant one, and the character was recoded to reflect this observation. A relatively large such gap was noted for *Histriophoca* by Scheffer (1960), and for *Homiphoca* and *Leptonychotes* by de Muizon & Hendey (1980).

Again, this character was only applied to the phocids due to the difficulties of establishing postcanine homologies between the phocids and the putative outgroups. Primitively, the phocids possess subequal gaps among all the postcanines (state 1). The phocines internal to *Cystophora* largely derive a relatively enlarged gap, with only *Pagophilus* and *Pusa hispida* re-obtaining subequal gaps. Virtually all monachines retain the primitive phocid morphology, with only *Leptonychotes* paralleling the phocine condition.

146) crowding of postcanines (upper and/or lower): 0 = not touching / overlapping; 1 = touching or overlapping (Ridgway 1972).

This character is to some degree an age-dependent one. In phocids, the deciduous dentition is shed or resorbed around the time of birth (Allen 1887; Bertram 1940; Ling & Bryden 1981; King 1983; Stewart & Stewart 1987), causing the adult teeth to initially be crowded and overlapping in the smaller juvenile skull (Doutt 1942; Chapskii 1967). [In most other mammals, such crowding is avoided by having a reduced deciduous dentition associated with the shorter rostrum of immature individuals (Hillson 1986).] As the animal reaches

maturity, the skull grows, allowing the postcanines more room (Doutt 1942), as was clearly demonstrated in an age series of *Phoca largha* (Chapskii 1967).

This character may also be susceptible to the potential case of paedomorphosis in the phocids, and especially in the phocines (see King 1972; Wyss 1994). As it applies to this character, two main skull types have been observed to exist. The skulls of the smaller phocids have been described as possessing a more "juvenile" appearance due to their relatively large crania and relatively small rostra (King 1972). With their smaller rostra, these "juvenilé" skulls may demonstrate a higher incidence of postcanine crowding. Conversely, the skulls of the larger phocids present a more "adult" appearance, with relatively smaller crania and longer rostra (King 1972). This skull type might therefore be expected to lack crowding of the postcanines.

Finally, this character has been noted to be sexually dimorphic in *Phoca vitulina* (Allen 1902), but not *Phoca largha* (Chapskii 1967), two otherwise closely related species. Despite these problems, the crowding of the postcanines has been used by Ridgway (1972) to distinguish between the genera *Phoca* (state 1) and *Pusa* (state 0).

As evidenced by the fissipeds observed in this study, the Caniformia are primitively characterized by having the postcanines in contact with one another (but typically merely touching and not overlapping). The converse condition is proposed as a synapomorphy of the Pinnipedia, with reversals in *Monachus monachus, M. schauinslandi* (a possible synapomorphy of *Monachus* spp.; ACCTRAN optimization), and *Phoca vitulina*, all of which possess the juvenile skull type. However, numerous other phocines (most notably *Pusa* spp.) with the same skull type do not demonstrate this trait, placing the correlation between skull type and postcanine crowding in some doubt. Bearing this in mind, the observation that the postcanines are not in contact in the phocids primitively may contradict King's (1972) hypothesis that the ancestral phocids possessed a juvenile skull type, while supporting Wyss's (1994) interpretation of it being a secondary derivation.

147) obliqueness of postcanine implantation relative to long axis of tooth row (upper and lower): 0 = straight; 1 = anterior / posterior end of postcanine directed laterally (de Muizon 1982a).

This character is related in many ways to the previous one. In young animals, or those with a juvenile skull type, the relatively short tooth row will crowd the postcanines and push them out of line. With an increase in age (or a change to the adult skull type), the postcanines should fall back into line in the relatively longer tooth row (Doutt 1942; de Muizon 1982a). Apart from those species listed under the previous character, de Muizon (1982a) claimed a tendency towards oblique implantation of the postcanines as a synapomorphy of *Monachus* spp. (but relatively greater in *M. monachus* than in either *M. schauinslandi* or *M. tropicalis*) due to the relative shortness of their tooth rows. King (1972) noted an oblique orientation of the lower teeth of *M. monachus* in particular. This condition may also characterize other phocids with a juvenile skull type. In particular, Chapskii (1955a) comments that *Phoca* spp. is often noted for the obliqueness of its postcanines.

The apomorphic condition, in which the postcanines are obliquely implanted, displays a virtually identical distribution as the previous character: *Monachus* spp. (but including *M.*

tropicalis), *Phoca vitulina*, and possibly *Leptonychotes*. Again, the absence of this trait in other species with a juvenile skull type further weakens any supposed correlation between skull type and postcanine crowding.

148) obliqueness of postcanine implantation (upper and lower) relative to vertical: 0 = straight; 1 = slanted (de Muizon 1982a; pers. obs.).

In addition to angling away from the axis of the tooth row, as in the previous character, the postcanines are also occasionally slanted, typically along the lingual-labial axis. Chapskii (1955a) states that this is virtually universal in *Phoca vitulina*. This condition is likely not associated with postcanine crowding and may, in fact, be enhanced when the postcanines are widely separate, due to their reduced association with each other. However, this apomorphic condition is restricted in distribution to convergent appearances in *Lobodon* (lower postcanines #1 and #2 slanted lingually) and *Mirounga angustirostris* (various postcanines, usually slanted labially).

149) curvature of upper tooth row (postcanines only): 0 = sigmoidal; 1 = arched; 2 = straight; 3 = kinked between $PC^{1,2}$, otherwise straight; 4 = reverse arch (Ridgway 1972).

A character dealing with the curvature of the upper tooth row was used by Ridgway (1972) to distinguish between the genera *Histriophoca* and *Pagophilus*. *Histriophoca* is often noted for its strongly curved upper tooth row (Scheffer 1958; Burns & Fay 1970), which occasionally approaches a lyrate (= sigmoidal) morphology (Burns & Fay 1970). However, Burns & Fay (1970) do caution that this extreme curvature is not consistent within *Histriophoca*, and that it also occurs within other members of the Phocini, albeit to a lesser extent. Howell (1928) describes an apparently straight tooth row in *Zalophus*.

Our observations revealed that a presence versus absence coding of upper tooth row curvature is too simplistic and does not accurately represent the range of variation present within the phocids. The major recurring patterns were ones where the tooth row arched laterally (state 1), medially (state 4), or laterally anteriorly and medially posteriorly (state 0). The kinked condition (state 3) is obviously an extreme case of one of the other states, but exactly which one is not clear a priori. Thus, this morphology was left as a distinct state.

The plesiomorphic condition is of a sigmoidal upper tooth row, which is possessed by the majority of the non-lutrine fissiped outgroups. The derivation of this character in the lutrines and ancestrally within the pinnipeds is unclear. Either a straight tooth row is synapomorphic for *Lutra* plus the pinnipeds (ACCTRAN optimization), or the ancestral condition for the pinnipeds is equivocal between states 2 and 4, an uncertainty which is preserved into each phocid subfamily (DELTRAN optimization). In any case, the majority of the pinnipeds possess the straight morphology, and, despite its possible ancestral status, a reverse arch is limited to *Cystophora, Mirounga* spp., and *Monachus monachus* (where it must appear independently). *Odobenus* obtains a laterally arched tooth row, as does *Enhydra* among the fissipeds. *Erignathus* uniquely reverses to the plesiomorphic sigmoidal tooth row. The kinked morphology was found only in *Monachus schauinslandi* plus *M. tropicalis*, and appears to be a derivative of the straight condition.

Mandible (3 characters)

Although it is frequently mentioned in species descriptions, the mandible exclusive of the teeth has not been a common source of characters in recent systematic studies of the phocids. This has not always been the case. Chapskii (1955a) asserts that the general form of the mandible (and especially of its posterior margins) contains important taxonomic information, a source of information previously exploited primarily by Russian systematists. Another possible character, which was not examined here, deals with the mandibular symphysis which appears to be generally more robust in the monachines than in the phocines (pers. obs.).

150) shape of lingual face of mandible at middle postcanines: 0 = concave; 1 = flat; 2 = convex (Ridgway 1972).

This character has been employed to distinguish between the genera *Phoca* spp. (state 2) and *Pusa* spp. (state 0) (Ridgway 1972). A flat morphology is plesiomorphic among caniforms, with the remaining apomorphic states possessing limited distributions, and among the pinnipeds only. A concave morphology appears independently on a number of occasions: *Odobenus, Lobodon, Mirounga* spp., and *Monachus tropicalis*. The convex morphology was only noted for *Cystophora* and *Halichoerus*. This arises either as a synapomorphy of the phocines as a whole, with the remaining taxa reversing to the plesiomorphic condition (ACCTRAN optimizations), or independently in the two taxa (DELTRAN optimization). *Phoca* spp. and *Pusa* spp. were not distinguished by this character, as both genera were characterized by a flat morphology.

151) shape of posteroventral edge of mandible: 0 = rounded; 1 = jagged (Ridgway 1972).

In effect, this character deals with the size of the angular process. A rounded posteroventral edge of the mandible (small angular process) has been noted independently for *Hydrurga* (Ridgway 1972) and *Omnatophoca* (Mivart 1885). However, this apomorphic condition generally seems to be a synapomorphy of the monachines minus the elephant seals (*Mirounga* spp.) as a whole. Although a reduction of the angular process seems to characterize all phocids to some degree, a substantial reduction (to the apomorphic condition) occurs only in *Cystophora* and *Erignathus* among phocines.

Taylor (1914) holds the reduction of the angular process to be an aquatic adaptation, with the support provided by the aquatic medium allowing for reduced muscle masses, and therefore reduced muscle attachment points. However, why this would affect the angular process is unclear. The angular process is the posteromost extent of the insertion of the pterygoideus internus (= lateralis) (Davis 1964), but neither a relative reduction, nor a shift in the insertion of this muscle has been described in the phocids (see Howell 1928; Bryden 1971; Piérard 1971). This character may, in fact, be homoplastic as a true reduction of the process (e.g., as in *Leptonychotes*), or an expansion of the angle of the jaw subsuming the process (e.g., as in *Monachus monachus*) will both give the appearance of a reduced angular process.

152) distinct medially directed flange along ventral edge of jaw located posterior to mandibular symphysis and ventral to posterior postcanines: 0 = absent; 1 = present (King 1972).

A mandibular flange (or an elongated symphysis) was noted by King (1972, 1983) for *Odobenus, Erignathus, Lobodon, Pagophilus, Phoca* spp., and *Pusa* spp., where the resultant scoop-like mandible was postulated to be an adaptation for a "sucking" mode of feeding [best described for *Odobenus*; see Fay (1982)]. This flange may represent either a vestigial portion, or the precursor of a more robust mandibular symphysis, as this flange was often observed to grade smoothly anteriorly into the symphysis. As well, the flange is generally absent in the monachines, which, on the whole, possess a more robust symphysis (pers. obs.).

The distribution of the flange here closely matches that listed by King (1972, 1983). It appears to be an apomorphic condition shared by all phocines internal to *Halichoerus*, except for *Phoca largha*, but including *Histriophoca*. It was also independently obtained in *Lobodon*, but not consistently in *Odobenus*, which, like *Monachus monachus*, was polymorphic for this trait.

Forelimb (17 characters)

Post-cranial material has only sparingly been used to elucidate the systematics of the phocids. Only King (1966) and Wyss (1988a) have used such material to any degree. This reflects a number of factors. First, the comparative complexity of the mammalian skull yields a disproportionately high number of (obvious) characters. As well, there is a tendency for skins and skulls to be preferentially preserved over post-cranial material for mammals in many museum collections. Often, mammalian taxa are represented only by cranial material, making the inclusion of post-cranial material impossible in a practical sense. Finally, when post-cranial material has been preserved, it is usually disarticulated, making identification of the smaller isolated elements difficult and less desirable for study.

Hendey & Repenning (1972) consider many phocine post-cranial features to be primitive, an interpretation also implied by Wyss (1988a). Within the phocids, the generally good diagnostic value of the humerus has been noted (Ray 1976a; de Muizon & Hendey 1980).

153) relative size of scapular spine: 0 = reduced to prominent acromion; 1 = medium; 2 = prominent (King 1966; Wyss 1988a).

The reduction of the scapular spine (both in length and height) in most monachines was initially noted by King (1956, 1966). However, Wyss (1988a) correctly observed that the spine exhibits three morphologies within the phocids: a prominent form in the phocines where it extends virtually the full dorsoventral length of the scapula, the reduction to a knob-like acromion in the lobodontines, and an intermediate condition in *Mirounga* spp. and *Monachus* spp. Although Wyss (1988a) hesitantly equated this intermediate morphology with the phocine pattern, we have chosen to leave it separate. Among the outgroups, a reduced spine occurs only in ursids (Davis 1964) and the otarioids (Wyss 1988a). Wyss (1988a) has taken this distribution to indicate that a reduced spine is primitive for the pinnipeds [assuming an ursid outgroup; see Wyss (1987)].

A prominent scapular spine is plesiomorphic among the Caniformia and largely retained throughout, including *Ursus*. The intermediate condition only appears in *Odobenus, Mirounga* spp., and polymorphically with state 2 in *Zalophus*. This could arise through parallel evolution (DELTRAN optimization), but may also indicate a synapomorphy of

the pinnipeds, with subsequent modification in the remaining forms (ACCTRAN optimization). The apomorphic reduction to a prominent acromion unites all monachines except *Mirounga* spp. All phocines possess a prominent scapular spine.

154) relative shape of axillary (= caudal) border of scapula: 0 = straight; 1 = curved (Wyss 1988a; pers. obs.).

This character stems from the following one which was used by Wyss (1988a) to indicate a synapomorphy of the phocids exclusive of *Mirounga* spp. and *Monachus* spp. The shape of the teres major process notwithstanding, we noted that the axillary border of the scapula exhibits one of two distinctive morphologies. In most fissiped carnivores, the axillary border is reasonably straight (Miller 1962; Davis 1964; Crouch 1969). In contrast, the strongly curved border of most pinnipeds appears to be derived from an enlargement of the gleno-vertebral (posterodorsal) portion of the infraspinous region of the scapula (Howell 1928).

The apomorphic curvature of the axillary border presented a more limited distribution here, primarily being a synapomorphy of the phocines (with and without the polymorphic *Cystophora*), with independent origins in *Lutra* and *Ursus* among the outgroups. Among the monachines, only *Monachus monachus* consistently displayed the derived state, although most species were polymorphic for this trait.

155) distinct hook-like teres major process on scapula: 0 = absent; 1 = present (Wyss 1988a).

The teres major process comprises the posterodorsal-most portion of the gleno-vertebral region mentioned by Howell (1928). Wyss (1988a) considered the enlargement of this process (over and above that of the gleno-vertebral region) to form a hook on the axillary border of the scapula a synapomorphy of the phocids exclusive of *Mirounga* spp. and *Monachus* spp. Instead, our analysis indicates that the apomorphic presence of a distinct hook-like teres major process is limited to certain phocines only. It appears as a synapomorphy at the level of either *Phoca largha* (ACCTRAN optimization) or *Phoca vitulina* (DELTRAN optimization), and is maintained for all phocines internal to this, with the exception of *Pusa sibirica* (possibly as a synapomorphy with *Pusa hispida*; ACCTRAN optimization).

*156) supinator (= lateral epicondylar) ridge on humerus: 0 = absent; 1 = present (Wyss 1988a).

With recoding, this character was included in character #157.

157) relative degree of development of supinator (= lateral epicondylar) ridge on humerus: 0 = weak; 1 = medium; 2 = strong; 9 = absent (King 1966; Wyss 1988a).

King (1966) initially used this character to distinguish between the phocines (state 2) and the monachines (state 0). While agreeing with this distribution, Wyss (1988a) added outgroup information. In noting the absence of the supinator ridge in the otarioids (also Howell 1928) and its generally strong development among fissiped carnivores, Wyss (1988a) considered the presence of the ridge in phocines to be a reversal to the primitive (possibly at the level of the carnivores) condition. In contrast, de Muizon & Hendey (1980) felt the supinator ridge to be a primitive feature among phocids.

The appearance of the supinator ridge among the caniforms appears to be much more complex than indicated by Wyss (1988a). The polarity is equivocal at the level of the Caniformia due to the absence of the ridge in *Canis*. However, a similar absence in the domestic cat, *Felis domestica* (Crouch 1969), increases the likelihood that this is the plesiomorphic condition. The arctoids derive a medium-sized ridge, which the phocids reduce somewhat (state 0). This weak supinator ridge is largely retained for the monachines, with the clade of *Monachus schauinslandi* and *M. tropicalis* losing the ridge completely. A strongly developed ridge is unusual among caniforms, being limited to the phocines exclusive of *Cystophora*, with a parallel appearance in *Procyon*. *Pusa caspica* uniquely derives state 1 among phocids.

*158) deltopectoral crest on humerus: 0 = absent; 1 = present (Wyss 1988a).

With recoding, this character was included in characters #159 and 160.

159) relative length of deltopectoral crest on humerus: 0 = less than or equal to one-half length of humerus; 1 = greater than one-half length of humerus; 9 = absent (Wyss 1988a).

In all pinnipeds, the pectoralis muscle is quite prominent, resulting in a strengthening of its insertion point on the humerus (Howell 1928; Bryden 1971; Hendey & Repenning 1972). Hendey & Repenning (1972) distinguished two main patterns for this strengthening. In phocines, the pectoralis inserts only on the proximal half of the humerus, resulting in a deltopectoral crest that extends towards the enlarged lesser tubercle proximally, and is quite robust at its distal end. The crest extends to slightly less than halfway along the length of the humeral shaft before ending abruptly in a sharp overhang. In contrast, the insertion of the pectoralis in monachines is extended distally on the humerus, resulting in a deltopectoral crest that is two-thirds to three-quarters of the length of the humerus and grades smoothly into its shaft (Hendey & Repenning 1972; Wyss 1988a). *Leptonychotes* apparently shows a disposition towards the phocine pattern (de Muizon 1982a). Otarioids tend towards the monachine pattern (Hendey & Repenning 1972; Wyss 1988a), leading Wyss (1988a) to postulate it as plesiomorphic for the pinnipeds. This character examines one aspect of this morphology, the length of the crest, while the following character looks at the merging of the crest with the humeral shaft.

The current character presents a rather uncertain evolutionary pathway, although the distribution of the states is well marked. The phocine pattern is present in all phocines, with additional appearances in *Canis, Procyon*, and *Hydrurga*. Meanwhile, the monachine pattern is found in those monachines internal to *Hydrurga, Lutra*, and the otarioids. *Enhydra* and *Mirounga* spp. are polymorphic for these two states. A distinct crest is uniquely absent in *Martes*. However, this distribution has the effect of rendering the polarity at the level of the Caniformia equivocal. This situation may persist through to the phocids, with the different morphologies arising independently within the family (DELTRAN optimization). Another scenario has the monachine pattern as a synapomorphy of the arctoids, before the phocine pattern is derived ancestrally for the phocids and retained into the basal members of each subfamily at least (ACCTRAN optimization).

160) merging of deltopectoral crest to shaft of humerus: 0 = smooth; 1 = abrupt; 9 = absent (Wyss 1988a).

As indicated by Wyss (1988a), the monachine pattern (state 0) represents the plesiomorphic condition, and this extends back to the level of the Caniformia. The phocine pattern, whereby the deltopectoral crest ends abruptly at a virtual right angle to the shaft, is a synapomorphy uniting all phocines, with a parallel appearance in *Leptonychotes*. Again, a distinct crest was uniquely absent in *Martes*.

161) entepicondylar foramen of humerus: 0 = absent; 1 = present (King 1966; Wyss 1988a).

One obvious distinguishing characteristic between phocines and monachines is the presence of an entepicondylar foramen in the former and its absence in the latter (King 1966; Wyss 1988a). However, it should be noted that this is a generalization applying primarily to extant forms. Early Pliocene monachines (e.g., *Homiphoca capensis*, various species of *Monotherium*) do possess an entepicondylar foramen (Hendey & Repenning 1972; Ray 1976b; de Muizon & Hendey 1980; de Muizon 1982a; Repenning 1990). Various authors take this to be evidence of a recent loss of the foramen by the monachines (Hendey & Repenning 1972; de Muizon & Hendey 1980; Repenning 1990). As well, we observed phocine specimens in which the foramen was unilaterally (*Pagophilus*, AMNH 180016) or bilaterally absent (*Halichoerus*, USNM 446408), something also infrequently observed in other phocines (King 1966). A polymorphic distribution for this character is also indicated for the Ursidae, where the foramen is generally absent, except for the genera *Ailuropoda* and *Tremarctos* (Davis 1964).

As mentioned by Wyss (1988a), the interpretation of the distribution of this character depends on the outgroup relationships assumed for the phocids. A diphyletic pinniped origin with lutrine affinities for the phocids, as advanced by de Muizon (1982a), yields the monachine pattern as being apomorphic. A monophyletic Pinnipedia with ursid affinities, as postulated by Wyss (1987, 1988a), instead holds the phocine pattern to be apomorphic. Our analysis indicates that the polarity of this character is equivocal at the level of the Pinnipedia. At the level of the Caniformia, however, the possession of an entepicondylar foramen is apomorphic, being found in *Procyon, Martes, Enhydra*, and *Lutra*, in addition to all phocines. The connection between these fissipeds and the phocines is dependent on the optimization criterion used. With ACCTRAN optimization, the lack of the foramen is a synapomorphy of the pinnipeds, with the phocines homoplastically re-deriving the foramen. Under DELTRAN optimization, the possession of the foramen is synapomorphic for these taxa, with the otarioids and monachines independently reversing to the plesiomorphic condition. Only this latter pattern can account for the proposal whereby the foramen is present in monachines primitively before being lost (see above).

162) distally projecting ledge (palmar process) on cuneiform of carpus: 0 = absent; 1 = present (King 1966; Wyss 1988a).

King (1966) used this character to group *Cystophora* with the phocines (state 1) and *Mirounga* spp. with the monachines (state 0). In noting the absence of the ridge in otarioids, Wyss (1988a) presumed the presence of the ridge to be a phocine synapomorphy at the level of the Pinnipedia. However, such an interpretation is upheld here only under ACCTRAN optimization. Under DELTRAN optimization, the otarioids and monachines independently lose the ridge to match the state found in *Canis*. Otherwise, the palmar

process is a synapomorphy of the arctoids (the polarity being equivocal for the caniforms) and is consistently found in *Ursus, Martes, Enhydra*, and *Lutra*.

163) general morphology of metacarpal shaft: 0 = no lateral shaft ridges; 1 = lateral shaft ridges (M.A. Cozzuol pers. comm.) (Fig.23).

M.A. Cozzuol (pers. comm.) kindly pointed out that the metacarpals in some phocines are marked by small longitudinal ridges on each side of the distal palmar surface. However, at best, many phocine taxa are only polymorphic for this plesiomorphic caniform feature. The loss of these ridges describes a synapomorphy of *Martes*, the lutrines, and the pinnipeds, with the tendency towards regaining this feature only appearing consistently in *Lutra* and *Pusa caspica*.

164) general morphology of metacarpal head: 0 = smooth; 1 = "palmar" ridges present (King 1966; Wyss 1988a) (Fig.23).

Character #18 of Wyss (1988a) describes a suite of features related to the morphology of the metacarpal-phalangeal articulation. We have chosen to subdivide Wyss's (1988a) character into its component parts (this character, characters #165 and 166). Wyss (1988a) described his first component, the longitudinal "palmar" ridge, as dividing the distal and palmar surfaces of the metacarpal head (also King 1966). If we have in fact observed the same feature intended by Wyss (1988a), we would amend his definition to something more akin to the keeled heads of Berta & Ray (1990): a longitudinal ridge (or keel) on the distal metacarpal head running between the palmar and anti-palmar surfaces. Among caniforms, this "palmar" ridge is absent only in otarioids and monachines (King 1966; Wyss 1988a), which Wyss (1988a) interprets as a synapomorphy of the pinnipeds, with a reversal to the primitive carnivore condition (state 2) by the phocines. However, our observation of "palmar" ridges among the otarioids renders the outright lack of any such ridges as a synapomorphy solely of the monachines as a whole (ACCTRAN optimization), or of the

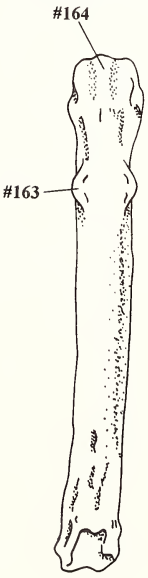

Fig.23: Ventral view of the third metacarpal of a canid *(Canis familiaris)* illustrating selected characters (indicated by their number; see **Character Analysis**) of this element. Distal is towards the top of the page. Adapted from Miller (1962).

monachines less the polymorphic *Mirounga* spp. (DELTRAN optimization). Note, however, that this slight discrepancy may hinge on our definition of this character being different from the one intended by King (1966) and Wyss (1988a).

165) cross-sectional shape of phalanges: 0 = flat; 1 = intermediate; 2 = round (King 1966; Wyss 1988a).

The second of Wyss's (1988a) metacarpal features examined the cross-sectional shape of the phalanges. In the monachines, as in the otarioids, the phalanges are distinctly flattened as opposed to the more rounded morphology of the phocines (Howell 1928; King 1966; Wyss 1988a). However, the phalanges of the phocines are still appreciably flatter than those found in fissiped carnivores (Wyss 1988a), and hence should represent more of an intermediate condition (state 1).

Generally, any apomorphic flattening of the phalanges is limited to the pinnipeds. Strongly flattened phalanges (state 0) arise on at least three main occasions: *Zalophus, Phoca vitulina* plus *Pusa* spp. (the two reconstructions indicate a conflicting assortment of independent origins and losses in this general region), and those monachines internal to *Leptonychotes*, minus *Monachus tropicalis* (which regains rounded phalanges). No phocine demonstrated slightly flattened phalanges (state 1). Instead the appearance of this morphology was limited to *Lutra* and *Mirounga leonina*.

166) morphology of proximal phalangeal articular surface: 0 = hinge-like; 1 = trochleated (King 1966; Wyss 1988a).

In most caniforms, the proximal articular surface of the phalanx is strongly trochleated to accommodate the "palmar" ridge of the distal metacarpal head (see character #164). The lack of such a ridge in otarioids and monachines results in a more hinge-like articular surface of the phalanx (King 1966; Wyss 1988a). As with the palmar ridges, Wyss (1988a) interprets this distribution so that a hinge-like articulation is synapomorphic for the pinnipeds, with the phocines reversing to re-obtain the primitive carnivore pattern. While the same distribution of states was observed here, such an interpretation is contingent upon the optimization criterion employed. Wyss's (1988a) scenario is applicable under ACCTRAN optimization, but under DELTRAN optimization, hinge-like articular surfaces are independently obtained in otarioids and monachines.

167) comparative length of metacarpals I and II: 0 = I > II; 1 = I subequal to II; 2 = I < II (King 1966; Wyss 1988a).

Both King (1966) and Wyss (1988a) observed that in phocine seals, as in most carnivores, metacarpals I and II are of approximately equal size. In contrast, the remaining pinnipeds are characterized by an elongated and comparatively thicker first metacarpal (King 1966; Wyss 1988a). This is a generalization, however, as *Cystophora* and *Halichoerus* are approximately intermediate between these extremes (see King 1966: 391). Again, Wyss (1988a) interprets this distribution to indicate a reversal, albeit incomplete (as the first metacarpal is slightly longer than the second in phocines, while the situation is reversed in fissiped carnivores), on the part of the phocines. We divided the original character (relative metacarpal size) into its two component parts: relative metacarpal length and relative metacarpal diameter (= robustness or thickness). As well, we have expanded the

number of character states to account for all permutations of the relative sizes of the two elements.

The plesiomorphic condition is for the second metacarpal to be the longer of the two, a situation found in all fissiped outgroups except for *Enhydra* and *Ursus*, where the metacarpals are subequal in length. The pinnipeds are united by the apomorphic condition whereby the first metacarpal is distinctly longer. As expected, most phocines are diagnosed by having metacarpals of equal length. *Cystophora* retains and *Pusa sibirica* reverts to the primitive pinniped morphology.

168) comparative overall diameter of metacarpals I and II: 0 = I > II; 1 = I subequal to II; 2 = I < II (King 1966; Wyss 1988a).

The comparative robustness of metacarpals I and II follows much the same pattern as their length, except that only scattered phocines reverse towards a more subequal arrangement. An enlarged first metacarpal is a pinniped synapomorphy, with the fissipeds characterized by a second metacarpal of equal (all fissiped arctoids) or greater (*Canis* only) diameter than the first. State 0 is found universally in the otarioids and monachines, and is largely retained throughout the phocines as well. Only *Erignathus, Phoca largha*, and *Pusa caspica* independently reverse to obtain the condition where the two elements are roughly equal in diameter.

169) relative degree of development of foreflipper claws: 0 = not well developed or absent; 1 = well developed, prominent (King 1966; Wyss 1988a).

There is the tendency within the pinnipeds (exclusive of the phocines) to reduce both the fore- and hind flipper claws (Wyss 1988a; see character #189). In the otarioids, the foreflipper claws are virtually absent, remaining only as small nodules (Wyss 1988a). Although only *Hydrurga* and *Ommatophoca* possess reduced foreflipper claws among monachines (King 1966), Wyss (1988a) holds them to be reduced for the subfamily, thus describing a pinniped synapomorphy with a reversal occurring in the phocines. For those species where adequate preserved material was lacking, we supplemented our observations with data from King (1966). Here the apomorphic reduction of the foreflipper claws occurred independently in only the otarioids, *Hydrurga*, and *Ommatophoca*.

Pelvis (8 characters)

The general form of the phocid pelvis is very distinctive from that of other carnivores (de Muizon 1982a), lending additional support to the monophyly of the group. However, rather than concentrate on the autapomorphic features of the phocid pelvis, we have attempted to examine characters that clarify either the ingroup (i.e., within the phocids) or outgroup relations of the family.

170) eversion of wing of ilium: 0 = distinctly less than 45°; 1 = roughly 45°; 2 = distinctly greater than 45° (King 1966; Wyss 1988a).

The phocids are uniquely characterized by a laterally everted ilium (King 1966; de Muizon 1982a; Wyss 1988a). The degree of eversion is markedly greater in phocines (exclusive of *Erignathus*) than in monachines, often reaching 90° (Howell 1928; King 1966; Wyss 1988a). In the phocines especially, this eversion benefits the tremendously enlarged iliocostalis portion of the back musculature which originates, at least in part, from the

former medial side of the ilium, as well as the gluteus group extending to the femur (Howell 1928; Bryden 1971; Hendey & Repenning 1972). McLaren (1975) holds that the subfamilial differences arise from the retention of a more primitive muscular arrangement in the monachines, a contention echoed by Hendey & Repenning (1972). The binary coding employed by most authors ("strongly everted or not") disguises the unique form of the ilium in all phocids by grouping the monachines with non-phocids. Therefore, we have subdivided this character more finely, with the categories roughly corresponding to "not everted", "weakly everted", and "strongly everted".

The apomorphic eversion of the ilial wing (states 1 or 2) is largely confined to the phocids, although a weakly everted ilium does occur in *Enhydra* and *Ursus*. As the phocids are characterized ancestrally by state 0, independent eversions of the ilial wing must occur in each subfamily, as implied by Hendey & Repenning (1972). The weakly everted ilium typical of many monachines describes a synapomorphy of those species internal to *Hydrurga*, with *Monachus schauinslandi* (possibly as a synapomorphy with *Monachus tropicalis*; ACCTRAN optimization) reverting to a flat ilium. The strongly everted ilium of the phocines arises ancestrally within this subfamily, with only *Erignathus* (states 0 and 1) largely reversing to the plesiomorphic caniform morphology.

*171) gluteal fossa on wing of ilium: 0 = absent; 1 = present (King 1966; Wyss 1988a). With recoding, this character was included in character #172.

172) depth of gluteal fossa on ilium: 0 = shallow; 1 = medium; 2 = deep; 9 = absent (King 1966; Wyss 1988a).

Apparently associated with the strongly everted phocine (exclusive of *Erignathus*) pelvis is a deep, compact gluteal fossa on the lateral side of the everted ilial wing (King 1966; Wyss 1988a). The majority of this fossa in phocines serves as the origin for the gluteus medius muscle (Howell 1928). The gluteal fossa is apparently absent in the remaining pinnipeds (Wyss 1988a), but exists in *Canis* and *Ursus* as a shallow, elongated trough (Miller 1962; Davis 1964).

A gluteal fossa of shallow or medium depth is found in all fissiped outgroups except possibly *Lutra* (ACCTRAN optimization). A deep fossa unites the phocines ancestrally with only *Erignathus* (state 9) and *Pusa sibirica* (state 1 – possibly as a synapomorphy with *Pusa hispida*; ACCTRAN optimization) deviating from this trend. Beyond this, however, the two optimization criteria used here provide strikingly different pathways for the evolution of this character. ACCTRAN optimization holds for the loss of the fossa uniting *Lutra* plus the pinnipeds with *Leptonychotes, Lobodon*, and *Mirounga* spp. independently deriving medium depth fossae. In contrast, DELTRAN optimization indicates that a shallow fossa is a synapomorphy of *Lutra* plus the pinnipeds, with the otarioids, *Hydrurga, Monachus* spp. and *Ommatophoca* losing the fossa in parallel. Of these two opposing hypotheses, the latter seems the more likely, as the previous (excluded) character indicates that the loss of the fossa is an apomorphic tendency occurring independently in the taxa mentioned above.

173) relationship of obturator nerve foramen to obturator foramen: 0 = distinctly separate, at least unilaterally; 1 = intermediate – foramina confluent, but individually recognizable; 2 = confluent – obturator nerve foramen not apparent (Wyss 1988a).

Although reasonably common among the otarioids [especially the arctocephaline otariids (the fur seals) and occasionally *Odobenus*], a distinct obturator nerve foramen separate from the obturator foramen is present only in *Monachus schauinslandi* among phocids (King & Harrison 1961; Ray 1976a; Repenning & Ray 1977; Wyss 1988a). Wyss (1988a) has interpreted this feature as being primitive among the pinnipeds, and used the above distribution to justify the sister taxon status of *M. schauinslandi* to the remaining phocids. An identifiable obturator nerve foramen is periodically present in *Cystophora* and *Monachus tropicalis*, but it is confluent with the obturator foramen (state 1), whereas it is displaced towards the cotyloid notch of the acetabulum in *Monachus schauinslandi* (state 0) (King & Harrison 1961; Repenning & Ray 1977; Wyss 1988a; pers. obs.). Any appearance of the obturator nerve foramen (states 0 or 1) is apomorphic among the caniforms. State 0 is only manifested in *Monachus schauinslandi*, while state 1 occurs convergently in the otarioids and *Monachus tropicalis*. *Cystophora* was notably polymorphic for states 1 and 2 for this character.

174) ridges in anterior portion of obturator foramen: 0 = absent; 1 = present (pers. obs.) (Fig.24).

We noted this feature in the pelves of a diverse range of taxa. These ridges may be related to the previous character, as their location closely approximated that of the incompletely separated obturator nerve foramen in species such as *Cystophora* and *Monachus tropicalis* (see previous character). In fact, these ridges may serve to segregate the obturator nerve from various muscles of the hip, most notably the craniad insertions of the obturatorius externus and internus muscles on the obturator membrane (Howell 1928; Miller 1962; Piérard 1971). Admittedly, the term "ridges" is inadequate as the ridges took on many forms, ranging from actual longitudinally oriented ridges that in effect constricted the anterior part of the obturator foramen, to small bony spurs.

In general, the ridges tend to be absent in the fissipeds, although their appearance in *Canis* renders the polarity of this character equivocal at the level of the Caniformia. The ridges mark a synapomorphy of the pinnipeds, with the phocids showing a tendency towards their loss. Ridges are consistently absent in *Monachus* spp. (possibly as a synapomorphy with *Lobodon*; ACCTRAN optimization), *Phoca vitulina*, and the clade of *Pusa hispida* plus *Pusa sibirica*, and polymorphically so in a number of other phocids.

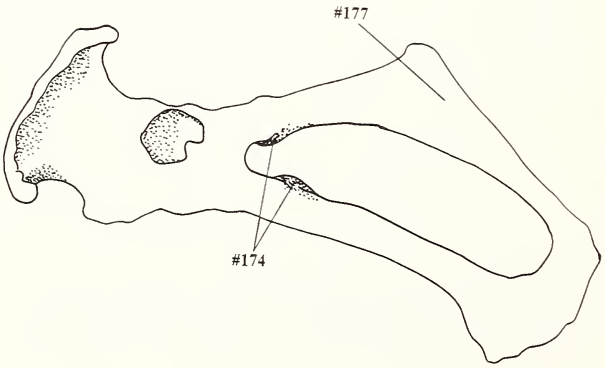

Fig.24: Lateral view of the left pelvic girdle of *Pusa hispida* illustrating selected characters (indicated by their number; see **Character Analysis**) of this element. Anterior is towards the left of the page and dorsal to the top. Adapted from de Muizon (1982a).

175) relative length of post-acetabular region of the pelvis: 0 = shortened (and rounded); 1 = elongated (and narrow) (King 1966; Hendey & Repenning 1972).

Compared with most other carnivores, the post-acetabular region of the pinniped pelvis is characteristically elongated (Howell 1928; de Muizon 1982a; King 1983). The extreme this condition reaches in the phocids (Howell 1928; de Muizon 1982a) is likely related to the lateral eversion of the phocid ilium (see character #170). Yet, even within the phocids, two different pelvis types can be differentiated. Phocines possess a relatively long and narrow post-acetabular region of the pelvis, as opposed to the relatively shorter and rounder form of the monachines (King 1966; Hendey & Repenning 1972). A relatively elongated pelvis is synapomorphic for the mustelids (including the lutrines) plus the pinnipeds. The two phocid subfamilies are clearly divided by this feature. The phocines universally possess an elongated pelvis, while the monachines reverse ancestrally towards a plesiomorphic short pelvis.

176) general curvature of pelvis around long axis: 0 = relatively straight; 1 = distinctly twisted (pers. obs.).

During our observations, we noted a peculiar morphology of the phocine pelvis. In all other caniforms, the pelvis is twisted around its long axis so that when the cranial portion is viewed directly dorsally (i.e., so that the acetabulum points laterally), the medial surfaces of the ischium and pubis are visible. In contrast, the phocine pelvis is reasonably straight, so that the ischium does not deflect appreciably from the long axis of the pelvis. King (1966) does note a lateral bowing of the pubis in female phocids, but this does not refer to the same feature. King's (1966) bowing is more obvious in phocines and involves a medial curvature of the pubis posteriorly so that the innominates are virtually in contact at their posterior ends. As well, we observed the twisting under discussion here in phocines of both sexes. This twisting of the pelvis is a synapomorphy of the phocines, with a parallel appearance in *Lobodon*.

177) relative location of ischiatic spine (= tuber ischiad): 0 = roughly midway along the post-acetabular region; 1 = located in posterior post-acetabular region (pers. obs.) (Fig.24).

In the caniforms, the relative location of the ischiatic spine appears to be associated with the relative length of the pelvis (see character #175). In taxa with relatively short pelves, the ischiatic spine tends to be located close to the posterior end of the pelvis. The apparent anterior shift of the ischiatic spine in taxa with long pelves possibly indicates a posterior elongation of the pelvis in these forms. However (compare with the distribution of character #175), an anterior shift of the ischiatic spine is indicated to be a synapomorphy of the pinnipeds, with a reversal in *Odobenus* (ACCTRAN optimization), or of the phocids only with a parallel appearance in *Zalophus* (DELTRAN optimization). This latter scenario accords well with observations of an elongated post-acetabular region in phocids (Howell 1928; de Muizon 1982a). Among phocids, only *Hydrurga* and *Lobodon* revert to the plesiomorphic state (state 1).

There is a possibility that the two states we identified for this character might be an artifact of the sexual dimorphism present in pinniped pelves. King (1983) states that the posterior outline of the pelvis in male pinnipeds is much more rectangular than the more rounded female morphology [see Fig.36 in King (1969)]. This would result in an apparent posterior

shift of the ischiatic spine in males. However, in noting the fairly consistent anterior shift of the spine throughout the pinnipeds here (in conjunction with our attempts to have an equal representation of males and females), we judge the effect of this potential error to be minimal.

Hind Limb (12 characters)

Certain features of the hind limb have been useful in defining the phocids as a family (e.g., lack of a lesser trochanter on the femur, presence of posterior process on the astragalus) (Howell 1928; de Muizon 1982a), but otherwise, the hind limb (exclusive of the pelvis) has not been used to a great extent to elucidate phocid phylogeny. This might be explained for the femur, at least, by it being assigned a generally low diagnostic value due to its high variability (e.g., Ray 1976a; de Muizon & Hendey 1980).

178) position of greater trochanter on femur: 0 = lower than head; 1 = equal with head; 2 = higher than head (King 1966; de Muizon 1982a).

This character has been briefly mentioned to define either of the phocid subfamilies. King (1966) notes that phocines tend to possess state 2, while de Muizon (1982a) used state 0 to define a synapomorphy of the monachines, a distribution echoed by de Muizon & Hendey (1980). Here, the morphologies whereby the greater trochanter is equal to or higher than the femoral head are apomorphic. State 1 characterizes the phocines ancestrally and is universal within the subfamily except for *Pagophilus, Phoca largha*, and *Pusa sibirica*, which independently derive state 2. State 1 also appears in the monachine *Monachus tropicalis* (possibly as a synapomorphy with *Monachus schauinslandi*; ACCTRAN optimization) and the fissipeds *Enhydra, Martes*, and possibly *Procyon*, either by convergence (DELTRAN optimization), or as a synapomorphy of the fissiped taxa, with a reversal to the primitive caniform condition in *Lutra* plus the pinnipeds (ACCTRAN optimization).

The slight discrepancy with previous observations (phocines generally possessing state 1 and not state 2) can be related to the fact that our observations of this character were made so that the distal condylar surfaces of the femur were level. However, the autapomorphic development of an epicondylar ridge in phocids causes the distal condylar surfaces to be slightly oblique with respect to the femoral shaft (de Muizon 1982a). Thus, with our technique, the greater trochanter would be shifted to a lower position relative to the femoral head. That this character still indicates a synapomorphy of the phocines speaks for the height to which the greater trochanter is raised in this group.

*179) distinct trochanteric fossa on femur: 0 = absent; 1 = present (King 1966; de Muizon 1982a).

With recoding, this character was included in character #180.

180) depth of trochanteric fossa on femur: 0 = shallow; 1 = medium; 2 = deep; 9 = absent (King 1966; de Muizon 1982a).

As compared to the modern monachines, another distinguishing feature of the phocine femur is the development of a distinct trochanteric fossa (King 1966; de Muizon 1982a). However, the value of this character may be limited by its inconsistent presence in phocines (e.g., it is absent in *Erignathus*) together with its presence in many fossil

monachines as well as *Lobodon* (de Muizon & Hendey 1980; de Muizon 1982a). A similar absence of the fossa in the otarioids, combined with its presence throughout the rest of the Carnivora led Wyss (1988a) to suggest that this character indicated yet another reversal on the part of the phocines. In contrast, de Muizon (1982a) held the monachine pattern to be apomorphic for the subfamily.

A deep trochanteric fossa is plesiomorphic among the Caniformia, being found in all major fissiped lineages. The above distribution for this character is largely borne out (with the exception of a shallow fossa in *Zalophus, Leptonychotes*, and *Monachus monachus*), but the evolutionary pathway is dependent on the reconstruction technique employed. DELTRAN optimization largely supports de Muizon (1982a), with the plesiomorphic condition being retained by the phocines, and parallel losses or reductions of the fossa occurring in the otarioids and monachines. In contrast, ACCTRAN optimization supports Wyss (1988a), in that the loss of the foramen is synapomorphic for the pinnipeds, with the phocines re-deriving a deep fossa. As expected, *Lobodon* regains a medium depth fossa.

181) lesser trochanter: 0 = absent; 1 = present (de Muizon 1982a).

The phocids are unique among mammals in lacking the lesser trochanter on the femur (Howell 1928; de Muizon 1982a). A slight discrepancy exists as to the resulting new insertion point of the psoas magnus. The majority opinion is that the insertion shifts to the posteroventral ischiatic spine (= pectineal tuberosity) on the ventral edge of the ilium, representing an adaptation to enhance the lateral undulatory movements employed in the phocid swimming style (Miller 1887; Bryden 1971; Piérard 1971; de Muizon & Hendey 1980; de Muizon 1981, 1982a). However, Howell (1928) indicates this to be a different muscle, the psoas tertius, and places the insertion of the psoas magnus on the medial tuberosity of tibia, together with the iliacus. In any case, the apomorphic loss of the lesser trochanter for the phocids is indicated here.

182) relative width of femur distally: 0 = gracile (less than medium breath); 1 = robust (greater than or equal to medium breadth) (M.A. Cozzuol pers. comm.).

In conjunction with his research into the possible paraphyletic nature of *Monachus* spp., M.A. Cozzuol kindly pointed out this character to us. He noted that the femur is very robust and broad distally in *M. monachus*, but much more gracile in *M. schauinslandi* and *M. tropicalis*. Additionally, de Muizon & Hendey (1980) hint at a wide distal end to the femur in the lobodontines. In applying this character to the other taxa in this study, a comparatively robust femur appears to be a synapomorphy of the monachines, missing only in *Mirounga leonina* and the clade of *Monachus schauinslandi* and *M. tropicalis* (ACCTRAN optimization). However, another possibility holds for independent origins of a wide distal end in *Mirounga angustirostris* and most of the remaining monachines (DELTRAN optimization).

183) proximal fusion of tibia and fibula: 0 = unfused; 1 = rudimentary – not fused all the way around; 2 = totally fused (Wyss 1988a).

The fusion of the proximal epiphysial heads of the pinniped tibia and fibula presumably represents an adaptation to strengthen and decrease the mobility of this region of the leg

to aid in swimming. This condition is obtained in virtually all Recent pinnipeds, the only exceptions being *Odobenus*, where they are rarely fused, and *Monachus schauinslandi*, where they are almost never fused (Ray 1976a; Repenning & Ray 1977; de Muizon & Hendey 1980; de Muizon 1982a; King 1983; Wyss 1988a). Complete fusion is typically observed in later fossil pinnipeds, but not in the earlier basal forms (Repenning & Ray 1977; de Muizon & Hendey 1980; Wyss 1988a), leading to suggestions that the unfused morphology is primitive for phocids (Ray 1976a; de Muizon 1982a). In addition to the two extreme morphologies, we noted that in some specimens, preliminary fusion had occurred between the epiphysial heads (typically in the anterodorsal region), but was incomplete in other regions. In accordance with King's (1956) suggestion that the fusion between the tibia and the fibula may be among the last to occur during ontogeny, this latter condition (state 1) may represent a developmental artifact.

Any fusion of the tibia and fibula is apomorphic within the Caniformia. *Martes* is unique among fissipeds in displaying the rudimentary fusion of these two elements (state 1). At the earliest, complete fusion occurs as a synapomorphy of the pinnipeds (with a reversal in *Odobenus*; ACCTRAN optimization), but for the phocids in any case (with a convergent appearance in *Zalophus*; DELTRAN optimization). Full or partial reversals within the phocids are reasonably limited. Partial reversals occur independently in the phocines *Phoca largha* and *Pusa sibirica* (possibly as a synapomorphy with *Pusa hispida*; ACCTRAN optimization). A full reversal unites the monachines *Lobodon* plus *Monachus* spp., although all species except *Monachus schauinslandi* are polymorphic for states 0 and 1.

184) relative degree of development of the post-tibial (= intercondyloid) fossa of tibia: 0 = weak; 1 = strong (King 1966; Wyss 1988a).

King (1966) distinguished between the phocines and monachines by noting a greater tendency for a more pronounced post-tibial fossa in the former (also de Muizon & Hendey 1980). Other than for a curious tendency towards the phocine condition in the fossil lobodontine *Homiphoca* (Hendey & Repenning 1972; de Muizon & Hendey 1980), this appears to be a unique feature for the phocines, with the fossa being shallow in the otarioids and most fissiped carnivores (Wyss 1988a). However, among the outgroups examined here, only *Canis* demonstrated a weak post-tibial fossa, rendering the polarity of this character equivocal at the level of the Caniformia. The strong fossa typical of fissipeds is largely retained in the pinnipeds, with only *Monachus schauinslandi* plus *Monachus tropicalis, Phoca largha*, and *Pusa sibirica* independently deriving a weak fossa. This outcome (plus the high incidence of polymorphism in this character) seriously detracts from the ability of this character to distinguish between the two phocid subfamilies, and may stem from the lack of any substantial difference between the two character states. This, in turn, might relate to the lack of any substantial differences among caniform astragalar trochleae, the structure that articulates with the post-tibial fossa.

*185) robustness of calcaneum: 0 = smaller than or subequal to astragalus; 1 = larger than astragalus (de Muizon 1982a).

The comparative robustness of the calcaneum, when the astragalus is used as a reference, merely reflects the presence or absence of the posterior process on the plantar aspect of the astragalus. As this duplicates character #186, this character was excluded.

186) posterior process on plantar aspect of astragalus: 0 = absent; 1 = present (de Muizon 1982a).

The condition of the phocid astragalus is unique among mammals. Firstly, the astragalus possesses a strong posterior process causing it and the calcaneum to assume roughly equal sizes (Howell 1928; de Muizon 1982a; pers. obs.; see character #185). Secondly, the plantar surface of this posterior process is marked by a distinct groove for the passage of the flexor hallucis longus tendon (see the following character). In phocids, this tendon is better developed than it is in other mammals and plays a key role in their swimming locomotion. In fact, the hypertrophy of this tendon is responsible for another diagnostic feature of the phocids, that of being unable to turn the hind feet forward while on land (Howell 1928; de Muizon 1982a; King 1983). As indicated, the development of a posterior process is synapomorphic for phocids, and is possessed by all extant species (including *Monachus tropicalis*).

187) depth of groove on plantar aspect of posterior process of astragalus: 0 = groove absent; 1 = shallow; 2 = moderate; 3 = deep; 9 = posterior process absent (de Muizon 1982a).

As indicated by the previous character, the groove on the plantar aspect of the astragalus is unique to the phocids (Howell 1928; de Muizon 1982a; King 1983). However, this groove is not equally developed among the phocids, ranging from shallow to deep, and even virtually absent in many monachines (pers. obs.). The differential expression of this feature in the two phocid subfamilies renders the ancestral state for the phocids uncertain. The phocines are characterized ancestrally by a deep groove. This is reduced to a shallow groove in *Phoca* spp. and *Pusa* spp., before the primitive phocine morphology is regained in *Erignathus, Histriophoca*, and *Pagophilus*. The monachines are defined by a lack of the groove, although most taxa within this subfamily are polymorphic between this state and states for grooves of various depths.

188) length of metatarsal III relative to remaining metatarsals (shape of posterior flipper margin): 0 = metatarsal III longest; 1 = metatarsal III intermediate; 2 = metatarsal III subequal or slightly shorter; 3 = metatarsal III distinctly shorter (King 1966; Wyss 1988a).

All phocids are characterized by a shortening of the third metatarsal relative to the remaining metatarsals, with the reduction tending to be more extreme in the monachines than in the phocines (King 1966; Wyss 1988a). However, rather than view this as a synapomorphy of the monachines, Wyss (1988a) was more inclined to view shortening as primitive for the phocids, with the phocines partially reversing to approach the typical carnivore pattern (states 0 or 1). This was supported by the observation that *Cystophora* does not group with the phocines, but instead displays a monachine degree of reduction (Wyss 1988a). A reduced third metatarsal is not present in the otarioids, where all metatarsals are of about equal length (Wyss 1988a). Together with the relative reduction of all bones of the third digit of the hind foot (King 1983), the shortening of the third metatarsal also has coincident effects on the shape of the posterior flipper margin as a whole. All phocids possess a concave outline to the posterior flipper to some degree, and, again, it is much more marked in the monachines and the phocines *Cystophora* and *Histriophoca* (King 1983; Wyss 1988a). Phocines, and *Erignathus* in particular, tend

towards a straighter posterior flipper margin (Wyss 1988a). As the outline of the posterior flipper could not be observed directly, we concentrated instead on the relative size of the third metatarsal.

Most fissipeds are characterized by the plesiomorphic state, whereby the third metatarsal is the longest, although *Enhydra* and *Ursus* independently obtain state 1. A shortened third metatarsal is diagnostic of the pinnipeds, with the otarioids generally obtaining state 2 while the phocids derive state 3 ancestrally. No separation between the two phocid subfamilies was obtained here, as virtually all taxa retained a distinctly shortened third metatarsal. Again, this is due, in large measure, to the historically rather arbitrary distinction between the phocine and monachine morphologies ("slightly shorter" versus "distinctly shorter") that was difficult to quantify here. Only *Pusa caspica* [as obtained from Wyss (1988a)] and *Histriophoca* convergently reverse towards the typical fissiped pattern by obtaining state 2. If this observation for *Histriophoca* is accurate, then a severe shortening of the phalanges of the third hind digit must account for the concave posterior flipper margin reported for this genus (see above).

189) relative degree of development of hind flipper claws: 0 = not well developed or absent; 1 = well developed, prominent (King 1966; Wyss 1988a).

As with the foreflippers (see character #169), there exists a tendency towards reduction of the hind flipper claws in the pinnipeds. For the phocids at least, the pattern is more unmistakable. Phocines again have well developed hind flipper claws, while those of all monachines are markedly reduced (King 1966, 1983; Wyss 1988a). The otariids now present something of a categorical problem, as the hind flipper claws are large, but are only present on the middle three digits (Howell 1928; King 1983; Wyss 1988a). *Odobenus* presents less of a problem. Although it likewise possesses the three grooming claws, they are quite small (King 1983; Wyss 1988a). Missing data were again supplemented with observations from King (1966).

The apomorphic reduction of the hind flipper claws occurs independently on three occasions within the Caniformia: *Enhydra*, the otarioids generally (*Zalophus* is regarded here as being polymorphic for this character), and the monachines. This may be a synapomorphy of these taxa, with *Lutra* and the phocines re-obtaining large claws (ACCTRAN optimization), or be the result of parallel evolution (DELTRAN optimization).

Miscellaneous (7 characters)

This section includes hard anatomical characters that did not fall into the other categories and selected soft anatomical features.

190) location of posterior end of cribriform plate: 0 = within interorbital region; 1 = posterior portion of interorbital region; 2 = anterior end of braincase (pers. obs.) (Fig.19).

Perhaps associated with the lateral compression of the interorbital region of the pinnipeds (Howell 1928; King 1972, 1983; see character #49), we noted that the posterior end of the cribriform plate in this group is generally shifted posteriorly. Instead of lying distinctly within the (anterior end of the) interorbital region, as in most caniforms, the plate in all pinnipeds is located within the posterior end of the interorbital region, or, at its most

extreme, at the point where the interorbital region merges with the braincase (pers. obs.). This posterior shift arises somewhere within the lutrines and is retained throughout the pinnipeds. The lutrines and basal monachines generally possess the intermediate condition (state 1), while the remaining pinnipeds are characterized by the more extreme morphology. This shift to the anterior end of the braincase may be a synapomorphy of the pinnipeds, with state 1 being derived ancestrally in the monachines (ACCTRAN optimization), or the ancestral state for the pinnipeds and phocids may be equivocal between states 1 and 2 (DELTRAN optimization).

191) relative position of vertebrarterial (= intervertebral) foramen of atlas: 0 = visible in dorsal view; 1 = visible in posterior view (King 1966; Wyss 1988a).

Another distinction between the phocid subfamilies concerns the position of the vertebrarterial foramen of the atlas. In phocines, as in most carnivores, the foramen is only visible in posterior view. Only among canids and monachines does the foramen become visible in dorsal view (King 1966; Wyss 1988a). Some problems do exist with this character. *Monachus* spp. more closely approach the typical carnivoran pattern (King 1966; Wyss 1988a). As well, the unusually large size of the foramen in *Odobenus* and *Monachus tropicalis* makes it at least partially visible in both dorsal and posterior views. Here, a dorsally visible vertebrarterial foramen was only present for *Hydrurga* among the monachines, along with a convergent appearance in *Canis*. Although many monachines were polymorphic for this character, this distribution renders both the polarity of this character and its utility for elucidating phocid relationships questionable.

192) claw morphology in cross-section, I: 0 = semicircular; 1 = triangular (Doutt 1942; Ridgway 1972).

Together with the following character, Doutt (1942) used the shape of the claws in cross-section to distinguish between *Phoca vitulina* (state 0) and *Histriophoca, Pagophilus*, and *Pusa hispida* (all state 1). Ridgway (1972) applied the same character to distinguish between the genera *Phoca* spp. (state 0) and *Pusa* spp. (state 1). However, observations for both this and the following character were hindered by the general paucity of suitable material. Observations could not be made for *Mirounga angustirostris, Phoca largha*, and *Pusa caspica*, and the condition for a number of other specimens could only be estimated from the ungual processes of the terminal phalanges. Bearing this in mind, only *Mirounga leonina* consistently possessed the apomorphic triangular morphology, possibly as a synapomorphy with *Mirounga angustirostris* (ACCTRAN optimization). A fair number of other pinnipeds were polymorphic for this trait.

193) claw morphology in cross-section, II: 0 = dorsal ridge or annuli absent; 1 = dorsal ridge or annuli present (Doutt 1942; Ridgway 1972).

In combination with the previous character, Doutt (1942) used the presence of a dorsal ridge on the claw to distinguish between *Pusa hispida* (state 1) and *Histriophoca, Pagophilus*, and *Phoca vitulina* (all state 0). Again, Ridgway (1972) applied this character to distinguish *Phoca* spp. (state 0) from *Pusa* spp. (state 1). Heeding the problems mentioned under the previous character, an apomorphic dorsal ridge was present only in *Pusa sibirica* and then only polymorphically.

194) mystacial whiskers: 0 = smooth; 1 = beaded (Wyss 1988a).

Systematic differences in the form, distribution, and number of vibrissae are apparent throughout the pinnipeds (see Ling 1977). One striking morphology [although it may be dependent on the thickness of the whisker (Chapskii 1967)] is the apomorphic derivation of beaded mystacial whiskers. This condition, which gives the whisker a wavy outline, is found to varying degrees in all phocids except *Erignathus* and *Monachus* spp., which exhibit the typical carnivoran pattern (also found in the otarioids) of smooth whiskers (King 1983; Wyss 1988a). This distribution has been interpreted to support the primitive position of *Monachus* spp. within the phocids, with a convergent reappearance in *Erignathus* (Wyss 1988a). As suitable material was often lacking to make direct observations, we relied heavily upon the data of Wyss (1988a) to fill in any gaps.

The distribution above is indicated here. Beaded whiskers describe a synapomorphy of the phocids with *Erignathus* and *Monachus* spp. independently reversing to re-obtain the plesiomorphic condition. However, this character does not support a basal position for *Monachus* spp. as supposed by Wyss (1988a). Instead the two genera independently re-obtain smooth mystacial whiskers.

195) secondary hairs: 0 = (largely) absent; 1 = present (Wyss 1988a).

Carnivoran hair occurs in discrete units of a central primary hair surrounded by numerous, smaller secondary hairs (Scheffer 1964; Wyss 1988a). As noted by Wyss (1988a), characters involving either the morphology or the distribution of hair within these units appear to be a potentially valuable, but sadly neglected area of pinniped systematics (see Ling 1978). One interesting variation on the "monotonous" pinniped hair pattern (Scheffer 1964: 299) is the virtual lack of the secondary hairs in *Odobenus, Mirounga* spp., and *Monachus* spp. At best, secondary hairs appear in one out of every 10 hair units in these taxa, while some lack secondary hairs altogether (Scheffer 1964; Ling & Bryden 1981; Wyss 1988a). As we could not make direct observations for this character, the data of Wyss (1988a) were used. Parallel apomorphic losses of the secondary hairs in each of the three genera above are indicated.

196) relative overall size of males and females: 0 = females smaller than males; 1 = females subequal to males; 2 = females larger than males (Ralls 1976; Kovacs & Lavigne 1992; McLaren 1993).

Sexual dimorphism in which the male is larger than the female is common throughout the Caniformia. This sexual dimorphism tends to reach an extreme in the otariids, where the male may be four and a half times the size of the female in some species. Phocids exhibit both sexual dimorphism and monomorphism, but are unusual in that females are larger than males in certain species (Ralls 1976; Kovacs & Lavigne 1992). In some phocids, corresponding sexual differences are apparently noticeable with respect to the robustness of the skull (Allen 1887, 1902).

Data for this character were obtained exclusively from the literature. Sources include Bertram (1940), Ralls (1976), Bigg (1981), Bonner (1981), Burns (1981), Frost & Lowry (1981), Kenyon (1981a, 1981b), Kooyman (1981a, 1981b, 1981c), Ling & Bryden (1981), McGinnis & Schusterman (1981), Odell (1981), Ray (1981), Reeves & Ling (1981), Ronald & Healey (1981), King (1983), Nowak (1991), and McLaren (1993). Whenever

possible, preference was given to those sources employing growth curves (e.g., McLaren 1993) or statistics (e.g., Ralls 1976), as they presumably would be less prone to sampling effects than isolated descriptions. As well, lengths were preferentially used to judge size rather than the more commonly used, and often more appropriate, measure of mass. As noted by McLaren (1993), weights are often not recorded for pinnipeds, and the high seasonal variation in pinniped blubber stores makes mass a less reliable criterion for judging size in these animals.

The plesiomorphic condition among the Caniformia is for the male to be larger than the female. This is found universally among all outgroups and is retained into the basal members of each phocid subfamily. Beyond this, the trend within each subfamily is for parallel derivations of monomorphism. This occurs for the phocine clades *Erignathus, Histriophoca*, plus *Pagophilus*; and *Pusa hispida* plus *Pusa sibirica*. As well, it characterizes the lobodontines plus *Monachus* spp., with *Hydrurga* and *Ommatophoca* convergently deriving the condition whereby the female is the larger sex.

Summary

Several features of the character set presented above (and, indeed, the data matrix as a whole) need to be stressed. This data matrix is one of the most comprehensive ever compiled (with respect to the number of taxa and morphological characters) to answer the question of phocid phylogeny. To our knowledge, the only other comparable matrix is that of Berta & Wyss (1994). But, beyond its sheer size, another advantageous feature of the matrix lies in the wide range of osteological characters that were employed, originating from virtually all regions of the organism. Most of these characters appear to be phylogenetically informative (but see below), including many of the 28 that were excluded from the analysis. In most cases, these latter characters were excluded as they were deemed to be redundant when considered in the light of other characters. This primarily reflects presence of "character pairs", where the first character examined for the presence of a feature, while the second detailed the morphology of that feature. However, in some cases, redundant characters reflected an inferior coding scheme (characters #18, 32-36, and 100). Only five characters were excluded a priori because we felt that they were of a dubious nature (characters #1, 2, 90, 124, and 129). However, of those apparently phylogenetically informative characters that remained, many could be improved still further (i.e., have their information content increased) through recoding to remove the apparent a posteriori cases of homoplasy (i.e., non-homologous similarity) within them as advocated by Hennig (1966). (It should be noted that very few characters, discounting within terminal changes, can be seen to possess a "clean" distribution free of any homoplasy.) Largely, this involves a refinement of the coding scheme to distinguish between morphologically very similar, but non-homologous character states (e.g., see character #116).

Several discrepancies can be noted between historical observations of some characters and our observations. No doubt, this can be traced, in part, to the unusually high intraspecific variation among cranial features in pinnipeds. Thus, both sets of observations might well be accurate, but only with respect to the specimen(s) that they were obtained from [and within the bounds of the subjective judgement of different researchers for many qualitative

features (e.g., small versus medium versus large)]. However, another source for any discrepancies might be that we have recorded data for each individual species, whereas many previous studies attempted to describe features that were presumed to apply throughout, or felt to be primitive for, some higher level taxon (e.g., King 1966; Wyss 1988a; Wozencraft 1989; Berta 1991). By examining all phocid species, we believe that we have shown that some of these generalities of phocid (or phocine, or monachine, ...) morphology do not necessarily hold absolutely among all of the concerned species. Finally, some inconsistencies between the inferred evolutionary pathways can also be noted. In most cases, this is due to the pathways being derived from different cladograms. However, in a fair number of other cases [most notably, those arising from Wyss (1988a)], the historical evolutionary pathway was shown to be only one of two equally parsimonious possibilities, corresponding to the singular use of only one optimization criterion available for character reconstruction.

Yet, the most disconcerting contradiction arises when the characters are viewed individually, as opposed to collectively. Together, all of the 168 included characters produced a very clean solution, with a somewhat surprisingly low number of equally most parsimonious (and slightly less than most parsimonious) solutions (see **Overall Parsimony Analysis** and **Statistical Tests**). However, when viewed individually, as in this section, very few characters directly and unequivocally indicate the overall solution that they do as a group (i.e., Fig.5B). This is even more apparent when the entire data matrix is divided into process partitions (sensu Bull et al. 1993; i.e., the characters were roughly divided into distinct anatomical regions) and analyzed separately (Fig.25). (Note that in order to generate character sets of sufficient size to yield reasonable resolution, characters originating from the forelimb, pelvis, hind limb, and atlas were grouped as "post-cranial" characters, while those from the bony falx and tentorium, dorsal braincase, and mandible, and all soft-anatomical features were grouped as "miscellaneous" characters.) Although the resolution is surprisingly good given the very reduced number of characters per taxon (due, in part, to the unusually high number of multistate characters, which can support more putative synapomorphies per character), none of the indicated cladograms really supports a solution comparable to the overall solution. Monophyly of the phocids, one of the strongest nodes in the overall solution, is only indicated in the consensus solutions of the character sets from the basicranial, teeth (which is to some degree an artifact of our coding many teeth characters as being inapplicable for the outgroup taxa, thereby forcing a monophyletic Phocidae), and miscellaneous regions (Fig.25D, E, and G). Monophyly of the phocid subfamilies is even rarer, being indicated only by the basicranial (Phocinae only) and post-cranial (both Monachinae and Phocinae) character sets (Fig.25D and F).

Of the individual results worth noting, the now abandoned Cystophorinae (= *Cystophora* plus *Mirounga* spp.) is clearly supported by both snout and teeth characters (Fig.25A and E). This distribution of support corresponds quite nicely with the major features used to define the Cystophorinae – a 2/1 incisor formula and some form of inflatable nasal proboscis in the adult males, plus some additional minor characteristics from the same regions (see King 1966; Ridgway 1972) – which were based on feeding specializations and sexual selection (McLaren 1975). Additionally, it appears that even the distinctive

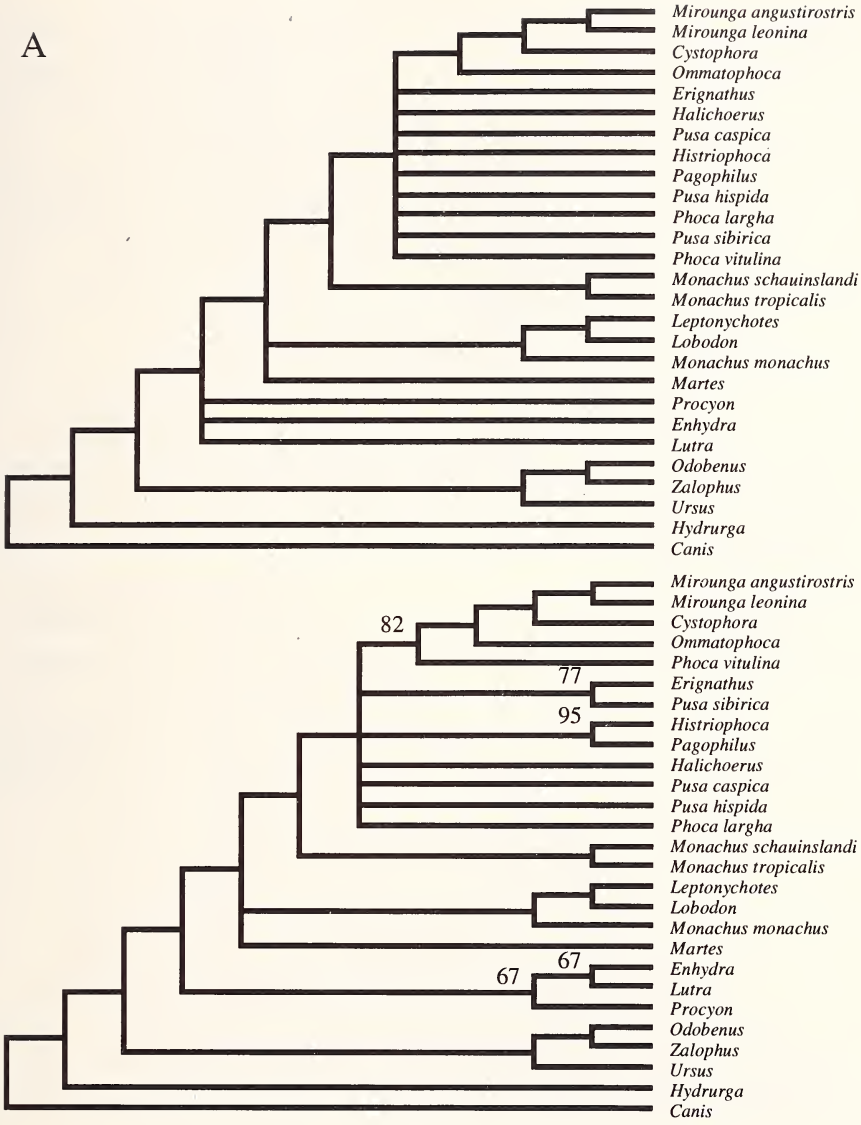

Fig.25A: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (A) snout (18 characters, n = 66 trees, length = 5,667 steps, CI = 0.486, HI = 0.710, RI = 0.701, RC = 0.474). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions.

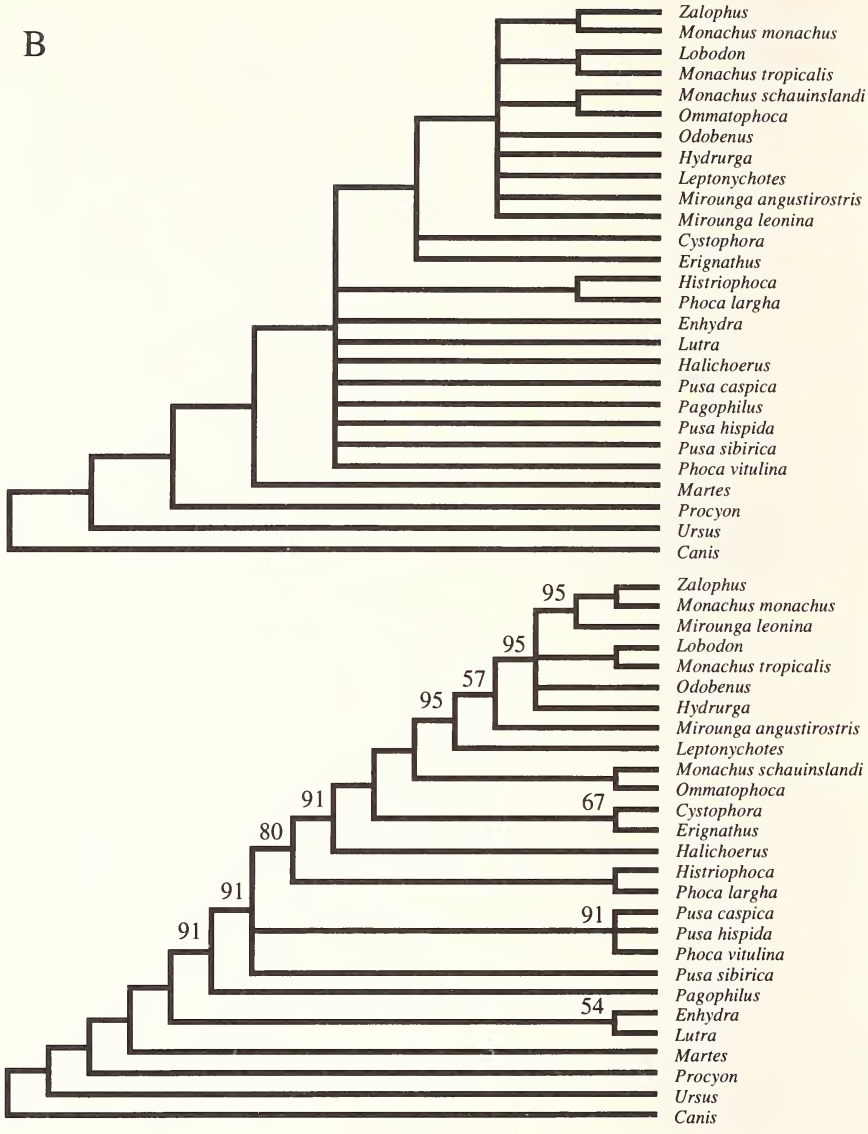

Fig.25B: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (B) orbit (25 characters, n = 334 trees, length = 10,032 steps, CI = 0.477, HI = 0.759, RI = 0.646, RC = 0.449). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions.

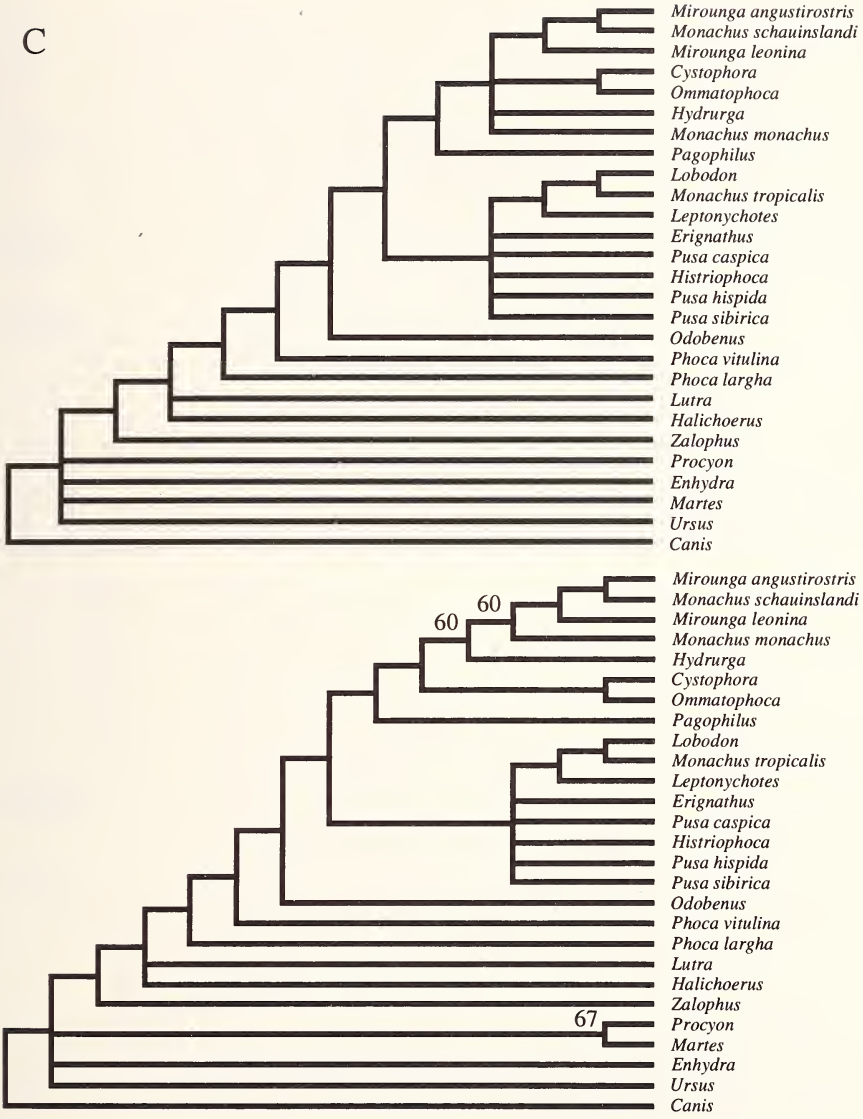

Fig.25C: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (C) palate and ventral side of snout (16 characters, n = 720 trees, length = 7,251 steps, CI = 0.718, HI = 0.784, RI = 0.664, RC = 0.477). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions.

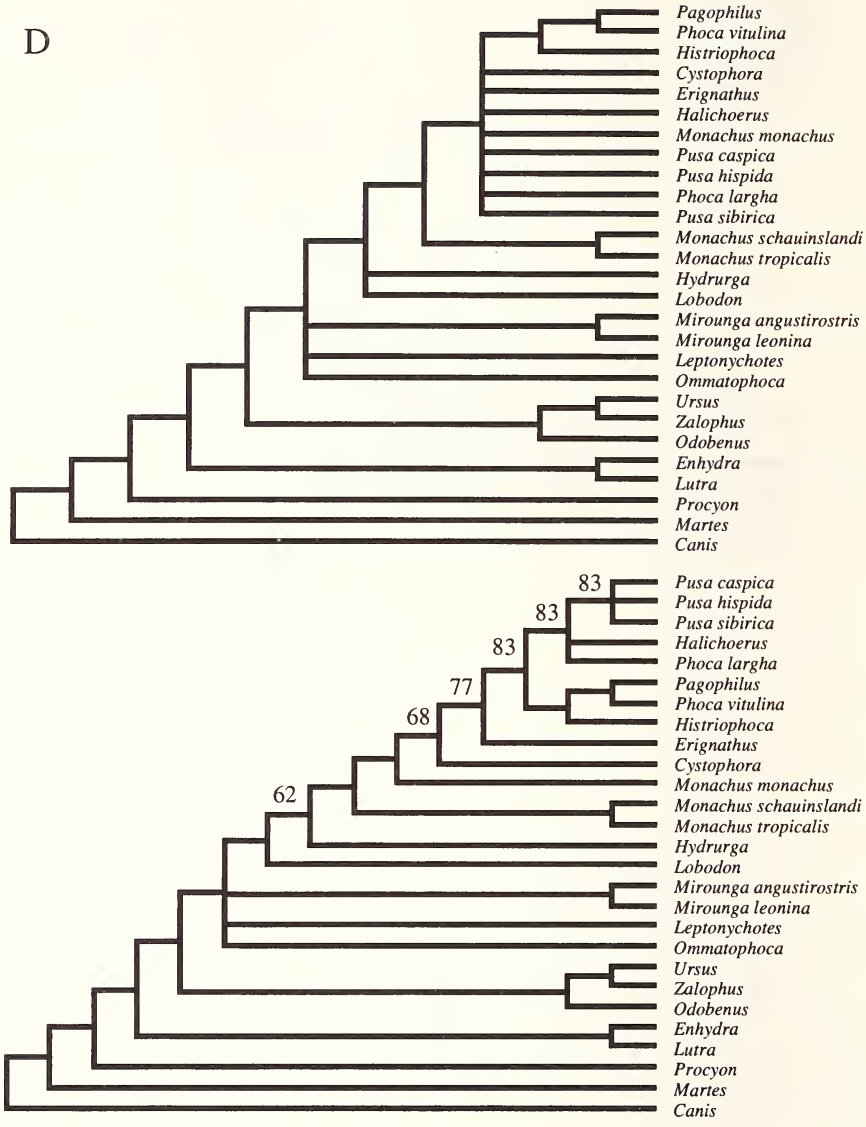

Fig.25D: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (D) basicranial region (38 characters, n = 195 trees, length = 12,360 steps, CI = 0.489, HI = 0.705, RI = 0.700, RC = 0.475). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions.

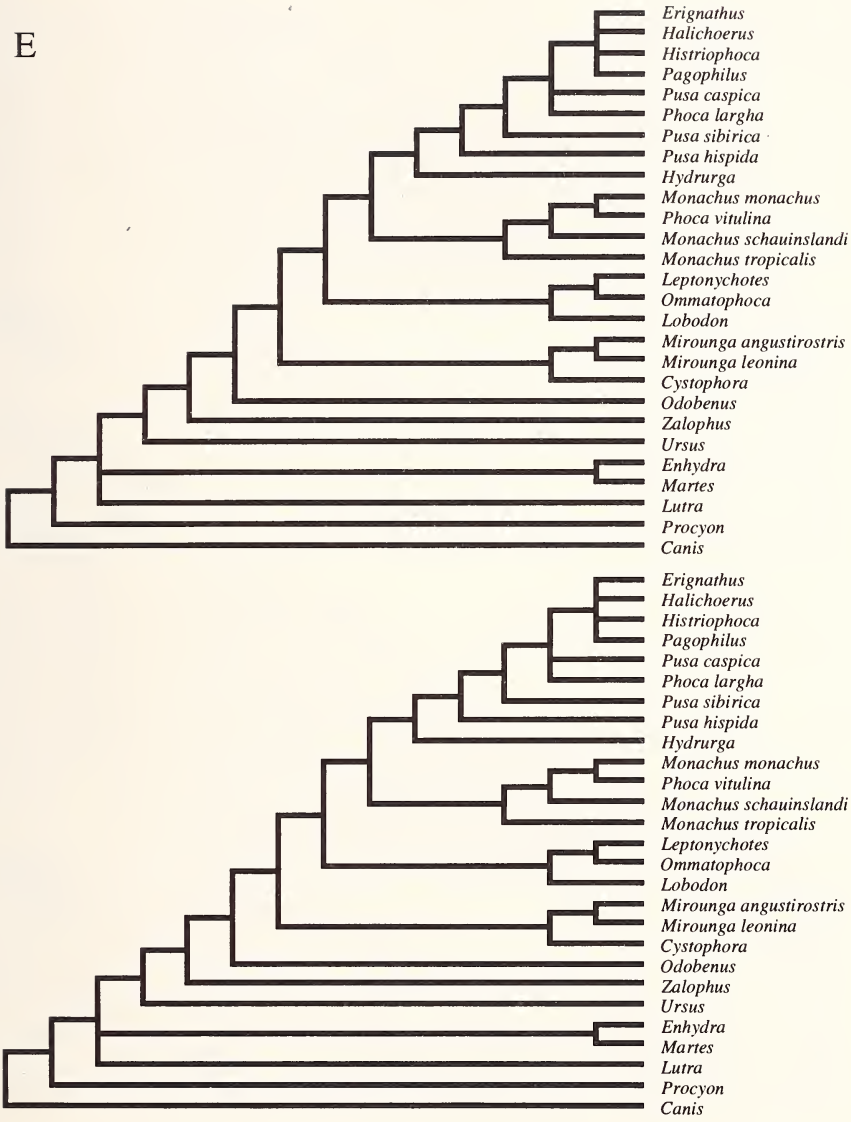

Fig.25E: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (E) teeth (22 characters, n = 12 trees, length = 6,912 steps, CI = 0.749, HI = 0.694, RI = 0.762, RC = 0.570). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where all nodes were found in 100% of the equally most parsimonious solutions.

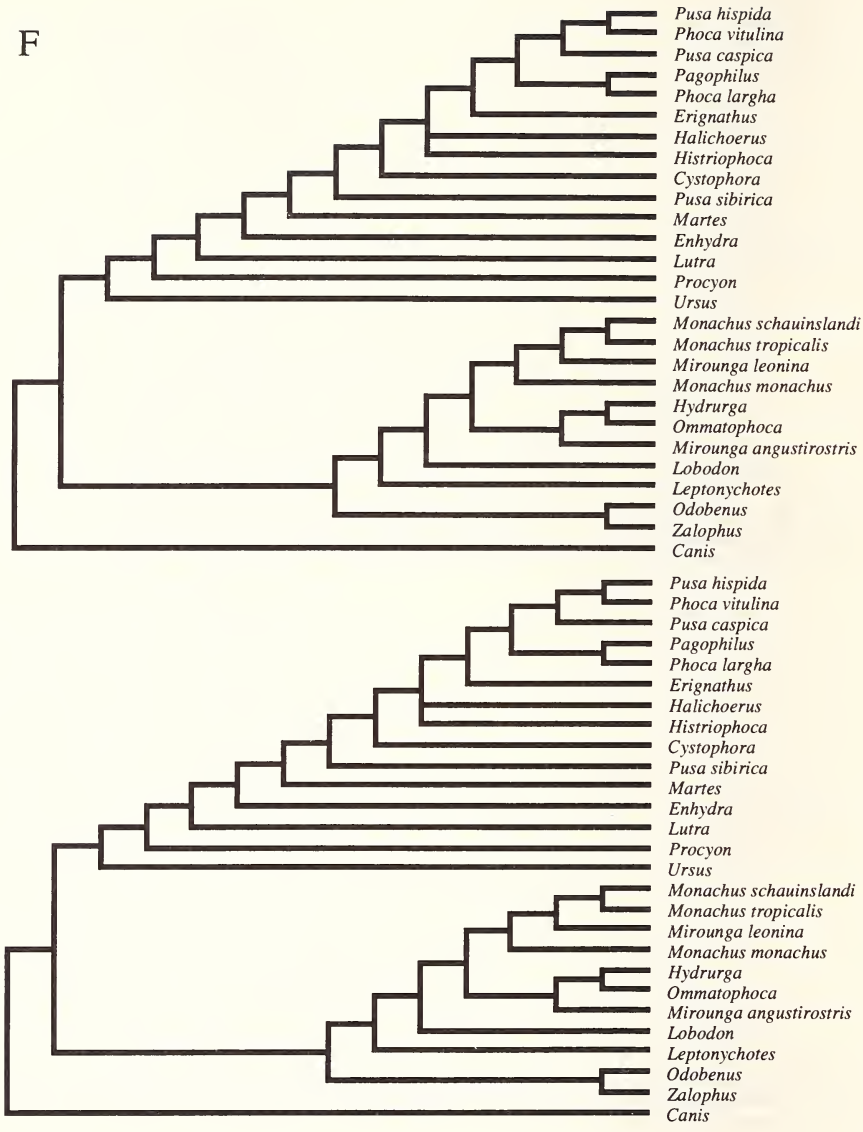

Fig.25F: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (F) postcranial region (32 characters, n = 3 trees, length = 14,883 steps, CI = 0.725, HI = 0.787, RI = 0.777, RC = 0.563). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where all nodes were found in 100% of the equally most parsimonious solutions.

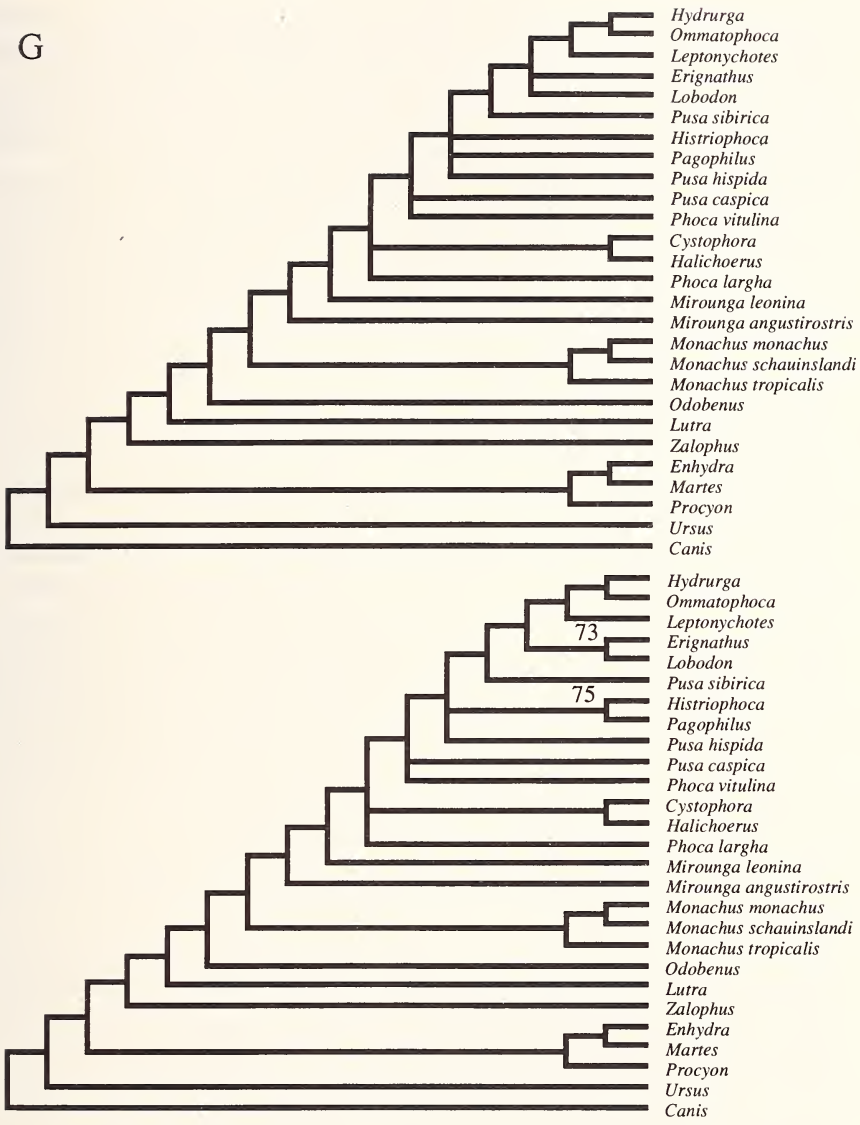

Fig.25G: Consensus solutions (top – strict algorithm; bottom – majority rule algorithm) resulting from a parsimony analysis of the inversely weighted data matrix subdivided according to the region of character origin: (G) miscellaneous features (17 characters, n = 44 trees, length = 6,366 steps, CI = 0.767, HI = 0.758, RI = 0.773, RC = 0.593). Lengths and goodness-of-fit statistics apply only to the majority rule consensus solution, where, unless otherwise indicated, all nodes were found in 100% of the equally most parsimonious solutions.

form of the phocid pelvis (de Muizon 1982a) is not sufficient to assure the monophyly of the phocids over the whole of the post-cranial features (Fig.25F). However, the apparently distinctive nature of the monachine post-cranial morphology as a whole (see Hendey & Repenning 1972; Wyss 1988a) is indicated here, with the monachines, together with the otarioids, being clearly separated from the remaining arctoid carnivores and the phocines.

This apparent conflict between the overall and regional solutions, and between the individual regional solutions, can be attributed to one of two causes: 1) sampling error, or 2) the presence of more than one signal within our data set. The potential effects of sampling error have perhaps been underestimated in phylogenetic analysis. It is possible that many competing hypotheses of phylogenetic relationships stem from a biased selection of characters from the universe of all possible characters. With the use of appropriately designed tests, such competing hypotheses may be shown to be statistically equivalent. Such may also be the case here. Although sampling error can never be eliminated, it can be minimized by selecting a random set of characters (or, at least, a wide range of characters) from the universe of all possible characters. The selection of a wide range of characters is the more practical option at this point in time; however, it is susceptible to the second, more serious error source, that of different signals within the process partitions.

The possibility of such additional, non-phylogenetic processes being a potential source of character covariation has been mentioned by Faith & Cranston (1992) and Hillis & Huelsenbeck (1992). An obvious example here is for the teeth, where the determining signal is likely a "functional" one, derived from the demands of food specialization within the phocids (see Chapskii 1955a; McLaren 1975). Within the more restricted and more localized regional character sets, these various signals are apparently sufficient to swamp the single (phylogenetic?) signal that predominates at the level of all characters. In all cases, these "regional signals" are also quite strong, indicating a less homoplasious solution (as indicated by the four goodness-of-fit statistics; see Fig.25) than does the "overall signal" (compare with Fig.5). This is especially true of the basicranial, teeth, post-cranial, and miscellaneous data sets. (The dramatic increase in CI for some regions is an artifact of there not being any uninformative characters included in their partitions of the entire data matrix.)

Given such strong "regional signals", we can see how the "overall signal" might have surfaced within the larger data set by examining a closely analogous situation. Wilkinson (1991) suggested that increasing numbers of homoplastic characters (which might be derived from the "regional signals" here) could be accommodated within a data set, so long as they are randomly distributed. Farris (1969) made an even stronger statement in that, given certain conditions (including the random distribution of homoplasy), the number of homoplastic characters could outnumber the number of informative ones (and by a considerable amount) without being detrimental. It would appear then that the various "regional signals" within our data matrix are so localized as to become "insignificant" at the level of the whole matrix. However, the conflicts between these "regional signals", and between each and the "overall signal", are still sufficiently strong to make the overall solution more homoplasious than any of the regional ones. The "overall signal" would appear to be a more widespread, but slightly more dilute signal than the regional ones, which are apparently very strong in certain restricted anatomical regions.

Therefore, if the desired signal in a phylogenetic analysis is the "overall signal" (see **Statistical Tests** section; although the "phylogenetic signal" could equally be one of the "regional signals"), then phylogenies based largely on a set of characters from a single localized region should be avoided. Although the morphologies of any characters obtained from this one region will likely be strongly correlated with one another, this correlation can very often arise from some non-phylogenetic process [e.g., the general resemblance of the snout in *Cystophora* and *Mirounga* spp., which is a manifestation of the morphological requirements of possessing a (convergently derived) inflatable proboscis]. Again, of the two solutions mentioned above, the more practical at this point is to examine a wide range of characters, possibly as a first step towards a total evidence approach. However, this should be done with some caution. The very different signals from the various, supposedly discrete anatomical regions beg the statistical question of whether these separate matrices should have been "pooled" in the first place (see Bull et al. 1993), a major limitation of the total evidence approach. Therefore, one would ideally want to generate a set of randomly distributed characters, as we have argued previously (see **Statistical Tests** section), but it is difficult to fathom how the degree of randomness of such a set could be ascertained. In any case, when properly applied, either method should increase the probability of generating a data matrix where the influence of the various non-phylogenetic signals is minimized, allowing the presumably more widespread phylogenetic signal to dominate and determine the resultant outcome.

It remains then for the final section to present a short summary of the phylogeny of the phocids indicated in this study, including identifying the areas of stronger and weaker support. Various selected implications of this phylogeny will also be examined, as will the lines of research still required in the area of phocid systematics.

DISCUSSION AND CONCLUSIONS

We here recap this study by first presenting an overall summary of the phylogenetic findings in light of the results of the many statistical tests performed and comparative tools employed in the **Statistical Tests** and **Comparative Tools** sections. Possible sources of error affecting the validity of any conclusions thereby reached will be analyzed, before the remainder of this section is given to such miscellaneous topics as the taxonomic implications of our proposed phylogeny of the phocids, concordance of our proposed phylogeny with other lines of evidence (primarily biogeographical and fossil), and, finally, possible future lines of research suggested by this study.

Summary of results

Virtually all of the analyses conducted in the **Overall Parsimony Analysis, Statistical Tests** and **Comparative Tools** sections point to a single common pattern, which Faith (1992) would equate with a form of Popperian corroboration. With respect to the overall solution (Fig.5B), outgroup relations clearly possess the strongest support within the cladogram, demonstrating alterations in their topology only when specifically forced to do so. However, as indicated by the constraint analyses (see **Comparative Tools** section),

and as suggested by Sarich (1976), Wayne et al. (1989), Perry et al. (1995), and C.A. Repenning (pers. comm.), the specific pattern advocated here for the outgroup interrelationships might be an unnatural resolution of what should really be a polytomy. Reasonably strong support was also obtained for the phocids as a whole and for each phocid subfamily, but, beyond this, support drops off markedly. Yet, despite relatively weak statistical support, the pattern of monachine interrelationships (and the monophyly of *Monachus* in particular) appears to be exceptionally robust, emerging unaltered in virtually every analysis (again, unless specific changes were imposed upon the subfamily). Relationships within the phocines, and especially within the Phocini (plus *Erignathus*), were demonstrably more labile, showing slightly different patterns with almost every analysis. Topological changes within the Phocini (plus *Erignathus*) could also be effected by imposing changes within the Monachinae. The analogous reverse situation was never observed.

Although many novel, non-traditional relationships are indicated within the phocids by this study, it is worth noting that most studies of phocid phylogeny that employed some form of rigorous methodology (e.g., King 1966; Burns & Fay 1970; Wyss 1988a) have, for their respective times, also advocated some fairly non-traditional relationships. As well, the novel relationships advocated here enjoy reasonable support throughout the many analyses within this study. This is particularly true of the more terminal position within the phocines advocated herein for *Erignathus*. In fact, this historically-regarded "primitive" and "monachine-like" phocine is apparently responsible for causing *Histriophoca* and *Pagophilus* to occupy a more terminal position, and possibly even a relationship based on synapomorphies and not symplesiomorphies, than they might otherwise possess without its influence. The new relationships presented for *Erignathus* likely arise from a fairer appraisal of its overall morphology, without an undue emphasis on some of its (undisputed) more primitive, monachine-like characters. Instead, *Cystophora* is proposed as the sister taxon to the remaining phocines. The similar role played by *Mirounga* within the monachines suggests that the now defunct Cystophorinae may display a large number of phocid symplesiomorphies, especially in features originating from the nasal region. This supposition is strengthened by the appearance of similar features in the fossil pinniped *Allodesmus* (Mitchell 1975), especially with its re-interpreted position as part of the sister group to the phocids (Wyss 1987; Berta 1991; Wyss & Flynn 1993; Berta & Wyss 1994). This distinctive nasal region morphology is also apparently responsible for the moderately strong tendency of *Cystophora* to form the sister taxon of the monachines. The species level approach adopted here permits paraphyly of the lobodontines, a reasonably poorly examined group whose assumed monophyletic status had apparently never been rigorously examined. However, paraphyly of this tribe is dependent on the invasion of the monophyletic *Monachus*. Like *Erignathus*, a more terminal position for *Monachus* may have been hindered historically by a disproportionate emphasis on the (again undisputed) more primitive features of this genus. But, like the other relationships within the monachines, this more terminal position for *Monachus* appears to be fairly robust.

Thus, of the five questions raised in the **Introduction**, we propose the following answers: 1) *Monachus* is monophyletic, with *M. schauinslandi* and *M. tropicalis* sharing a common

ancestor to the exclusion of *M. monachus*; 2) the Phocini are paraphyletic, as are its constituent genera *Phoca* (both sensu stricto and Burns & Fay 1970), and possibly *Pusa*; 3) the Monachinae are monophyletic; 4) the species level relationships of the phocids are as indicated in Fig.5B; and, 5) the pinnipeds are monophyletic, with lutrine affinities.

Potential sources of error

Obviously, the above conclusions must be viewed in the light of a number of qualifying statements. Perhaps the key such qualification is that we have merely presented a summary of one particular data set, using one particular method of tree reconstruction, and whose underlying distribution need not necessarily coincide with the actual phylogeny of the phocids (see also **Statistical Tests** section). Therefore, any judgment as to the accuracy of the results presented herein must ultimately derive from an assessment of the overall quality of the data set, and whether the characters examined in this study constitute a reasonably random sample from the universe of all possible characters. Given these restrictions, however, we believe that both the size and scope of our data matrix give this study several advantages over previous analyses of phocid phylogeny. To our knowledge, this study is the only species level analysis of the entire phocid family. Thus, no potential pairings of species were prevented by the assumed monophyly of any higher level taxa. As well, multiple specimens were examined for each species to attempt to account for the unusually high amount of intraspecific variation within the pinnipeds (Mivart 1885; Doutt 1942; King 1966; Ray 1976b). A wide range of characters, representing most of the osseous skeleton, were also employed, the use of which allowed for a data matrix with very few missing data points. This range of characters, moreover, provided a better overall representation of the suite of all possible characters, the impetus behind the total consensus approach to phylogenetic analysis (see Kluge 1989; Kluge & Wolf 1993). In contrast, the use of sets of characters derived primarily from single anatomical regions yielded solutions even more in conflict with the "traditional wisdom" regarding phocid phylogeny. Finally, simplifying and/or biasing assumptions (e.g., use of only a single outgroup, avoidance of polymorphic data) were avoided, hopefully resulting in a more realistic analysis.

Yet, the sources of information employed in this study still possess inherent limitations. The imposed exclusion of any fossil taxa (due to their general unavailability) could prove detrimental due to the possible effects of the exclusion of any taxa in a low level analysis such as this (Arnold 1981). Be that as it may, the extremely poor fossil record of the pinnipeds, and of the monachines in particular (Hendey & Repenning 1972; Ray 1976a), equates to a high proportion of missing (i.e., undiscovered) fossil taxa. As well, the exclusion of fossil pinniped taxa does not appear to alter the basic topology of pinniped relationships as determined from extant forms only (Flynn et al. 1988; Berta & Wyss 1994). Nonetheless, it would have been interesting at the very least, and informative in any case (particularly with respect to elucidating the evolutionary pathway of certain characters), to have included various fossil pinnipeds and putative fossil pinniped ancestors (e.g., the lutrine-like *Potamotherium*).

Of more concern is the high intraspecific variation characteristic of the pinnipeds mentioned above. This variability is so severe with respect to cranial anatomy in particular,

that Ray (1976b) regards any conclusions based on a limited number of skulls as being extremely tentative (also Davies 1958b). This potential source of error impacts primarily on such species as *Mirounga angustirostris* and *Monachus monachus*, where only a limited number of specimens were available for study (see Appendix A). Fortunately, Kesner (1994) indicates that beyond some minimal number of specimens, it is more advantageous (with respect to error and statistical power) to increase the total number of characters rather than to examine more specimens (to reduce the probability of including an incorrect character state). As well, the modified majority rule algorithm used to determine the consensus character states for each species should reduce the presence of any outright erroneous or trivial states in the data matrix, while hopefully retaining the more important polymorphisms.

As well, the type of data employed in this study might have had some effect on the overall result obtained. The discordance between phylogenies derived from morphological versus biochemical or molecular data has long been noted (see Hillis 1987; Patterson et al. 1993). This conflict has been attributed to the different assumptions and methods of analysis inherent for each data type (Hillis 1987), but may also derive from the fact that morphological and molecular data are apparently the most effective at phylogenetic reconstruction at different taxonomic levels. In assessing attempts to resolve the phylogenetic relationships of the even-toed ungulates (Mammalia: Artiodactyla), Novacek (1993) pointed out that molecular data have produced good resolution for the internal (intra-ordinal) relationships of the group, but not for its outgroup (inter-ordinal) relationships, where morphological data have performed better.

Apparently, molecular data appear to work better at the lower taxonomic levels (see Irwin & Arnason 1994: 53). At progressively higher levels, the accumulation of neutral changes should tend to obscure any phylogenetic signal, being visualized either as a reasonably high amount of homoplasy, or as a general lack of resolution (although conservative molecular regions may be more immune to this potential problem). Conversely, morphological data appear to work better at higher taxonomic levels. As well as being potentially afflicted by some or all of the problems mentioned by Arnold (1981), morphological data do not appear to be discriminatory enough to pick out some of the fine differences required for a species level analysis. Largely, this seems to stem from the traditional use of fairly obvious, but simple morphological characters (e.g., presence or absence of various processes, foramina, ...), which, when combined with the general predisposition towards binary characters, will ignore a vast assemblage of more complex, and potentially more finely discriminating, features (e.g., shape features as elucidated by some form of morphometric analysis). Apart from the increased effort required to acquire these more complex characters, their acceptance has been hindered by the perception that the features are somehow not "real" or discrete, and therefore not subject to natural selection in the same way. This latter point arises from our supposed functional and evolutionary "understanding" of morphological features, allowing us to a priori eliminate potential characters that might be unsuitable for various reasons (e.g., too homoplastic, too trivial).

This conflict between the two data types may have been manifested somewhat in this study with the acknowledgement that the pattern of outgroup relationships was generally

more strongly supported than that of the ingroup relationships. However, reasonable resolution was still found within the phocids, perhaps due to an increased number of more discriminating, non-traditional and/or multistate characters. Increased resolution is still possible, especially within the Phocini (plus *Erignathus*), where even more finely discriminating data are required to dissect the evolutionary pattern out of the rapid adaptive radiation of the group (see below).

Finally, one limitation of cladistic analysis as it applies here, and specifically as it applies to the determination of homologous features, needs to be addressed. The increasing evidence for, and consequent acceptance of pinniped monophyly (e.g., Wyss 1987; Flynn 1988; Flynn et al. 1988; Berta 1991; Cozzuol 1992; Novacek 1992; Wyss & Flynn 1993; Vrana et al. 1994; Arnason et al. 1995; Lento et al. 1995; this study), together with the interpretation that the aquatically related features of the group are homologous, and not convergent (Wyss 1988b), needs to be reconciled with available fossil evidence. Currently, the fossil record of the pinnipeds strongly indicates distinct, if not diphyletic, origins of the otarioids and the phocids, whose first appearances in the fossil record are separated by the North American continent and some seven million years (Repenning et al. 1979). However, assuming for the moment that the known fossil evidence does provide an accurate picture of pinniped origins (but see below for alternative possibilities), note that it does not automatically imply the diphyly of the pinnipeds (as has been held in the past). Granting that the modern pinnipeds all originated from the same ancestral lineage, they would still fit under the strict cladistic definition of a monophyletic group – "a group of species that includes an ancestral species and all of its descendants" (Wiley et al. 1991: 3) – so long as their common ancestor did not also give rise to some other lineage that we would not classify as a pinniped.

Of more concern, however, is that the acceptance of the scenario given above by Repenning et al. (1979) would require us to re-interpret some otherwise apparently homologous features. Even if the pinnipeds are truly (strictly) monophyletic, their separate origins from a presumably terrestrial (or, at best, only partially aquatic) ancestor (as would likely be the case given their geographic separation) would mean that most of their aquatically related characters identified here and elsewhere (e.g., Wyss 1988b) as homologies, would have to have evolved in parallel. The common appearance of such features (and possibly of some non-aquatically related ones as well) would then be a consequence of the adaptational limitations imposed by the inheritance of a common, ancestral body plan (i.e., developmental constraints; see Maynard Smith et al. 1985), possibly based on some key innovation (sensu Liem & Osse 1975; see discussion in Russell 1979), combined with the necessity of adapting to an aquatic environment. (Naturally the case for convergent characters due to developmental and functional constraints becomes even more widespread if the Pinnipedia are diphyletic.) An interesting test of this scenario involves the lutrines and the polar bear [*Thalarctos maritimus*; Corbet & Hill (1991)], species becoming increasingly adapted to an aquatic environment. Given their derivation from a reasonably similar arctoid body plan, and a continued tendency towards an increasingly aquatic existence, these species may become indistinguishable from the pinnipeds in a few million years, despite their clearly

independent origin. It is often forgotten that the interpretation of apparent homologies as true homologies in a cladistic analysis is based on parsimony. Given other lines of evidence (which need not necessarily be additional cladistic analyses), such features may turn out to be homoplastic.

We do wish to add that we do not necessarily subscribe to the view that the aquatically related features of pinnipeds are convergently derived. We merely want to point out that the potential paleobiogeographical ramifications of a monophyletic Pinnipedia have largely been ignored to date (see below).

Taxonomic implications

One inescapable consequence of any systematic study is its potential impact on the taxonomy of the group being examined. The many novel relationships posited here for the phocids would argue for a fairly dramatic re-organization of the taxonomy of this group. Although we will outline what some of these changes should be (or at least provide a list of equally acceptable options), we do not intend to propose these changes in a formal manner. They are merely presented as the logical extension of the phylogeny that we have presented.

The monophyly of both *Monachus* and of the Monachinae as a whole allows for these entities to retain their taxonomic status (as a genus and subfamily respectively), without having their names placed in quotation marks (as in Wyss 1988a; Berta & Wyss 1994). The paraphyly of the Lobodontini, meanwhile, argues for one of two solutions. The first has the Monachini (= *Monachus* spp.) subsumed within the Lobodontini, which has priority [see historical review in Scheffer (1958)]. The Miroungini (= *Mirounga* spp.) would remain as a distinct tribe. The second option is for the Lobodontini to be abolished, possibly together with all tribal designations in the monachines as suggested by Hendey & Repenning (1972) and King (1983).

Within the phocines, a similar list of choices is available for the paraphyletic Phocini: either outright abolition or the inclusion of *Erignathus*. The former option seems more tenable, as there appears to be no legitimate reason to exclude only *Cystophora* from the fairly wide range of morphological variation encompassed by such a newly defined Phocini. [Arnason et al. (1995) also indicate that the distinction between *Cystophora* and the Phocini (excluding *Erignathus*) appears to be fairly minor.] The more derived position of *Erignathus* also renders *Phoca* (sensu Burns & Fay 1970) paraphyletic. The elevation of the various subgenera to full generic status, as was done in this study, is not permissible as *Phoca* (sensu stricto), and possibly *Pusa*, would be paraphyletic. This is true regardless of whether *Phoca largha* is granted species status or not. Again, there are two possible solutions to this problem. The first, and the simplest, involves subsuming *Erignathus* as a subgenus within *Phoca* (sensu Burns & Fay). There is some precedence for this, as *Phoca* is the senior synonym for *Erignathus* (as is the case for most phocids) (see Scheffer 1958). A similar procedure has also been advocated for *Halichoerus* by Arnason et al. (1993, 1995). The second solution involves the elevation of all subgenera back to generic status, but with new generic appellations being found for *Phoca largha* and possibly *Pusa caspica*, neither of which possess available generic synonyms.

Other obvious changes are required outside of the phocids (e.g., the pinnipeds should no longer be a carnivoran suborder, but a tribe within the lutrines), but the wholesale alterations to arctoid taxonomy that this would require, even ignoring the difficulties in the application of the term "monophyly" to the pinnipeds (see above), are beyond the scope of this study.

Biogeography and fossil evidence

As a group, the phocids possess one of the more interesting biogeographical distributions among mammals. They are found in both hemispheres, but, excepting *Monachus* spp. which are the only phocids to inhabit tropical climes, are largely limited to the polar and sub-polar regions of each [see Scheffer (1958) and King (1983) for precise species ranges]. This, coupled with a postulated North Atlantic origin for the family (McLaren 1975; Ray 1976a; Repenning et al. 1979), has led to many theories as to the development of the current species distribution. It is not our intent here to develop a new biogeographic hypothesis for the phocids based on the phylogeny advocated herein, but rather to compare this phylogeny with some of the biogeographic hypotheses that have already been put forth.

The basic biogeographic theory for the phocids holds for a North Atlantic origin of the family around the early middle Miocene [15 million years before present (MYBP)]. Fully-fledged representatives of both the monachines and phocines are found in this initial fauna. The remainder of the Miocene saw the isolation of a group of phocines (later to give rise to *Pusa* spp.), and possibly isolated monachines, in the Paratethys Sea, a large ancient sea covering much of what is now eastern Europe. Other phocines and monachines continued to inhabit the North Atlantic at this time, with the monachines being the dominant form, especially on the North American side (Hendey & Repenning 1972; Grigorescu 1976; Ray 1976a; Repenning et al. 1979). Climatic deterioration during the Pliocene evoked different responses on the part of the North Atlantic phocids. The monachines largely retreated southward, retaining their pagophobic habits, while the phocines, although also retreating southward to some degree, responded more by adapting to the cooler climate (Hendey 1972; Ray 1976a).

Within the monachines, *Monachus* spp. (or ancestors thereof) are posited to have remained behind as the remainder of the subfamily continued moving southward. Two competing hypotheses exist as to how the three species of monk seal arose: a progressive westward waif dispersal from the northwest coast of Africa (Hendey 1972; de Muizon 1982a), or the interruption of the gene flow of a wide-ranging North Atlantic population (giving rise to Mediterranean and Caribbean populations), followed by waif dispersal to the Hawaiian islands (Ray 1976a). In either case, *M. schauinslandi* and *M. tropicalis* are held to share a common ancestor to the exclusion of *M. monachus* (in contrast to more recent opinion). The remaining monachines continued their southward migration either on the Pacific side of South America (Repenning et al. 1979), the Atlantic side (Hendey 1972), or on both sides (Ray 1976a; de Muizon 1982a).

Less is known about the phocines, as their poor fossil record combined with a recent post-early Pliocene and/or Pleistocene adaptive radiation (Ray 1976a) largely hinder any detailed description of the dispersal pattern within the subfamily. One theory advocates two separate dispersal movements (McLaren 1975; Ray 1976a; Repenning et al. 1979). The first movement involves an initial northward migration from the *Pusa*-like ancestors of the Paratethys Sea into the Arctic basin, followed by an eastward migration to give rise to modern *Pusa* spp. The land-locked *Pusa caspica* and *Pusa sibirica* are thus apparently remnant populations of this initial Paratethyan stock (although the case is not as clear for *P. sibirica*), rather than migrating in from the Arctic basin during the Pleistocene (see below; also McLaren 1960a; Grigorescu 1976). The second movement involves a westward migration of the remaining phocines from the North Atlantic to their current ranges. Both migrations used the Arctic basin to traverse the North American continent. A second theory (Davies 1958b), although not mentioned per se, apparently holds for a North Atlantic origin for all phocines, with subsequent migrations into the Arctic basin during interglacial periods. Repeated glacial events then divided the different species into their Atlantic and Pacific subspecies, or pushed them away from their original North Atlantic range (as was felt to be the case for *Histriophoca, Pusa caspica*, and *Pusa sibirica*). *Pagophilus* and *Histriophoca*, in particular, were posited to be sister species separated by the most recent glaciation event (Davies 1958b).

Altogether, the phylogeny of the phocids presented in this study raises several conflicts with the biogeography of the family as outlined above. These conflicts are present throughout the cladogram. Among outgroup relationships, the potential discrepancy between the increasingly accepted monophyly (likely in a strict cladistic sense) of the pinnipeds, and the separate origins of the otarioids and phocids indicated by the fossil record might be due to the inadequacies of the latter. The most parsimonious solution is for a common origin for all pinnipeds (presumably in the earlier North Pacific site), with our first record of a phocid not being until seven million years later, by which time its ancestors had migrated to the North Atlantic, either northward through the Arctic basin or southward through the Central American Seaway. Surprisingly, to our knowledge, only Costa (1993) has recently suggested such a scenario (and specifically via the southerly route), despite the continual recent allying of the Atlantic phocids with the Pacific desmatophocids (an extinct group of pinnipeds comprised of the genera *Allodesmus, Desmatophoca*, and *Pinnarctidion*) within a monophyletic Pinnipedia (Wyss 1987; Berta 1991; Wyss & Flynn 1993; Berta & Wyss 1994). Indeed, the possible biogeographical ramifications of a monophyletic Pinnipedia have been virtually ignored (e.g., see Wyss 1987:25), possibly in light of the strong counter-arguments provided by Ray (1976a: 396-397).

Of the two possible routes to the Atlantic, the southerly route is the more probable. A migration through the Arctic basin does not even appear to be feasible as the Bering land bridge generally blocked access to it from about the late Oligocene to the early Miocene (Hopkins 1967). Some northward migration might have occurred given that modern pinnipeds are capable of migrating surprising distances over land (see Scheffer 1967), something likely even more readily accomplished by their less aquatically adapted

ancestors (see also de Muizon 1982a). As well, the Bering Strait may have been infrequently open around this time (Hopkins 1967). However, a more severe obstacle to a migration through the Arctic basin is its colder climate, which would presumably hinder the progression of the pagophobic phocid ancestors (Scheffer 1967; Ray 1976a). In contrast, the Central American Seaway seems to be a more likely option. By all accounts, it was wide open throughout much of the late Oligocene to early Miocene and beyond (Davies 1958a; Berggren & Hollister 1974; Ray 1976a; de Muizon 1982a), and the use of this route does allow the phocid ancestors to maintain their warm water affinities in agreement with the supposed warm water origin of the phocids in the North Atlantic. Although the utter lack of any phocoid fossils in the reasonably well known Oligocene to Pleistocene fauna of the Pacific coast of North America has been used to argue against a common Pacific origin (Barnes & Mitchell 1975; Ray 1976a), the acceptance of a desmatophocid sister group to the phocids does much to ameliorate this. The various desmatophocid genera are known to have existed around the time of the first appearance of the phocids and their ranges extended at least to south central California for certain species of both *Allodesmus* and *Pinnarctidion* (Mitchell 1975; Repenning 1975; Barnes 1979). Thus, the phocids may represent an offshoot of one of these lineages that migrated through the Central American Seaway into the North Atlantic, as was later also held to have been done by the ancestors of the modern walrus (Repenning 1975; Repenning & Tedford 1977; Repenning et al. 1979).

Within the phocids (accepting the minimal position that the North Atlantic served as the common dispersal site of the family), the terminal position of *Monachus* spp. within the lobodontines demands either a northward re-invasion by this genus from some southern hemisphere locale, or for multiple southward invasions by the lobodontines. There is some precedent for either a northward re-invasion (albeit slight) by, or a more southerly extension of, the *Monachus* lineage. Hendey (1972) holds for a slight northward "re-invasion" by the ancestors of *M. tropicalis*, while *M. monachus* has been reported as far south as Senegal in historical times (Hendey 1972). As well, fossil allies of *Monachus* (i.e., fossil Monachini) have been reported from Peru (de Muizon 1982a), although they more likely represent an unsuccessful colonizing population. The case for *Mirounga* spp. is equivocal here, and does not speak for southward migrations on either the Pacific (e.g., Ray 1976a; de Muizon 1982a) or Atlantic coast (e.g., Hendey 1972) of South America (but see below).

The case for putative northern re-invasions becomes stronger if one examines the timing of parturition among the monachines. Among phocids, parturition typically occurs during the spring of their respective hemispheres (i.e., the beginning versus the end of the calendar year for the northern and southern hemispheres respectively). Curiously, however, the monachines *Mirounga angustirostris, Monachus monachus*, and *Monachus tropicalis* possess autumnal pupping times that coincide, in absolute terms, with those of the truly southern hemisphere monachines (Allen 1887; McLaren 1966; Hendey 1972; Bonner 1981; Kenyon 1981b; King 1983; also references in Hayssen et al. 1993). [Most European populations of *Halichoerus* also possess an autumnal pupping time (McLaren 1966; Bonner 1981; King 1983; also references in Hayssen et al. 1993), but this shift has been attributed to competition with *Phoca vitulina* for pupping sites (McLaren 1966).] The

atypical timing of parturition for the above monachines, combined with an apparent lack of alternative explanations such as competition for pupping sites, suggests a southern origin with a northern re-invasion (see Hendey 1972). In the case of *Mirounga angustirostris* in particular, this implies that *Mirounga* (or its ancestors) initially migrated southward along the Atlantic side of South America before rounding Cape Horn and moving northward along the Pacific side, as suggested by Hendey (1972).

Monachus schauinslandi presents several problems for this re-invasion hypothesis. It possesses a normal spring pupping time, although the observation that pupping may begin as early as December for this species (Kenyon 1981b; King 1983; also references in Hayssen et al. 1993) suggests that *M. schauinslandi* has perhaps shifted back towards a normal spring pupping time faster than the remaining northern monachines. Of more concern, however, is the requirement of placing *M. schauinslandi* in the Pacific. Only two routes are possible – through the Central American Seaway, as is universally suggested, or around Cape Horn, as has been postulated for *Mirounga* spp. (Hendey 1972) – and neither is adequate here. Use of the Central American Seaway possesses a time limit, with its closure to marine dispersal occurring at least three and a half to four MYBP (Ray 1976a; de Muizon 1982a). In order to accord with our proposed phylogeny, the northward migration of *Monachus* spp. from the higher southern latitudes (after their derivation from lobodontine stock) would have had to be very rapid indeed. This scenario may well be impossible when allied with the suggestion that the full adaptation of the lobodontines to the high Antarctic latitudes occurred no more than four million years ago (Ray 1976a). However, combined with the suggestion of multiple invasions of the Antarctic continent by the lobodontines (Hendey 1972; McLaren 1975; de Muizon 1982a), it may be that the divergence of the lobodontines and *Monachus* spp. occurred in the middle southern latitudes. The only other possibility, that of an early dispersal of *Monachus schauinslandi* through the Seaway (with little or no previous southward migration), would strongly contradict our cladogram, as it would presumably render this species as the sister group to the remaining monk seals, and very likely to the remaining monachines as well. This is the accepted route however, with the invasion occurring between 8.5 to 13 MYBP (Hendey 1972) or even earlier (Repenning and Ray 1977). Costa (1993) even goes so far to suggest that *M. schauinslandi* did not even migrate through the Central American Seaway with the remaining ancient phocids in the first place. An important point to keep in mind with such early dispersal hypotheses for *M. schauinslandi* is that the main Hawaiian islands are only about six million years old (although the more westerly islands of the chain such as Laysan and Midway do date from 20 to 28 MYBP respectively) (Clague & Dalrymple 1989). Therefore, if such a scenario holds, it is more than likely that the ancestors of *M. schauinslandi* remained tied to the American coast for some time before a founder population reached the Hawaiian islands.

The second route, encircling Cape Horn, is not a viable alternative either. Again, it implies an early separation of *Monachus schauinslandi* from the *Monachus* lineage, leaving *M. monachus* and *M. tropicalis* either as sister taxa, or requiring them to migrate northward in parallel, possibly on either side of the Atlantic. This latter option does have the advantage of agreeing with the current (or historical for *M. tropicalis*) distributions of the

Atlantic *Monachus* spp. However, if *M. schauinslandi* is really the sister group to the remaining monk seals [as advocated by Repenning & Ray (1977) and Wyss (1988a)], then its migration around Cape Horn into the Pacific becomes more plausible, given a terminally placed *Monachus*.

The situation for the phocines is even less clear, with the phylogeny indicated here for this subfamily supporting (or at least not outright contradicting) each of the two major hypotheses presented above. Both do possess problems, however. Monophyly of *Pusa* spp. cannot be assured here, as required for the dual Paratethyan-North Atlantic origin hypothesis, while the relatively basal position of *Phoca largha*, an exclusively western Pacific species, is problematic for a mass origin from the North Atlantic alone. Another possibility might be that only *Cystophora* and *Halichoerus* originated from the North Atlantic, while the remaining, monophyletic forms all arose from the isolated Paratethyan stock. Support for this hypothesis comes from the fact that only *Cystophora* and *Halichoerus*, together with *Pagophilus*, are normally found exclusively in the Atlantic. [The Atlantic-only distribution of *Pagophilus* might have arisen as a result of a recent split in the Arctic basin of an ancestral lineage into the sister species *Histriophoca* and *Pagophilus*, as envisaged by Davies (1958b).] Again, the reasonably basal position of *Phoca largha* is problematic, as this species would presumably be derived from the original *Pusa*-like inhabitants of the Paratethyan, whereas the reverse in indicated here. However, the *Pusa*-like nature of the Paratethyan fauna might be overstated due to the predominance of its fossil material. Other phocine lineages (primarily *Phoca*-like forms) are also represented in the Paratethyan fauna (Grigorescu 1976), and *Phoca largha* (as well as the remaining non-pusids) might have originated from one of them.

Although many of the possible biogeographical options listed here involve long distance migrations for several species, comparable movements for several extant pinniped species are known (see Scheffer 1967; Ray 1976a). These examples include stray individuals that have either been found in presumably less desirable habitats (e.g., too warm for normally pagophilic species, or too cold for the less pagophilic ones), or whose presumed travel route would require traversing such habitats.

Future directions

The study of the evolutionary biology of the phocids faces two major obstacles at the moment. Firstly, the phylogenetic relationships within the Phocini (with or without *Erignathus*) continue to be problematic. In all truth, the pattern that we advocate here is merely one in a long line of hypotheses (e.g., Chapskii 1955a; McLaren 1966, 1975; Burns & Fay 1970; de Muizon 1982a; Arnason et al. 1995; Mouchaty et al. 1995; Perry et al. 1995). More research is needed in this area with techniques better suited to such low level analyses.

One such technique involves the use of molecular data which, paradoxically, has been used more up to now to elucidate the position of the phocids within the pinnipeds (e.g., Sarich 1969a, 1969b, 1975; Arnason 1974, 1977; Haslewood 1978; de Jong 1982; de Jong & Goodman 1982). Instead, the internal phylogeny of the phocid seals has been elucidated largely through the use of (traditional) morphological data. Some initial work

has been performed using molecular data (e.g., Sarich 1976; Arnason & Widegren 1986; Shubin et al. 1990; Baram et al. 1991; Arnason et al. 1993, 1995; Mouchaty et al. 1995; Perry et al. 1995), but only a few biomolecules have been analyzed, and typically only for a very limited number of species. However, the analysis of molecular data seems to hold more promise than does morphological data [but see Cummings et al. (1995) for possible limitations of such data]. As mentioned above, molecular data appear to provide better resolution at the lower taxonomic levels, and therefore might be able to resolve the polytomy within the Phocini. As well, in contrast to their high morphological intraspecific variability, particularly with respect to the skull (Mivart 1885; Doutt 1942; Davies 1958b; Ray 1976b), pinnipeds, like most marine mammals, display an unusually low genetic variability (Arnason 1972, 1982; Shubin et al. 1990; Arnason et al. 1993). Presumably, this lower variability would allow for a clearer and stronger signal. Finally, the strong possibility of a molecular clock for some biomolecules (see Thorpe 1982) may allow for the dating of various divergence events, which, in turn, would allow for the examination of such ancillary questions as rates of speciation or extinction (see Harvey & Nee 1993).

Yet, resolution at the lower taxonomic levels within the phocids may also be provided by a morphometric analysis of morphological data. Such analyses are commonly used at the specific or intraspecific level to assess differences within or between taxa (e.g., Jolicoeur 1975; Thorpe 1975a, 1975b; Youngman 1982). By themselves, morphometric analyses only indicate degrees of similarity between taxa (Albrecht 1980); however, the results of such analyses could easily be transformed into cladistic characters [but see Farris (1990) for potential abuses of this]. This could make a vast suite of additional characters available for cladistic analyses that were previously avoided as their complexity (e.g., shape characters) makes them difficult to obtain and/or to code objectively, or because they were held to be phylogenetically uninformative. However, the phenomenon whereby two characters used in concert may show increased discriminatory power over when either is used in isolation (Lubischew 1962), allows for even seemingly uninformative characters to potentially play some phylogenetic role. As well, morphometric analyses may give us a more objective (i.e., statistical) means to judge the degree of information content in a character. Together, the cladistic analyses of both molecular data and morphological data using morphometric characters should enable a fully-resolved species level solution of the phocids. However, it should be realized that full resolution may not be possible, and that the indicated polytomy within the Phocini (plus *Erignathus* here) does, in fact, describe a real evolutionary event.

The second problem concerns the unusual biogeography of the phocids. The combination of a postulated North Atlantic origin for the phocids, plus the poor paleontological data for the family, has led to much uncertainty in attempts to explain the far-flung pattern of its extant members. These attempts are further hindered by being based largely on a rather superficial view of the phylogenetic relationships of the extant species. Of primary concern here is the tacit assumption of the monophyly of some higher level phocid taxa, the dangers of which are presented in this study. The monophyletic status of some of these taxa has also been called into question (Wyss 1988a; this study). However, with the lack of sufficient fossil evidence, any biogeographic hypothesis must minimally accord with current

systematic opinion. Ideally, the whole area of phocid biogeography needs to be re-examined, with an eye not only to paleontological and systematic data, but also to other historical lines of evidence (e.g., oceanic currents, potential migration routes, glaciation events, competition from other organisms). In the near future, however, any hypotheses will continue to be hindered by the poor fossil record of the family and that of the pinnipeds as a whole. Fortunately, interest in pinniped paleontology has increased in recent years, leading to many new finds, particularly in the southern hemisphere. We would suggest that additional effort should also be focused around the region of Central America to test the hypotheses of the initial eastward migration of the phocid ancestors through the Central American Seaway and the subsequent return migration of the ancestors of *Monachus schauinslandi*. Once all this new material is properly described and analyzed, a more comprehensive attempt at explaining the biogeographic distribution of the phocids can truly be made.

ABSTRACT

The phocid seals present an interesting puzzle within mammalian systematics. The undue attention focused on their contentious ancestral affinities (together with the ongoing debate over pinniped origins) has contributed, in part, to their internal phylogeny remaining reasonably poorly studied. Therefore, a species-level cladistic analysis was undertaken to resolve the overall phylogeny of this family. All recent phocid species were examined (including *Monachus tropicalis*), using representatives of all major extant caniform lineages as outgroups. 168 morphological characters (primarily osteological, and primarily those of the head skeleton) were examined.

A parsimony analysis using PAUP 3.1.1 revealed two equally most parsimonious solutions, each with a consistency index (corrected for uninformative characters) of 0.456. The recent supposition of a monophyletic Pinnipedia was upheld, albeit with lutrine, and not ursid affinities. However, this latter point may be an unnatural resolution of a real polytomy within the evolutionary history of the arctoids. A monophyletic Otarioidea formed the immediate sister group to the phocids. Within the phocids, reasonable support for both traditional subfamilies was found, albeit with novel relationships within each, particularly for their basal taxa. Both *Monachus* spp. and *Erignathus*, which have universally been viewed as the most primitive members of their subfamilies (Monachinae and Phocinae respectively), are held here to hold more derived positions (with strong support for a monophyletic *Monachus* as well), rendering the Antarctic Lobodontini and Arctic Phocini paraphyletic respectively. We suggest that perhaps undue attention has been focussed on the admittedly primitive features of both genera at the expense of other apparently more derived ones. Instead, the basal positions within each subfamily are suggested to be occupied by *Mirounga* spp. and *Cystophora* respectively, leading to the possibility that the diagnostic features of the now abandoned subfamily Cystophorinae may be based, to some degree, on phocid symplesiomorphies. Together with various statistical tests and comparative tools, reasonable support was indicated for this pattern of phylogenetic

relationships, albeit slightly higher among outgroup taxa. Demonstrably weak support (combined with poor resolution) was found only within the Phocini (plus *Erignathus*).

A detailed character analysis is also presented, including historical notes and the evolutionary pathway implied for each character from our cladogram. As well, comments regarding selected areas of cladistic methodology are also made.

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Authors' addresses:

Olaf R.P. Bininda-Emonds* and Anthony P. Russell Vertebrate Morphology Research Group, Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4, Canada

E-mail: olaf.bininda@zoology.oxford.ac.uk
arussell@acs.ucalgary.ca

* Current address: Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom

APPENDICES

APPENDIX A

Specimen List

A total of 286 specimens were examined. Specimens examined were skulls (including mandible) only, unless followed by: * = skeleton only; ** = skull and skeleton; *** = partial skull; **** = partial skull and skeleton; ***** = skin.

Institutions are abbreviated as follows: AMNH – American Museum of Natural History; ANSP – Academy of Natural Sciences of Philadelphia; BM(NH) – British Museum (Natural History); MCZ – Museum of Comparative Zoology, Harvard; PMA – Provincial Museum of Alberta; UAMZ – University of Alberta Museum of Zoology; UCMZ(M) – University of Calgary Museum of Zoology (Mammalia); USNM – United States National Museum (Smithsonian); UWBM – University of Washington Burke Museum.

Common and Latin names follow Wozencraft (1993) and Corbet & Hill (1991), except for the phocids, which follow Scheffer (1958) with *Phoca vitulina largha* elevated to the full species *Phoca largha*. The number in parentheses following the taxon name refers to the total number of specimens that were examined for that taxon.

Canidae

Canis lupus – grey wolf (8)
UCMZ(M): 1975.185; 1982.94; 1982.95; 1982.97; 1982.100; 1982.103; 1987.16; 1990.35**

Mustelidae

Enhydra lutris – sea otter (6)
AMNH: 215274**; 215275**
UAMZ: "A"**; "2"**; "4"**
USNM: 287288*****

Lutra canadensis – Canadian river otter (8)
AMNH: 135500; 150306**; 184646**
MCZ: 8849***
UCMZ(M): 1975.211**; 1983.5*; 1984.28**; 1993.38**

Martes americana – American pine marten (12)
AMNH: 11421; 11459; 11468; 21544**; 29057**; 29058**
MCZ: 55554***; 55555***
UCMZ(M): 1975.217; 1975.219; 1975.220**; 1992.24*

Odobenidae

Odobenus rosmarus – walrus (8)
AMNH: 15092; 19278**; 70099*
MCZ: 1723***
USNM: 396932*; 500252**; 550409
UWBM: 35215

Otariidae

Zalophus californianus – California sea lion (11)
AMNH: 18066**; 63946*; 73664; 238321*
MCZ: 6164***

Appendix A (continued)

USNM: 23332***; 49425**; 200847**; 504613*****
UWBM: 34980; 34995

Phocidae

Cystophora cristata – hooded seal (11)
AMNH: 95; 184659**; 212174***; 212185
BM(NH): 1890.8.1.4; 1956.11.7.1**
MCZ: 1084**
USNM: 188914; 188964; 241360**; 550317**

Erignathus barbatus – bearded seal (14)
AMNH: 28*; 10135; 18165; 18167; 73328***
BM(NH): 1887.9.28.1**; 1896.9.23.6; 1938.11.26.1
MCZ: 7679
USNM: 16116**; 188830; 275046; 288353*****; 396801

Halichoerus grypus – grey seal (10)
AMNH: 69487; 100191**; 125592***; 173535
BM(NH): 1951.11.28.1
MCZ: 51488**
USNM: 19837; 446405; 446408**; 504481

Histriophoca fasciata – ribbon seal (16)
AMNH: 130245**; 130246***; 182746*
BM(NH): 1965.7.19.7; 1965.7.19.9; 1966.12.7.2****
MCZ: 6545***; 52239; 52240; 52241**
USNM: 16484**; 311771***; 399449; 504959**; 504960****; unnumbered*****

Hydrurga leptonyx – leopard seal (13)
AMNH: 34920; 36200**; 77914
ANSP: 2488
BM(NH): 1901.1.4.15; 1959.12.17.4**
MCZ: 51853**
USNM: 3647***; 14492***; 32564*****; 270326**; 275208*; 550358*

Leptonychotes weddelli – Weddell seal (12)
AMNH: 32450*; 88446; 88548; 212172; 212181***
BM(NH): 1908.2.20.26**
MCZ: 51710
USNM: 269526; 270319*****; 395816***; 504875**; 550075

Lobodon carcinophagus – crabeater seal (12)
AMNH: 85513; 88494; 212179***; "C-2"
ANSP: 20557
BM(NH): 1908.2.20.57**; 1935.3.29.2
MCZ: 51851*; 52287**
USNM: 269722**; 550078; 550082*****

Mirounga angustirostris – northern elephant seal (7)
AMNH: 32676**; 32677; 32679**
USNM: 21890**; 38208***; 255975**; 260867**

Appendix A (continued)

Mirounga leonina – southern elephant seal (13)
AMNH: 48153; 48154; 48155; 70240; 77916***; 77925
BM(NH): 1908.2.20.44****; 1912.9.28.1**; 1951.7.17.1*; 1954.5.20.21
MCZ: 1178****; 1179****
USNM: 504927

Monachus monachus – Mediterranean monk seal (8)
AMNH: 73607**; 73608**
BM(NH): 1863.4.1.1**; 1894.7.27.1**; 1894.7.27.2**; 1894.7.27.3**
MCZ: 7281**
USNM: 219059*

Monachus schauinslandi – Hawaiian monk seal (11)
BM(NH): 1958.11.26.1**
MCZ: 20562; 59230**
USNM: 181250; 181252*; 243838; 243842; 243845***; 243849; 395991***; 395997***

Monachus tropicalis – West Indian or Caribbean monk seal (10)
AMNH: 10421**; 19600**; 77741**
ANSP: 4561**; 4616*; 4963**
BM(NH): 1889.11.5.1
MCZ: 7264**; 8605**
USNM: 102536

Ommatophoca rossi – Ross seal (11)
BM(NH): 1901.1.4.12; 1949.2.3.1; 1965.8.2.1*****; 1965.12.20.1*
MCZ: 51852**; 52305**
USNM: 270316**; 275206**; 302975**; 339989**; 550088*****

Pagophilus groenlandicus – harp seal (17)
AMNH: 10142; 10155; 100373***; 100377***; 150419; 180016*
ANSP: 17151***
BM(NH): 1843.6.23.8; 1938.12.10.4; 1951.11.28.2****
USNM: 188766****; 188774; 188816; 188890*****; 257031*; 504476****; 504477

Phoca largha – spotted or larga seal (9)
AMNH: 15817**; 18169; 19843; 212250
BM(NH): 1891.12.18.6; 1893.1.27.2****; 1965.7.19.12; 1965.7.19.14
MCZ: 11455

Phoca vitulina – harbour seal (11)
AMNH: 183135**; 232391**
BM(NH): 1867.10.5.4**; 1951.3.2.3*
MCZ: 5285***; 26861**
USNM: 140401*****; 188826**; 219876**
UWBM: 20224; 36047

Pusa caspica – Caspian seal (8)
AMNH: 206593
BM(NH): 1963.7.19.10; 1963.7.19.11; 1963.7.19.12; 1963.7.19.15
USNM: 341615**; 341616; 341617

Appendix A (continued)

Pusa hispida – ringed seal (13)
AMNH: 19308; 19310; 73306*
BM(NH): 1938.11.26.6; 1938.12.10.5**
MCZ: 6296***; 6297**; 7744***; 11506***
USNM: 49472*; 230854; 251645**; 305088

Pusa sibirica – Baikal seal (11)
AMNH: 185195; 185595**
BM(NH): 1963.7.19.8; 1965.9.6.1**; 1965.9.6.2**
MCZ: 29571
USNM: 175689****; 504941*****; 550028; 550034**; 550037****

Procyonidae

Procyon lotor – common raccoon (6)
UCMZ(M): 1975.206; 1982.1*; 1985.75**
PMA: 89.40.2**; 90.34.5**; 90.34.6**

Ursidae

Ursus americanus – American black bear (10)
MCZ: 675***; 3509***; 56979**; 59938**
UCMZ(M): 1975.189; 1975.191; 1975.192*; 1975.198; 1984.32
USNM: 303193*****

APPENDIX B

List of Characters

The following is the complete list of characters (and associated character states) examined in this study. A more detailed discussion of each character is found in the **Character Analysis** section. Excluded characters are preceded by an asterisk.

Snout (21 characters)

*1) relative position of external nares on snout: 0 = relatively dorsal ("high"); 1 = relatively ventral ("low").

*2) relative orientation of external nares on snout: 0 = vertical; 1 = horizontal.

3) shape of anterior margin of premaxilla in dorsal view: 0 = flat, square, or bi-lobed; 1 = tapered and/or rounded.

4) triangular lateral extensions of premaxilla into maxilla in dorsal view: 0 = absent; 1 = rudimentary or present.

5) visibility of ventral portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible.

6) visibility of middle portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible; 9 = n/a – middle portion not present.

7) visibility of dorsal portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible; 9 = n/a – dorsal portion not present.

8) shape of ventral portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex.

9) shape of middle portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – middle portion not present.

10) shape of dorsal portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – dorsal portion not present.

11) contact between nasal processes of premaxilla and nasals: 0 = none; 1 = little (less than width of nasal processes); 2 = broad (greater than or equal to width of nasal processes).

12) length of nasal processes of premaxilla along maxilla: 0 = extend only part way to nasals; 1 = extend fully or virtually fully to nasals.

13) shape of anterior margin of nasals (ignoring contribution of nasal suture): 0 = flat or broadly indented; 1 = lobular (uni-, bi-, or tri-lobed).

14) relative lengths of anterior prongs of nasal bones with a trident-shaped (= tri-lobular) morphology: 0 = lateral prongs greater than medial prong; 1 = lateral prongs subequal with medial prong; 2 = lateral prongs less than medial prong; 9 = n/a – nasal bones not trident-shaped.

15) visibility of nasal septum in dorsal view: 0 = does not extend beyond nasals (not visible); 1 = extends beyond nasals (visible).

16) shape of posterior edge of nasals, I: 0 = v-shaped (convergent); 1 = w-shaped (divergent).

17) shape of posterior edge of nasals, II: 0 = pointed; 1 = rounded.

*18) shape of posterior edge of nasals, III: 0 = pointed v-shape; 1 = rounded v-shape; 2 = rounded w-shape; 3 = pointed w-shape.

19) distinct caninus fossa: 0 = absent; 1 = present.

20) depth of unnamed fossa on ventrolateral side of premaxilla: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

21) anterior opening of infraorbital canal relative to nasolacrimal foramen: 0 = anterior; 1 = ventral (or posterior).

Orbit and zygomatic arch (35 characters)

22) swelling of maxilla anterior to zygomatic arch: 0 = absent; 1 = present.

*23) distinct preorbital process of maxilla: 0 = absent; 1 = present.

24) size of preorbital process of maxilla: 0 = small; 1 = medium; 2 = large; 9 = absent.

*25) distinct postorbital process of maxilla: 0 = absent; 1 = present.

26) size of postorbital process of maxilla: 0 = small; 1 = medium; 2 = large; 9 = absent.

*27) nasolacrimal (= lacrimal) foramen: 0 = absent; 1 = present.

28) size of nasolacrimal foramen: 0 = small; 1 = medium or greater; 9 = absent.

29) location of inferior oblique muscle origin relative to nasolacrimal foramen: 0 = widely separate; 1 = closely adjacent.

30) lacrimal: 0 = absent / not visible; 1 = visible.

31) amount of bone reduction along maxillo-frontal suture in interorbital region: 0 = none / irregular perforations; 1 = little – small foramen or narrow fissure; 2 = great – large foramen and/or greatly widened suture.

*32) morphology of bone reduction along maxillo-frontal suture in interorbital region: 0 = none; 1 = irregular perforations; 2 = round / ovoid; 3 = inverse teardrop-shaped; 4 = roughly rectangular; 5 = crescent-shaped.

*33) shape of maxillary (anteroventral) edge of widened maxillo-frontal suture: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – maxilla and frontal in contact.

*34) shape of frontal edge (posterodorsal) of widened maxillo-frontal suture: 0 = concave; 1 = straight; 2 = convex; 9 = n/a – maxilla and frontal in contact.

*35) degree of invagination of maxillary edge (anteroventral) of widened maxillo-frontal suture: 0 = none to slight; 1 = medium or greater; 9 = n/a – maxilla and frontal in contact.

*36) degree of invagination of frontal edge (posterodorsal) of widened maxillo-frontal suture: 0 = none to slight; 1 = medium or greater; 9 = n/a – maxilla and frontal in contact.

*37) anterior process of orbitosphenoid: 0 = absent / barely extends onto palatine; 1 = present.

38) degree of anterior extension of orbitosphenoid: 0 = extends to distinctly less than one-half length of palatine; 1 = extends to about one-half length of palatine; 2 = extends to distinctly greater than one-half length of palatine; 9 = absent / barely extends onto palatine.

39) ethmoid / turbinal bones in wall of interorbital region: 0 = absent; 1 = present.

40) approach of palatine to lacrimal region: 0 = does not reach lacrimal region; 1 = reaches or almost reaches lacrimal region.

41) location of sphenopalatine vacuity: 0 = enclosed in palatine; 1 = not enclosed in palatine.

42) relationship of sphenopalatine foramen and pterygopalatine canal: 0 = totally confluent, only single foramen visible; 1 = confluent, but individually distinguishable; 2 = separate.

43) continuity of sphenopalatine vacuity and widened maxillo-frontal suture: 0 = separate; 1 = confluent; 9 = n/a – widened maxillo-frontal suture absent.

44) relative vertical position of optic foramina: 0 = in lower third of interorbital region; 1 = between lower third and upper two-thirds of interorbital region; 2 = in upper two-thirds of interorbital region.

45) intracranial openings of optic foramina of orbitosphenoid: 0 = separate; 1 = converging / intermediate; 2 = confluent.

46) interorbital septum anterior to optic foramina: 0 = absent; 1 = present.

47) continuity of bilateral optic foramina in interorbital region: 0 = not continuous, no common passage; 1 = continuous, form passage through interorbital region.

48) alisphenoid canal: 0 = absent; 1 = present.

49) location of least interorbital width: 0 = distinctly anterior to middle of interorbital region; 1 = approximately in the middle of interorbital region; 2 = distinctly posterior to middle of interorbital region.

50) location of greatest zygomatic width: 0 = anterior to glenoid fossa (i.e., within zygomatic arch proper); 1 = at level of glenoid fossa (i.e., at squamosal).

51) relative position of zygomatic arches: 0 = lower than tooth row; 1 = level with tooth row; 2 = higher than tooth row.

52) direction of arch of anterior portion of jugal: 0 = downwards; 1 = flat, no distinct arch; 2 = upwards.

53) degree of overlap of maxillary and squamosal processes of zygomatic arch, on medial surface of zygomatic arch: 0 = little or none; 1 = approach closely – maxilla and squamosal almost or in contact.

54) approach of jugal to lacrimal region: 0 = does not approach lacrimal region; 1 = reaches lacrimal region / almost touches or does touch anterior wall of orbit.

*55) dorsal process of squamosal process of zygomatic arch: 0 = absent; 1 = present.

56) degree of interlock between jugal and dorsal process of squamosal process of zygomatic arch: 0 = weak; 1 = medium; 2 = strong; 9 = dorsal process of squamosal absent.

Palate and ventral side of snout (18 characters)

*57) incisive foramina (= palatine fissure / foramen): 0 = absent; 1 = present.

58) size of incisive foramina: 0 = small; 1 = medium; 2 = large; 9 = absent.

59) posterior extension of incisive foramina: 0 = enclosed within premaxilla; 1 = contact premaxillary-maxilla suture; 2 = extend into maxilla; 9 = incisive foramina absent.

60) number of incisive foramina: 0 = one; 1 = two; 9 = absent.

61) reduction of incisive foramina: 0 = absent; 1 = present.

62) position of major palatine foramen relative to maxillo-palatine suture: 0 = anterior; 1 = on; 2 = posterior.

63) shape of maxillo-palatine suture: 0 = flat / square; 1 = rounded / triangular.

64) outline of palatine bones in ventral view: 0 = square; 1 = "butterfly-shaped".

65) shape of posterior edge of palatine: 0 = (roughly) triangular; 1 = arched; 2 = straight.

66) presence of posteriorly directed process in midline of posterior edge of palatine: 0 = absent; 1 = present.

67) morphology of notching in posterior edge of palatine: 0 = rounded; 1 = triangular; 2 = incision; 9 = none.

68) size of notching in posterior edge of palatine: 0 = small; 1 = medium; 2 = large; 9 = absent.

69) relationship of bony nasal septum to posterior edge of palate: 0 = does not reach posterior edge of palate; 1 = closely approaches / reaches posterior edge of palate.

70) orientation of pterygoid hamuli: 0 = directed laterally; 1 = in midline; 2 = directed medially.

*71) relationship of ethmoid to pterygoid on ventral surface of skull: 0 = does not contact pterygoid; 1 = contacts pterygoid.

72) degree of contact between ethmoid and pterygoid process of basisphenoid: 0 = narrow; 1 = greater than or equal to medium breadth; 9 = none.

73) relationship between pterygoid process of basisphenoid and auditory bulla: 0 = does not extend to auditory bulla; 1 = extends to auditory bulla.

74) bony constituents of wall of foramen ovale with respect to alisphenoid and squamosal: 0 = alisphenoid only; 1 = both alisphenoid and squamosal; 2 = squamosal only.

Basicranial region (43 characters)

75) visibility of the mastoid process in dorsal view: 0 = not visible; 1 = visible.

76) relative shape of basioccipital-basisphenoid region: 0 = concave; 1 = flat; 2 = convex.

*77) postglenoid (= glenoid) foramen in squamosal: 0 = absent; 1 = present.

78) size of postglenoid (= glenoid) foramen in squamosal: 0 = small; 1 = medium; 2 = large; 9 = absent.

79) shape of anterior edge of auditory bulla: 0 = concave; 1 = flat; 2 = convex.

80) inflation of ectotympanic: 0 = not inflated; 1 = slightly / moderately inflated; 2 = inflated.

81) inflation of caudal entotympanic along anteroposterior axis: 0 = not inflated; 1 = slight / moderate inflation; 2 = inflated.

82) inflation of medial portion of caudal entotympanic: 0 = not inflated; 1 = slight / moderate inflation; 2 = inflated.

83) distinct sulcus dividing ectotympanic and entotympanic portions of auditory bulla: 0 = absent; 1 = present.

84) relationship between auditory bulla and petrosal: 0 = does not cover petrosal; 1 = covers petrosal.

85) relationship between auditory bulla and paroccipital process: 0 = does not reach process; 1 = reaches (or very closely approaches) process.

86) groove separating mastoid bulla and petrosal: 0 = absent; 1 = present.

*87) hypomastoid fossa (found along posteroventral edge of the auditory bulla and containing the stylomastoid groove): 0 = absent; 1 = present.

88) depth of hypomastoid fossa: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

89) distinct petromastoid ridge connecting paroccipital and mastoid processes: 0 = absent; 1 = present.

*90) source of "paroccipital" process: 0 = occipital; 1 = occipital and mastoid; 2 = mastoid.

91) morphology of paroccipital processes: 0 = absent; 1 = elongated ridges; 2 = bumps / pillars.

92) size of paroccipital processes: 0 = small / not prominent; 1 = intermediate; 2 = large / prominent; 9 = processes absent.

93) relationship between paroccipital processes and mastoid bone: 0 = separate; 1 = adjacent / continuous; 9 = n/a – paroccipital processes absent.

94) relationship between paroccipital processes and nuchal (= lambdoidal) crest: 0 = separate; 1 = adjacent / continuous; 9 = n/a – paroccipital processes absent.

95) relative size and shape of posterior lacerate foramen: 0 = not confluent with petrobasilar fissure; 1 = confluent with petrobasilar fissure; 9 = petrobasilar fissure absent.

96) relationship between petrobasilar fissure and basioccipital-basisphenoid suture: 0 = in contact, suture unexpanded; 1 = in contact, suture greatly expanded and confluent with fissure; 9 = petrobasilar fissure absent.

97) visibility of posterior opening of carotid canal in ventral view: 0 = not visible; 1 = visible; 9 = carotid canal absent.

98) visibility of foramen of posterior opening of carotid canal in ventral view: 0 = not visible; 1 = visible; 9 = carotid canal absent.

99) direction of posterior opening of carotid canal, I: 0 = distinctly greater than 45° medially (i.e., roughly medially); 1 = roughly 45° medially; 2 = distinctly less than 45° medially (i.e., roughly posteriorly); 9 = absent.

*100) direction of posterior opening of carotid canal, II: 0 = roughly 90° (i.e., medially); 1 = distinctly greater than 45° medially but distinctly less than 90°; 2 = roughly 45° medially; 3 = distinctly less than 45° medially but distinctly greater than 0°; 4 = roughly 0° (i.e., posteriorly); 9 = carotid canal absent.

101) posteromedial bony shelf of auditory bulla extending from aperture of carotid canal to posterior lacerate foramen: 0 = absent; 1 = rudimentary or present; 9 = carotid canal absent.

102) dorsal wall of carotid canal: 0 = open; 1 = closed; 9 = carotid canal absent.

103) unidentified bone encircling posterior opening of carotid canal: 0 = absent; 1 = present; 9 = carotid canal absent.

104) opening of carotid canal in auditory bulla: 0 = anterior or anteroventral to posterior lacerate foramen; 1 = adjacent to posterior lacerate foramen; 9 = carotid canal absent.

*105) median lacerate foramen in auditory bulla: 0 = absent; 1 = present.

106) size of median lacerate foramen: 0 = small; 1 = medium; 2 = large; 9 = absent.

107) mastoid lip in region of external cochlear foramen: 0 = absent; 1 = rudimentary or present.

108) external cochlear foramen: 0 = open; 1 = closed; 9 = absent.

109) relationship between stylomastoid and auricular foramen: 0 = confluent / common; 1 = intermediate; 2 = separate; 9 = auricular foramen absent.

110) relationship of tympanohyal and stylomastoid foramen: 0 = separated; 1 = closely associated.

111) location of tympanohyal relative to stylomastoid foramen: 0 = anterior; 1 = posterior.

112) position of petrosal relative to intracranial ridges of basioccipital continuous anteriorly with the dorsum sellae: 0 = widely separate; 1 = intermediate; 2 = closely adjacent.

113) relative size of dorsal region of petrosal: 0 = unexpanded; 1 = intermediate; 2 = expanded.

114) relative size and shape of petrosal apex: 0 = absent / unexpanded and pointed; 1 = intermediate; 2 = dorsoventrally thickened and bulbous.

115) roof of internal auditory meatus: 0 = reduced; 1 = full internal auditory meatus.

116) bony spur of roof of internal auditory meatus: 0 = absent; 1 = present.

117) inflation of bullar chamber: 0 = not inflated; 1 = inflated.

Bony tentorium and bony falx (5 characters)

118) contribution of parietal to bony tentorium: 0 = none / processus tentoricus absent; 1 = contributes.

119) contribution of parietal to bony falx: 0 = none; 1 = contributes; 9 = bony falx absent.

120) ventral extension of bony tentorium: 0 = does not approach floor of braincase; 1 = approaches dorsal region of petrosal; 2 = approaches or contacts floor of braincase.

121) morphology of bony falx proper: 0 = absent; 1 = sail-shaped; 2 = vertical; 3 = inverse sail.

122) partial bony falx: 0 = absent; 1 = present.

Dorsal braincase (4 characters)

123) shape of fronto-parietal suture: 0 = flat; 1 = unilobe; 2 = bi-lobed; 3 = tri-lobed or greater.

*124) separate temporal ridges: 0 = widely spaced; 1 = approximately in midline; 9 = absent.

*125) sagittal crest: 0 = absent; 1 = present.

126) size of sagittal crest: 0 = absent, but separate temporal ridges present; 1 = small; 2 = medium; 3 = large; 9 = absent.

Teeth (23 characters)

127) number of upper incisors in one-half of jaw: 0 = zero; 1 = one; 2 = two; 3 = three.

128) number of lower incisors in one-half of jaw: 0 = zero; 1 = one; 2 = two; 3 = three.

*129) morphology of incisors: 0 = peg-like; 1 = unicuspate; 2 = caniform; 3 = complex; 9 = absent.

130) shape of upper incisors in cross-section: 0 = round; 1 = intermediate; 2 = (strongly) laterally compressed; 9 = absent.

131) relative size of upper incisors: 0 = outermost incisor about equal in size to remaining incisor(s); 1 = outermost incisor of much greater size than remaining incisor(s); 9 = n/a – only one upper incisor present per quadrant.

132) relative size of lower incisors: 0 = outermost incisor about equal in size to remaining incisor(s); 1 = outermost incisor of much greater size than remaining incisor(s); 9 = n/a – one or fewer lower incisors present per quadrant.

133) displacement of incisors (upper or lower): 0 = absent – all in line with one another; 1 = present – incisor series slanted; 9 = n/a – incisors absent or singular.

134) procumbency of incisors (upper or lower): 0 = absent; 1 = present; 9 = n/a – upper or lower incisors absent.

135) number of upper postcanines: 0 = three; 1 = four; 2 = five; 3 = six.

136) number of lower postcanines: 0 = three; 1 = four; 2 = five; 3 = six; 4 = seven.

137) morphology of postcanines: 0 = peg-like / unicuspate; 1 = triconodont; 2 = multicuspate.

138) tendency to form additional cusps in triconodont postcanines: 0 = absent; 1 = present; 9 = n/a – postcanines not triconodont.

139) tendency to lose accessory cusps in triconodont postcanines: 0 = absent; 1 = present; 9 = n/a – postcanines not triconodont.

140) size of accessory cusps in triconodont or multicuspate postcanines: 0 = small, continuous with major cusp; 1 = larger, distinct from major cusp; 9 = n/a – postcanines not triconodont or multicuspate.

141) relative size of upper postcanines: 0 = all subequal; 1 = #1 (PM^1) noticeably smaller than rest, which are subequal; 2 = #5 (M^1) noticeably smaller than rest, which are subequal; 3 = #1 and #5 noticeably smaller than rest, which are subequal; 4 = #1 and/or #5 noticeably larger than rest, which are subequal; 9 = n/a – postcanine homology uncertain.

142) relative size of lower postcanines: 0 = all subequal; 1 = #1 (PM_1) noticeably smaller than rest, which are subequal; 2 = #5 (M_1) noticeably smaller than rest, which are subequal; 3 = #1 and #5 noticeably smaller than rest, which are subequal; 4 = #1 and/or #5 noticeably larger than rest, which are subequal; 9 = n/a – postcanine homology uncertain.

143) tendency to single-rooting of upper postcanines: 0 = absent; 1 = present.

144) tendency to single-rooting of lower postcanines: 0 = absent; 1 = present.

145) relative size of gap between upper postcanines 4 and 5: 0 = smaller than other gaps; 1 = subequal to other gaps; 2 = larger than other gaps; 9 = n/a – postcanine homology uncertain.

146) crowding of postcanines (upper and/or lower): 0 = not touching / overlapping; 1 = touching or overlapping.

147) obliqueness of postcanine implantation relative to long axis of tooth row (upper and lower): 0 = straight; 1 = anterior / posterior end of postcanine directed laterally.

148) obliqueness of postcanine implantation (upper and lower) relative to vertical: 0 = straight; 1 = slanted.

149) curvature of upper tooth row (postcanines only): 0 = sigmoidal; 1 = arched; 2 = straight; 3 = kinked between $PC^{1,2}$, otherwise straight; 4 = reverse arch.

Mandible (3 characters)

150) shape of lingual face of mandible at middle postcanines: 0 = concave; 1 = flat; 2 = convex.

151) shape of posteroventral edge of mandible: 0 = rounded; 1 = jagged.

152) distinct medially directed flange along ventral edge of jaw located posterior to mandibular symphysis and ventral to posterior postcanines: 0 = absent; 1 = present.

Forelimb (17 characters)

153) relative size of scapular spine: 0 = reduced to prominent acromion; 1 = medium; 2 = prominent.

154) relative shape of axillary (= caudal) border of scapula: 0 = straight; 1 = curved.

155) distinct hook-like teres major process on scapula: 0 = absent; 1 = present.

*156) supinator (= lateral epicondylar) ridge on humerus: 0 = absent; 1 = present.

157) relative degree of development of supinator (= lateral epicondylar) ridge on humerus: 0 = weak; 1 = medium; 2 = strong; 9 = absent.

*158) deltopectoral crest on humerus: 0 = absent; 1 = present.

159) relative length of deltopectoral crest on humerus: 0 = less than or equal to one-half length of humerus; 1 = greater than one-half length of humerus; 9 = absent.

160) merging of deltopectoral crest to shaft of humerus: 0 = smooth; 1 = abrupt; 9 = absent.

161) entepicondylar foramen of humerus: 0 = absent; 1 = present.

162) distally projecting ledge (palmar process) on cuneiform of carpus: 0 = absent; 1 = present.

163) general morphology of metacarpal shaft: 0 = no lateral shaft ridges; 1 = lateral shaft ridges.

164) general morphology of metacarpal head: 0 = smooth; 1 = "palmar" ridges present.

165) cross-sectional shape of phalanges: 0 = flat; 1 = intermediate; 2 = round.

166) morphology of proximal phalangeal articular surface: 0 = hinge-like; 1 = trochleated.

167) comparative length of metacarpals I and II: 0 = I > II; 1 = I subequal to II; 2 = I < II.

168) comparative overall diameter of metacarpals I and II: 0 = I > II; 1 = I subequal to II; 2 = I < II.

169) relative degree of development of foreflipper claws: 0 = not well developed or absent; 1 = well developed, prominent.

Pelvis (8 characters)

170) eversion of wing of ilium: 0 = distinctly less than 45°; 1 = roughly 45°; 2 = distinctly greater than 45°.

*171) gluteal fossa on wing of ilium: 0 = absent; 1 = present.

172) depth of gluteal fossa on ilium: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

173) relationship of obturator nerve foramen to obturator foramen: 0 = distinctly separate, at least unilaterally; 1 = intermediate – foramina confluent, but individually recognizable; 2 = confluent – obturator nerve foramen not apparent.

174) ridges in anterior portion of obturator foramen: 0 = absent; 1 = present.

175) relative length of post-acetabular region of the pelvis: 0 = shortened (and rounded); 1 = elongated (and narrow).

176) general curvature of pelvis around long axis: 0 = relatively straight; 1 = distinctly twisted.

177) relative location of ischiatic spine (= tuber ischiad): 0 = roughly midway along the post-acetabular region; 1 = located in posterior post-acetabular region.

Hind Limb (12 characters)

178) position of greater trochanter on femur: 0 = lower than head; 1 = equal with head; 2 = higher than head.

*179) distinct trochanteric fossa on femur: 0 = absent; 1 = present.

180) depth of trochanteric fossa on femur: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

181) lesser trochanter: 0 = absent; 1 = present.

182) relative width of femur distally: 0 = gracile (less than medium breath); 1 = robust.

183) proximal fusion of tibia and fibula: 0 = unfused; 1 = rudimentary – not fused all the way around; 2 = totally fused.

184) relative degree of development of the post-tibial (= intercondyloid) fossa of tibia: 0 = weak; 1 = strong.

*185) robustness of calcaneum: 0 = smaller than or subequal to astragalus; 1 = larger than astragalus.

186) posterior process on plantar aspect of astragalus: 0 = absent; 1 = present.

187) depth of groove on plantar aspect of posterior process of astragalus: 0 = groove absent; 1 = shallow; 2 = moderate; 3 = deep; 9 = posterior process absent.

188) length of metatarsal III relative to remaining metatarsals (shape of posterior flipper margin): 0 = metatarsal III longest; 1 = metatarsal III intermediate; 2 = metatarsal III subequal or slightly shorter; 3 = metatarsal III distinctly shorter.

189) relative degree of development of hind flipper claws: 0 = not well developed or absent; 1 = well developed, prominent.

Miscellaneous (7 characters)

190) location of posterior end of cribriform plate: 0 = within interorbital region; 1 = posterior portion of interorbital region; 2 = anterior end of braincase.

191) relative position of vertebrarterial (= intervertebral) foramen of atlas: 0 = visible in dorsal view; 1 = visible in posterior view.

192) claw morphology in cross-section, I: 0 = semicircular; 1 = triangular.

193) claw morphology in cross-section, II: 0 = dorsal ridge or annuli absent; 1 = dorsal ridge or annuli present.

194) mystacial whiskers: 0 = smooth; 1 = beaded.

195) secondary hairs: 0 = (largely) absent; 1 = present.

196) relative overall size of males and females: 0 = females smaller than males; 1 = females subequal to males; 2 = females larger than males.

APPENDIX C
Character Matrix

Polymorphic data are represented as follows: A = (01), B = (012), C = (0123), D = (013), E = (019), F = (02), G = (023), H = (0234), J = (029), K = (03), L = (09), M = (12), N = (123), P = (129), Q = (13), R = (14), S = (19), T = (23), U = (234), V = (2345), W = (24), X = (245), Y = (25), Z = (29), * = (34), and 1 = (45).

The main data matrix is represented by the first 27 taxa. The remaining four taxa (Lobodontini, *Mirounga, Monachus*, and *Phoca*) replaced the species *Hydrurga, Leptonychotes, Lobodon*, and *Ommatophoca; Mirounga angustirostris* and *Mirounga leonina; Monachus monachus, Monachus schauins-*

Taxon	Characters
	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9
Canis	? ? 1 0 0 0 0 0 0 0 2 2 1 1 0 0 0 1 1 1 1 0 0 A L 1 M 1 1 **0** 1 0 0 9 9 9 9 1 2 0 1 0 2 9 0 0 0 0 1 2 1 2 2 0 1 0 9 1 2 2 1 0 1 1 0 1 1 9 9 0 1 0 9 0 0 0 2 1 2 2 1 2 2 0 1 1 ? 1 0 0 ? 2 2 0 0 0 0 0 9 9 9
Procyon	? ? 1 0 0 0 0 0 A 2 2 1 1 0 0 0 1 1 0 0 1 0 0 9 1 0 1 0 **0** 1 0 0 9 9 9 9 1 2 0 1 0 2 9 0 A 0 0 0 1 1 2 2 0 1 0 9 1 1 0 1 0 1 A 0 1 1 9 9 1 1 1 1 0 0 1 M 1 1 M 0 2 2 0 1 1 ? 1 F 0 ? 2 1 A 0 1 0 1 A 2
Enhydra	? ? 1 A 0 A 0 1 1 F 2 1 1 0 0 0 1 1 0 L 1 1 1 1 1 0 1 0 **0** A 0 0 9 9 9 9 1 M 0 1 0 0 9 0 0 0 0 0 M A 2 2 0 0 0 9 1 1 2 1 0 1 1 A B 1 9 9 0 1 0 9 A 0 0 2 A L A 0 0 2 0 0 0 0 0 0 9 0 ? 1 0 0 0 A 0 1 1 2
Lutra	? ? A 0 0 0 0 0 M 2 2 1 1 0 0 A 1 M 0 A 1 1 1 A 1 1 1 A **0** 1 0 0 9 9 9 9 1 2 0 0 0 F 9 1 A 0 0 0 2 0 2 2 0 0 0 9 1 2 2 1 0 0 0 0 1 0 9 9 0 1 0 9 1 0 0 1 1 M 0 0 0 2 0 0 0 0 A L 0 ? 1 A A 0 0 0 1 A 2
Martes	? ? 1 0 0 0 0 0 A F 2 1 1 0 0 0 0 0 0 0 1 0 1 0 1 A 1 1 **0** 0 0 0 0 9 9 9 9 1 1 0 0 0 2 9 0 1 0 1 0 1 0 2 2 0 1 0 9 1 A 0 1 0 1 1 0 1 A 9 9 0 M A E 0 1 0 1 0 9 1 1 2 2 1 1 1 ? 0 9 0 ? 2 0 1 0 9 9 0 0 0
Ursus	? ? 1 A 0 0 0 0 0 0 2 1 1 2 0 1 1 2 0 1 0 0 1 0 1 M 1 1 1 **1** 1 1 2 0 0 0 0 1 2 0 1 0 2 0 A 0 0 0 1 F 1 2 M 0 1 0 9 1 2 0 1 0 1 1 0 1 1 9 9 0 1 0 9 0 0 0 1 1 2 1 0 0 1 0 1 1 ? 1 M 1 ? 2 2 1 0 1 0 0 0 2
Odobenus	? ? 1 0 0 A 1 1 1 1 2 1 0 9 0 1 1 2 **0** 9 1 0 1 1 1 1 A S **0** 0 0 0 0 9 9 9 A S 0 0 1 0 9 2 2 0 0 1 2 0 1 M 0 0 0 9 1 A 2 0 0 0 A 0 2 0 9 9 0 2 1 A A 0 0 1 A Z 1 0 0 0 A 1 0 1 **1** 0 1 ? 1 0 1 0 1 0 1 A 2
Zalophus	? ? 1 0 0 0 0 0 0 0 0 2 1 0 9 0 1 0 3 **0** B 1 0 1 1 1 2 0 9 **0** 0 2 * 1 A 0 1 1 2 1 0 1 0 1 0 1 2 2 1 1 1 2 1 2 2 0 0 0 9 1 0 0 1 0 0 0 0 1 0 S S 0 M A L 0 0 0 1 1 0 1 0 0 A 0 1 0 0 1 2 1 ? 2 2 1 0 1 0 0 0 2
Cystophora	? ? 0 0 0 0 9 0 0 9 0 0 1 Z 0 0 1 1 1 0 1 0 1 1 A L 0 9 **0** 0 1 5 0 1 0 0 1 2 0 0 0 M 0 1 0 0 0 0 B 0 2 1 0 0 1 2 1 0 0 1 0 1 0 0 M 0 9 9 1 M 1 1 1 2 1 1 1 1 1 2 2 2 0 0 0 1 1 M 0 ? 1 1 0 0 1 0 1 0 1
Erignathus	? ? 0 0 0 0 0 0 1 B 2 1 1 0 0 0 1 1 1 9 1 0 1 0 0 9 0 9 **0** 0 1 U 0 B A 0 0 9 0 0 0 1 0 2 1 0 0 0 1 1 2 1 1 0 1 1 1 1 1 1 1 0 2 0 1 1 0 9 9 0 1 1 1 1 0 1 M 1 A M 2 2 2 0 0 0 1 1 A 0 ? 1 1 1 0 9 9 1 0 0
Halichoerus	? ? 0 0 0 0 0 1 1 0 0 1 1 1 0 0 0 0 1 0 1 A 0 9 0 9 0 9 **0** 0 1 5 0 M A 0 A Z 0 0 A 0 A 1 0 0 0 0 1 0 2 2 0 0 1 0 1 2 2 1 0 1 0 A 1 0 9 9 0 0 A S 1 0 1 2 1 B 0 2 2 2 0 0 0 1 0 9 0 ? 2 0 1 0 1 0 1 0 0
Histriophoca	? ? 0 0 0 A 0 0 0 F 2 1 1 A 0 0 0 0 1 9 1 0 1 0 0 9 0 9 **0** 0 1 ₀ 0 M 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 2 M 0 0 1 B 1 1 1 1 0 1 0 1 2 0 A 0 0 A 1 1 1 0 1 M 1 2 1 B 2 2 0 0 0 1 0 9 0 ? 2 M 1 0 1 0 1 0 1
Hydrurga	? ? 1 0 0 1 0 0 0 2 0 1 1 0 0 0 1 1 1 A 1 0 1 M 0 9 0 9 **0** 0 M 5 0 2 A 0 A E 0 0 1 0 0 2 2 0 0 0 2 0 1 1 0 0 1 1 1 M 2 1 A 0 0 A 1 0 S Z 1 1 1 1 1 0 2 0 9 0 2 1 0 A 1 0 1 1 A 0 ? 1 2 0 0 0 0 1 1 2
Leptonychotes	? ? 1 0 1 1 0 0 0 F 2 1 1 0 0 0 0 0 0 9 1 0 1 0 0 9 0 9 **0** 0 M * 0 0 A A 1 1 0 0 1 A 0 1 2 0 0 0 1 0 1 1 1 0 1 1 1 0 1 1 A 0 0 A 0 0 9 9 0 0 1 A 1 1 0 M 1 0 A 0 2 2 A 1 0 1 1 A 0 ? 1 A 0 0 0 0 1 0 2
Lobodon	? ? A 0 1 1 0 0 A 2 0 1 1 2 0 0 0 0 0 9 1 0 1 0 0 9 0 9 **0** 0 2 2 0 0 1 1 1 F A 0 1 0 1 M 2 0 0 0 2 1 1 0 0 0 1 0 1 0 1 1 0 0 A 1 0 0 1 0 1 0 0 9 1 1 0 2 1 0 1 2 2 2 0 1 0 1 1 0 0 ? 1 M 0 0 0 0 1 0 1
Mirounga angustirostris	? ? 1 0 0 1 9 0 0 9 0 0 1 9 0 0 1 1 **1** 2 1 0 1 M 0 9 0 9 **0** 0 1 5 0 F A A 1 1 1 0 1 0 0 1 0 0 0 0 2 0 M M 0 0 1 1 0 9 9 9 1 0 0 1 1 0 1 2 1 2 1 2 1 1 1 0 0 1 M 0 0 2 2 0 0 1 0 9 0 ? 2 A 0 0 0 1 A 2
Mirounga leonina	? ? 1 0 0 9 9 0 9 9 0 0 1 9 0 0 0 0 1 2 1 0 1 2 0 9 0 9 **0** 0 2 5 0 M 1 0 1 1 0 0 1 A 1 2 0 0 0 0 1 0 2 1 0 0 1 1 A L E S 1 0 1 0 1 1 9 9 1 2 1 1 1 A 0 0 1 0 0 B 2 2 0 1 0 1 0 9 0 ? 1 0 0 0 0 0 A 0 2
Monachus monachus	? ? A 0 1 1 0 0 0 2 B 1 1 9 0 0 0 0 0 0 1 0 1 1 0 9 0 9 **0** 0 2 Y 0 0 1 1 1 1 0 0 A A 1 1 2 1 1 0 1 0 2 2 0 0 1 1 1 A 1 1 1 0 A 0 1 0 1 1 1 1 0 9 1 2 1 2 1 A A 2 2 A 0 0 0 1 1 2 0 ? 1 1 0 A A 0 1 0 2
Monachus schauinslandi	? ? 0 1 A 1 0 0 0 2 2 1 1 1 0 0 1 1 0 L 1 0 0 9 0 9 0 9 **0** 0 M 4 B 2 A 0 1 0 0 0 0 0 1 A 1 0 0 0 1 0 1 1 0 0 1 1 0 9 9 9 1 A 0 0 1 0 1 2 0 0 0 9 1 2 0 M A L 1 1 1 1 1 0 0 1 1 2 0 ? M 2 0 0 0 0 1 0 2
Monachus tropicalis	? ? 0 1 A 0 0 0 0 2 2 1 1 0 1 0 0 0 0 L 1 0 A L 0 9 0 9 **0** 0 2 2 0 0 1 0 0 9 0 0 1 A 1 B 2 1 0 0 0 0 1 0 0 0 1 2 1 1 M 1 0 A 0 1 0 0 2 0 0 0 0 9 1 M 0 M A L 1 1 2 0 1 A 0 1 1 2 0 ? M 2 0 A 0 0 1 0 2
Ommatophoca	? ? 0 0 1 0 9 0 0 9 0 0 1 0 0 0 0 0 A 9 1 0 1 1 0 9 0 9 **0** 0 M 4 0 0 1 0 1 2 0 0 0 0 1 1 1 0 0 0 1 0 1 0 0 A 1 1 1 A F 1 0 1 A 0 1 0 9 9 1 A 1 A 1 A 1 1 1 0 0 0 2 1 0 1 0 1 1 A 0 ? 1 A 0 0 0 0 1 0 2
Pagophilus	? ? 0 0 0 0 0 0 0 0 2 1 1 1 0 0 A A 1 9 1 A 0 9 0 9 0 9 **0** 0 0 0 0 9 9 9 9 1 2 0 0 0 B 9 0 0 0 0 0 A 0 M M 0 0 1 A 1 M 1 1 0 0 0 0 2 0 9 9 1 1 1 1 1 0 1 M 1 2 1 0 2 2 0 0 0 1 A L 0 ? 2 1 1 0 1 0 1 0 1
Phoca largha	? ? 0 0 0 0 0 0 0 0 2 2 1 1 0 0 0 0 0 1 A 1 A 0 9 0 9 0 9 **0** 0 1 5 0 F 0 0 1 1 0 0 A A A 0 0 0 0 0 0 0 2 M 0 0 1 1 1 2 2 1 0 A 0 A 0 0 9 9 0 A 1 0 1 0 1 M 1 1 1 2 2 2 0 0 0 1 0 9 0 ? 2 0 1 0 1 0 1 0 A
Phoca vitulina	? ? 0 0 0 0 0 0 0 2 **A** 1 1 0 0 0 0 0 1 0 1 A 0 9 0 9 0 9 **0** 0 M 5 0 M 1 0 1 2 0 0 0 M 0 0 0 0 0 0 A 0 2 M 0 0 1 A 1 1 2 1 0 0 0 0 0 0 S E 0 1 0 9 1 0 1 2 1 M A A 2 2 0 0 0 1 A L 0 ? 2 0 1 0 1 0 1 0 0
Pusa caspica	? ? 0 0 0 0 0 0 0 1 2 2 1 1 A 0 0 0 0 0 1 0 1 1 0 9 0 9 0 9 **0** 0 1 5 0 2 0 0 A P 0 0 0 1 1 0 0 0 0 0 A 0 2 2 0 0 1 2 1 1 M 1 0 1 A 1 1 0 9 9 0 1 1 0 1 1 A 1 1 0 1 2 2 2 0 0 0 1 0 9 0 ? 0 9 9 9 1 1 1 0 0
Pusa hispida	? ? 0 0 0 0 0 0 0 B 2 1 1 A 0 0 0 0 1 0 1 A 0 9 0 9 0 9 **0** 0 1 5 0 2 0 0 1 M 0 0 0 1 A 0 0 0 0 0 A 0 M 2 0 0 1 1 1 M 1 0 1 0 1 A 0 9 9 0 1 A 1 0 1 M 1 1 1 2 2 2 0 0 0 1 0 9 0 ? 2 0 1 0 1 1 0 0 0
Pusa sibirica	? ? 0 0 0 0 0 0 0 A 1 2 1 1 0 0 0 0 0 1 9 1 1 0 9 0 9 0 9 **0** 0 1 5 0 2 A 0 1 2 0 0 0 0 A 0 0 0 0 0 1 0 M 2 0 0 1 0 1 1 M 1 0 1 1 0 1 1 0 S L 0 1 1 0 1 0 A 1 1 A 1 2 2 2 0 0 0 1 0 9 0 ? F L S L 1 1 1 0 0
Lobodontini	? ? A 0 1 1 0 0 0 2 0 1 1 0 0 0 0 0 A 9 1 0 1 B 1 0 9 0 9 0 9 0 M V 0 0 1 A 1 B 0 0 1 0 A M 2 0 0 0 M 0 1 A 0 0 1 1 1 A B 1 0 0 0 A A 0 S J 1 A 1 A 1 1 0 M 1 0 A F 2 B 0 1 0 1 1 A 0 ? 1 B 0 0 0 0 1 0 2
Mirounga	? ? 1 0 0 S 9 0 L 9 0 0 1 9 0 0 A A 1 2 1 0 1 M 0 9 0 9 0 0 M 5 0 B A A 1 1 A 0 1 A A M 0 0 0 0 M 0 M M 0 0 1 1 A L E S 1 0 A A 1 A S Z 1 2 1 1 1 A 0 0 1 B 0 B 2 2 0 1 0 1 0 9 0 ? M A 0 0 0 0 A A 2
Monachus	? ? 0 A A A 0 0 0 2 2 1 1 E A 0 A A 0 L 1 0 A E 0 9 0 9 0 0 2 X 0 F 1 A A E 0 0 A A 1 A M A A 0 A 0 M B 0 0 1 M A E P S A A 0 A A 0 M B A A 0 9 1 2 A M A L 1 M M A A 0 0 1 1 2 0 ? M 2 0 A 0 0 1 0 2
Phoca	? ? 0 0 0 0 0 0 0 0 2 2 1 1 0 0 0 0 0 1 L 1 A 0 9 0 9 0 9 0 0 1 5 0 2 0 0 1 M 0 0 0 A A 0 0 0 0 0 A 0 2 2 0 0 1 A 1 1 M 1 0 1 0 1 B 0 9 9 0 1 1 A 1 0 1 M 1 M 1 2 2 2 0 0 0 1 0 9 0 ? 2 0 1 0 1 A 1 0 0

APPENDIX C
Character Matrix

landi, and *Monachus tropicalis*; and *Histriophoca, Pagophilus, Phoca largha, Phoca vitulina, Pusa caspica, Pusa hispida*, and *Pusa sibirica* respectively in the condensed analysis examining the effects of the constrained monophyly of higher level taxa on phocid phylogeny.

Observations obtained from, or based primarily upon, literature values are indicated in bold face. A question mark indicates a missing observation.

Taxon	Characters
	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9
	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6
Canis	9 9 9 9 9 1 1 0 9 9 1 1 2 0 0 1 0 1 1 1 0 0 1 A 9 1 3 3 3 1 0 1 0 0 0 3 4 2 9 9 9 9 9 0 0 9 1 0 0 0 1 1 0 2 0 0 0 9 1 0 0 0 0 1 1 2 1 2 2 1 0 1 0 2 1 0 1 1 0 1 2 1 0 0 0 1 0 9 0 1 0 0 0 0 0 1 0
Procyon	4 0 1 0 0 1 0 0 9 9 1 1 2 0 0 1 0 1 1 9 2 0 0 0 1 0 0 3 3 1 0 0 0 0 0 3 3 2 9 9 9 9 9 0 0 9 1 0 0 0 1 1 0 2 0 0 1 2 1 0 0 1 A 1 1 2 1 2 1 1 0 1 1 2 A 0 1 1 A 1 2 1 0 0 1 1 0 9 0 1 0 1 0 0 0 1 0
Enhydra	4 A 1 0 0 1 0 A 9 9 0 1 2 0 0 1 0 0 1 S 2 A A 1 9 1 1 3 2 0 2 1 0 A 0 1 2 2 9 9 9 9 9 0 0 9 1 0 0 1 1 1 0 2 0 0 1 M 1 A 0 1 1 0 1 0 1 1 1 1 1 1 0 2 0 1 1 1 1 1 2 1 0 0 1 1 0 9 1 0 A 1 0 0 0 1 0
Lutra	4 0 1 0 0 1 0 A 9 9 0 1 2 0 0 1 0 0 1 0 2 2 0 ? 9 0 9 3 3 0 A 1 A 1 0 2 2 2 9 9 9 9 9 0 0 9 1 0 0 F 1 1 0 2 1 0 1 M 1 1 0 1 1 1 1 1 1 2 1 1 0 A L 2 0 1 1 1 A 1 1 1 0 0 A 1 0 9 0 1 1 1 0 0 0 1 0
Martes	0 0 0 0 0 1 0 0 9 9 1 1 2 M 0 1 0 1 1 9 2 0 0 1 9 A S 3 3 1 2 1 A 0 0 2 3 2 9 9 9 9 9 0 0 9 1 0 0 0 M 1 0 2 0 0 1 0 0 9 9 1 1 0 1 2 1 2 1 1 0 1 1 2 0 1 1 1 1 1 2 1 0 1 1 1 0 9 0 1 0 1 0 0 0 1 0
Ursus	4 0 0 0 1 1 1 0 9 9 0 1 B 2 0 1 0 1 1 1 2 0 1 0 9 1 1 3 3 M 0 1 0 0 0 2 U 2 9 9 9 9 9 1 A 9 1 0 0 M 1 1 0 2 1 A 1 1 1 1 0 0 1 1 1 2 1 1 1 1 1 1 A 2 A 0 1 1 0 1 2 1 0 0 A 1 0 9 1 1 0 1 0 0 0 1 0
Odobenus	4 0 0 0 0 1 2 0 9 9 0 1 B 2 0 1 0 1 1 A 2 2 0 1 S 0 L 1 0 9 0 9 9 9 9 0 0 0 9 9 9 9 9 1 1 9 0 0 0 1 0 1 A 1 0 0 1 1 1 1 0 0 0 0 A 2 0 0 0 0 0 0 9 1 1 1 1 1 0 0 9 1 0 0 A 1 0 9 T 0 2 1 0 0 0 0 0
Zalophus	4 0 0 0 0 1 2 0 9 9 0 1 0 0 0 1 0 0 1 1 2 2 0 0 9 1 3 3 2 0 F 1 0 0 0 T 2 A L S L 9 9 1 1 9 0 0 0 W 1 1 0 M 0 A 1 A 1 1 0 0 A 0 1 0 0 0 0 0 0 0 9 1 1 1 1 0 A 1 0 1 0 2 A 1 0 9 2 A M 1 A 0 0 1 0
Cystophora	2 0 1 0 0 1 2 0 0 2 0 0 A 2 2 0 0 1 0 0 0 1 0 2 1 0 0 2 1 0 B 1 9 0 0 2 2 A L S L 0 0 1 A 1 0 0 0 4 2 0 0 2 A 0 1 0 1 0 1 1 1 A 1 F 1 0 0 1 M 1 M M 1 1 0 0 1 1 M 0 0 2 A 0 1 3 3 1 2 1 0 0 1 1 0
Erignathus	0 1 1 0 0 1 0 0 1 2 0 0 A 2 2 0 0 1 0 A A 2 A 2 9 0 9 3 2 0 0 1 A 0 0 2 2 1 0 1 0 1 1 0 0 2 0 0 0 0 1 0 1 2 1 1 1 M 1 0 1 1 1 0 1 2 1 1 1 1 A 0 9 2 A 1 A 0 1 1 0 0 0 2 1 0 1 T 3 1 2 1 A 0 0 1 1
Halichoerus	1 0 1 0 0 1 0 A 0 2 0 0 0 2 2 0 0 1 0 0 1 1 0 G 9 1 F 3 2 0 2 1 A 0 0 2 2 1 0 1 0 Q Q 1 1 2 0 0 0 F 2 1 0 2 1 0 1 M 1 0 1 1 1 0 1 2 1 1 0 1 2 1 2 2 1 1 0 0 1 1 2 0 A 2 1 0 1 3 T 1 2 1 0 0 1 1 0
Histriophoca	2 0 1 0 0 1 0 0 0 2 0 0 0 2 2 0 0 1 0 1 1 T 0 3 0 0 0 3 2 0 M 1 1 0 0 2 2 1 0 1 0 0 R 0 0 2 0 0 0 F 1 1 1 2 1 A 1 2 1 0 1 1 1 0 1 2 1 1 0 1 2 1 2 2 A 1 0 0 1 1 2 0 0 2 1 0 1 3 2 1 2 1 0 0 1 1 1
Hydrurga	4 1 1 0 0 1 0 0 0 2 0 0 2 2 2 0 0 1 0 0 0 2 0 A 9 1 1 2 2 2 2 A 1 0 0 2 2 1 0 0 1 0 0 0 0 1 0 0 0 2 1 0 0 0 A A A L 1 0 0 0 0 0 0 F 0 0 0 0 0 0 9 2 1 0 1 1 0 0 9 0 1 2 1 0 1 F 3 0 1 0 0 0 1 1 2
Leptonychotes	4 A 1 0 0 1 M 1 1 2 0 0 2 2 M 0 0 1 0 0 0 2 0 B 9 1 1 2 M F 1 1 S 0 1 2 2 0 9 9 9 3 3 0 0 2 0 A 0 2 M 0 0 0 A 0 1 A 1 1 1 0 0 0 0 2 0 0 0 1 1 1 0 2 A A A A A 1 0 0 1 2 1 0 1 K 3 0 M 1 0 0 1 1 1
Lobodon	2 1 1 0 0 1 0 1 1 2 0 0 0 2 1 0 0 1 0 A 0 2 0 2 9 0 9 2 2 2 0 1 0 0 1 2 2 2 9 9 1 1 1 0 0 1 0 0 1 2 0 0 1 0 A 0 1 0 1 1 0 0 0 0 A 0 0 0 0 1 1 1 0 2 A 0 0 1 A 1 1 0 1 A 1 0 1 C 3 0 2 A 0 0 1 1 1
Mirounga angustirostris	4 0 1 0 0 0 9 0 0 0 0 0 0 2 2 0 0 1 0 1 A 2 0 2 9 0 9 2 1 0 0 A 9 0 0 2 N 0 9 9 9 W 3 1 1 1 0 0 1 4 0 1 0 1 0 0 A L 1 A 0 0 0 0 A F 0 0 0 1 A A L 2 A 0 1 0 0 0 9 0 1 2 A 0 1 0 3 0 1 1 ? ? 1 0 0
Mirounga leonina	4 0 1 0 A 0 9 0 0 0 0 0 0 2 2 0 0 1 0 A 0 2 0 M 1 0 0 2 1 2 0 1 9 0 0 2 2 A L L L 4 H 1 1 1 0 0 0 4 0 A 0 A A 0 A L 1 A 0 0 0 0 A 1 0 0 0 1 A 1 0 2 A 0 1 0 0 0 9 0 0 F 1 0 1 D 3 0 M 1 1 0 1 0 0
Monachus monachus	4 0 1 0 0 1 0 0 0 2 0 0 0 1 0 0 0 1 0 0 0 M 0 F 9 1 1 2 2 1 0 1 1 A 0 2 2 1 0 1 0 K A 0 0 1 1 1 0 4 1 0 A 0 1 0 1 0 1 1 0 0 0 0 0 0 A A 1 1 0 9 2 0 0 1 0 0 1 0 0 1 A 1 0 1 0 3 0 2 1 0 0 0 0 M
Monachus schauinslandi	4 1 1 1 0 1 1 0 0 2 0 0 0 0 0 0 1 1 0 0 0 1 0 1 L 0 L 2 2 0 0 1 A A 0 2 2 1 1 0 0 3 1 0 0 M 1 1 0 3 1 0 0 0 0 0 0 9 1 1 0 0 0 0 0 0 0 0 0 1 0 0 9 0 0 A 1 0 A A L 0 0 0 0 0 1 0 3 0 2 A 0 0 0 0 1
Monachus tropicalis	4 1 1 0 0 1 0 0 1 2 0 0 0 0 0 0 1 1 0 0 0 2 0 1 S A E 2 2 0 0 1 1 0 0 2 2 A S E L 3 3 0 0 1 0 1 0 3 0 0 0 A 0 A 0 9 1 1 0 0 0 0 A 2 0 0 0 1 A 0 9 1 0 0 1 0 1 0 9 0 0 A 0 0 1 F 3 0 2 1 A 0 0 0 1
Ommatophoca	4 1 1 0 A 1 2 0 1 F 0 0 0 0 2 0 0 1 0 A 0 T 0 M S 0 L 2 2 0 1 1 1 0 1 2 2 A L S L 0 0 0 0 1 0 0 0 T B 0 0 0 A 0 A L 1 A 0 0 0 0 0 0 0 0 0 0 1 0 9 2 1 0 A 0 0 0 9 0 1 M 1 0 1 N 3 0 2 A 0 0 1 1 2
Pagophilus	2 0 1 0 0 1 0 0 0 2 0 0 2 2 2 0 0 1 0 0 A 2 0 3 0 0 0 3 2 0 2 0 1 0 0 2 2 1 0 1 0 Q 1 0 0 1 0 0 0 2 1 1 1 2 1 1 1 2 1 0 1 1 1 A 1 F 1 A A 1 2 1 2 2 1 1 0 0 2 1 M 0 0 2 A 0 1 C 3 1 2 1 0 0 1 1 1
Phoca largha	M 0 1 0 0 1 0 0 0 2 0 0 0 2 2 0 0 1 0 A 0 2 0 2 S 0 L 3 2 0 2 1 1 0 0 2 2 1 1 1 0 Q 1 0 0 M 0 0 0 2 1 1 0 2 1 A 1 2 1 0 1 1 1 ? 1 2 1 1 1 1 2 1 M 2 1 1 0 0 2 1 2 0 0 1 0 0 1 1 3 1 2 1 ? ? 1 1 0
Phoca vitulina	1 0 1 0 0 1 0 0 0 2 0 0 2 2 2 0 0 1 0 A 0 2 0 M A 0 0 3 2 0 1 1 ? 0 0 2 T 1 1 1 0 1 1 0 0 2 1 1 0 2 1 1 1 2 1 1 1 2 1 0 1 1 1 0 1 0 1 1 0 1 2 1 M 2 0 1 0 0 1 1 2 0 0 2 1 0 1 A 3 1 2 1 A 0 1 1 0
Pusa caspica	0 0 1 0 0 1 0 A 0 2 0 0 F 2 2 0 0 1 0 0 A 1 0 ? A 0 0 3 2 0 2 A A 0 0 2 2 1 1 1 0 1 1 0 0 2 0 0 0 2 1 1 1 2 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 2 1 2 2 1 1 0 0 M 1 2 0 0 2 A 0 1 M 2 1 2 1 ? ? 1 1 0
Pusa hispida	1 0 1 0 0 1 0 1 A 2 0 0 0 2 2 0 0 1 0 A 0 2 0 1 0 0 0 3 2 0 2 1 A 0 0 2 2 1 1 A 0 1 1 0 0 1 0 0 0 2 1 1 1 2 1 A 1 2 1 0 1 1 1 A 1 0 1 1 0 1 2 1 M 2 0 1 0 0 1 1 2 0 0 M 1 0 1 1 3 1 2 1 0 0 1 1 1
Pusa sibirica	1 0 1 0 0 1 0 1 1 0 0 0 1 2 2 0 0 1 0 0 A 1 0 M 9 0 9 3 2 0 M 1 0 0 0 2 2 1 1 0 0 3 1 0 0 2 0 0 0 2 1 1 1 2 1 0 1 2 1 0 1 1 1 0 1 M 1 0 0 1 2 1 1 2 0 1 0 0 2 1 1 0 0 1 0 0 1 N 3 1 2 A A A 1 1 1
Lobodontini	4 1 1 0 0 1 B A 1 2 0 0 F 2 M 0 0 1 0 0 0 2 0 B 9 A S 2 2 F B 1 1 0 1 2 2 B L L E D D 0 0 1 0 0 0 2 B 0 0 0 A 0 1 0 1 A 0 0 0 0 0 F 0 0 0 A 1 A L 2 1 0 A A 0 A E 0 1 M 1 0 1 C 3 0 M A 0 0 1 1 M
Mirounga	4 0 1 0 A 0 9 0 0 0 0 0 0 2 2 0 0 1 0 A A 2 0 M S 0 L 2 1 F 0 A 9 0 0 2 N A L L L W H 1 1 1 0 0 A 4 0 A 0 A A 0 A L 1 A 0 0 0 0 A B 0 0 0 1 A A L 2 A 0 1 0 0 0 9 0 A F A 0 1 D 3 0 M 1 1 0 1 0 0
Monachus	4 A 1 A 0 1 A 0 A 2 0 0 0 A 0 0 A 1 0 0 0 M 0 B 9 A S 2 2 A 0 1 1 A 0 2 2 1 A A 0 3 D 0 0 1 A 1 0 * A 0 0 0 A 0 A L 1 1 0 0 0 0 0 F 0 0 0 1 A 0 9 B 0 0 1 0 A A L 0 A A A 0 1 0 3 0 2 1 0 0 0 0 1
Phoca	M 0 1 0 0 1 0 0 0 2 0 0 F 2 2 0 0 1 0 0 0 2 0 N 0 0 0 3 2 0 2 1 1 0 0 2 2 1 1 1 0 1 1 0 0 2 0 0 0 2 1 1 1 2 1 1 1 2 1 0 1 1 1 0 1 F 1 1 0 1 2 1 2 2 A 1 0 0 M 1 2 0 0 2 A 0 1 1 3 1 2 1 0 0 1 1 A

APPENDIX D

Branch lengths and linkages

The information contained in this appendix applies to the overall (consensus) solution presented in Fig.5B. Assigned (inversely weighted) branch lengths are listed according to accelerated transformation / delayed transformation optimization criteria. Outgroup taxa are indicated by an asterisk.

Node	Connected to node	Assigned branch length	Minimum possible length	Maximum possible length
Canis (1)*	50	1448/874	874	1448
Procyon (2)*	49	540/623	391	806
Enhydra (3)*	47	516/1123	416	1306
Lutra (4)*	46	724/1024	400	1390
Martes (5)*	48	1032/1415	799	1465
Ursus (6)*	50	1124/1390	1074	1390
Odobenus (7)*	28	1181/1564	882	2097
Zalophus (8)*	28	1223/1339	857	1755
Cystophora (9)	35	556/1005	498	1088
Erignathus (10)	30	1265/1348	1265	1348
Halichoerus (11)	34	482/665	399	715
Hydrurga (12)	41	965/1115	733	1323
Leptonychotes (13)	40	669/822	586	930
Lobodon (14)	38	1368/1268	1065	1401
Mirounga angustirostris (15)	42	574/844	416	977
Mirounga leonina (16)	42	633/749	533	957
Monachus monachus (17)	37	832/1232	674	1298
Monachus schauinslandi (18)	36	748/1181	615	1281
Monachus tropicalis (19)	36	919/802	536	1102
Ommatophoca (20)	39	844/957	658	1060
Pusa caspica (21)	32	681/831	681	831
Histriophoca (22)	29	202/385	202	385
Pagophilus (23)	29	583/666	550	699
Pusa hispida (24)	31	100/183	100	183
Phoca largha (25)	33	383/383	383	383
Pusa sibirica (26)	31	677/1093	627	1143
Phoca vitulina (27)	32	800/850	800	850
28	45	1066/1432	750	2397
29	30	332/149	149	415
30	32	590/274	274	590
31	32	699/300	300	799
32	33	183/383	133	533
33	34	608/325	275	891
34	35	955/772	356	1413
35	44	1790/791	533	2065
36	37	982/927	749	1243

Node	Connected to node	Assigned branch length	Minimum possible length	Maximum possible length
37	38	1124/816	533	1560
38	39	519/402	286	888
39	40	508/275	250	724
40	41	736/716	533	1018
41	43	874/708	433	1315
42	43	1129/993	685	1495
43	44	633/1141	333	1724
44	45	1780/1855	1272	2521
45	46	2065/766	500	2497
46	47	665/483	383	1048
47	48	1282/541	541	1548
48	49	616/532	366	948
49	50	931/824	549	1239

APPENDIX E

Apomorphy Lists (unweighted)

The information contained in this appendix applies to the overall (consensus) solution presented in Fig.5B. The changes listed are consistent between optimization criteria unless followed by: (A) = accelerated transformation (ACCTRAN) only, or (D) = delayed transformation (DELTRAN) only. Some changes were indicated by PAUP as being equivocal, but were observed to be identical between ACCTRAN and DELTRAN optimizations. The ambiguity arises from a different possible reconstruction under a third optimization criterion (MINF) that wasn't examined here, PAUP listing most within terminal changes as being ambiguous, or because the node immediately preceding the branch was ambiguous. These options are denoted by (F), (?), and (?) respectively.

Note that steps are listed as the number of changes in state for each transition (= unweighted steps). Excluded characters are preceded by an asterisk.

Branch	Character	Steps	CI	Change	
Canis ↔ node 50	19	1	0.500	1 ⇔ 0	
	59	1	0.625	2 ⇔ 0	
	76	1	0.688	2 ⇔ 1	
	79	1	0.727	2 ⇔ 1	
	80	1	0.538	1 ⇔ 0	
	88	1	0.667	0 ↔ 2	(A)
	93	1	0.625	0 ↔ 1	(A)
	95	1	0.571	0 ⇔ 1	
	97	1	0.500	9 ↔ 0	(A)
	98	1	0.857	9 ⇔ 0	
	99	1	0.571	9 ⇔ 2	
	*100	1	0.556	9 ⇔ 4	
	101	1	0.667	9 ⇔ 0	
	102	1	0.500	9 ↔ 0	(A)
	103	1	1.000	9 ⇔ 0	
	104	1	1.000	9 ↔ 0	(A)
	120	1	0.778	0 ⇔ 2	
	126	1	0.579	3 ⇔ 1	
	135	1	0.800	3 ↔ 2	(A)
	136	1	1.000	4 ↔ 3	(A)
	*156	1	0.833	0 ⇔ 1	
	157	1	0.765	9 ⇔ 1	
	159	1	0.667	0 ↔ 1	(A)
	162	1	0.600	0 ⇔ 1	
	168	1	0.571	2 ⇔ 1	
	172	1	0.625	0 ↔ 1	(A)
	174	1	0.692	1 ↔ 0	(A)
	184	1	0.750	0 ↔ 1	(A)
	191	1	0.833	0 ⇔ 1	
Canis (within terminal)	*23	1	0.429	1 ⇒ 01	(?)
	24	1	0.571	0 ⇒ 09	(?)
	26	1	0.875	1 ⇒ 12	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	123	1	0.778	0 ⇒ 01	(?)
node 50 → *Ursus*	10	1	0.647	2 ⇒ 0	
	14	1	0.538	0 ⇒ 2	
	16	1	0.667	0 ⇒ 1	
	*18	1	0.455	1 ⇒ 2	
	29	1	1.000	0 ⇒ 1	
	31	1	0.636	0 ⇒ 1	
	*32	1	0.643	0 ⇒ 2	
	*33	1	0.667	9 ⇒ 0	
	*34	1	0.750	9 ⇒ 0	
	*35	1	0.692	9 ⇒ 0	
	*36	1	0.500	9 ⇒ 0	
	43	1	0.545	9 ⇒ 0	
	81	1	0.400	2 ⇒ 0	
	82	1	0.500	2 ⇒ 1	
	88	1	0.667	0 → 12	(D)
	89	1	0.500	0 ⇒ 1	
	93	1	0.625	0 → 1	(D)
	97	1	0.500	9 → 0	(D)
	102	1	0.500	9 → 0	(D)
	104	1	1.000	0 → 1	(A)
	104	1	1.000	9 → 1	(D)
	110	1	0.500	1 ⇒ 0	
	113	1	0.375	0 ⇒ 2	
	135	1	0.800	3 → 2	(D)
	143	1	0.250	0 ⇒ 1	
	149	1	0.667	0 ⇒ 12	
	154	1	0.700	0 ⇒ 1	
	159	1	0.667	0 → 1	(D)
	167	1	0.571	2 ⇒ 1	
	170	1	0.636	0 ⇒ 1	
	188	1	0.625	0 ⇒ 1	
Ursus (within terminal)	4	1	1.000	0 ⇒ 01	(?)
	26	1	0.875	1 ⇒ 12	(?)
	44	1	0.636	0 ⇒ 01	(?)
	49	1	0.588	2 ⇒ 02	(?)
	52	1	0.692	2 ⇒ 12	(?)
	88	1	0.667	2 → 12	(A)
	88	1	0.667	1 → 12	(D)
	112	2	0.692	2 ⇒ 012	(?)
	*129	1	0.625	1 ⇒ 12	(?)
	136	2	1.000	3 → 234	(A)
	136	2	1.000	4 → 234	(D)
	144	1	0.600	0 ⇒ 01	(?)
	149	1	0.667	1 ⇒ 12	(?)
	155	1	0.889	0 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	172	1	0.625	1 → 01	(A)
	172	1	0.625	0 → 01	(D)
	174	1	0.692	0 → 01	(A)
	174	1	0.692	1 → 01	(D)
	184	1	0.750	1 → 01	(A)
	184	1	0.750	0 → 01	(D)
node 50 → node 49	9	1	0.583	0 → 1	(A)
	20	1	0.733	1 ⇒ 0	
	21	1	1.000	0 ⇒ 1	
	26	1	0.875	1 → 0	(A)
	28	1	0.800	1 → 0	(A)
	48	1	0.500	1 ⇒ 0	
	49	1	0.588	2 → 1	(A)
	58	1	0.625	2 ⇒ 1	
	78	1	0.682	2 → 0	(A)
	92	1	0.625	2 → 0	(A)
	97	1	0.500	0 → 1	(A)
	97	1	0.500	9 → 1	(D)
	102	1	0.500	0 → 1	(A)
	102	1	0.500	9 → 1	(D)
	104	1	1.000	9 → 0	(D)
	106	1	0.500	1 ⇒ 0	
	119	1	0.786	1 ⇒ 9	
	122	1	1.000	1 ⇒ 0	
	*125	1	0.333	1 → 0	(A)
	136	1	1.000	4 → 3	(D)
	161	1	0.333	0 ⇒ 1	
	178	1	0.643	0 → 1	(A)
	184	1	0.750	0 → 1	(D)
node 49 → *Procyon*	*23	1	0.429	1 ⇒ 0	
	24	1	0.571	0 ⇒ 9	
	26	1	0.875	1 → 0	(D)
	28	1	0.800	1 → 0	(D)
	49	1	0.588	2 → 1	(D)
	69	1	0.167	0 ⇒ 1	
	*71	1	0.571	0 ⇒ 1	
	72	1	0.667	9 ⇒ 1	
	75	1	0.500	0 ⇒ 1	
	78	1	0.682	0 → 1	(A)
	78	1	0.682	2 → 1	(D)
	92	1	0.625	0 → 1	(A)
	92	1	0.625	2 → 1	(D)
	*124	1	0.692	9 ⇒ 1	
	*125	1	0.333	1 → 0	(D)
	126	1	0.579	1 ⇒ 0	
	131	1	0.833	1 ⇒ 0	
	135	1	0.800	2 → 3	(A)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	157	1	0.765	1 ⇒ 2	
	159	1	0.667	1 → 0	(A)
	172	1	0.625	0 → 1	(D)
Procyon (within terminal)	9	1	0.583	1 → 01	(A)
	9	1	0.583	0 → 01	(D)
	45	1	0.500	0 ⇒ 01	(?)
	63	1	0.778	1 ⇒ 01	(?)
	76	1	0.688	1 ⇒ 12	(?)
	79	1	0.727	1 ⇒ 12	(?)
	88	1	0.667	2 → 02	(A)
	88	1	0.667	0 → 02	(D)
	93	1	0.625	1 → 01	(A)
	93	1	0.625	0 → 01	(D)
	98	1	0.857	0 ⇒ 01	(?)
	162	1	0.600	1 ⇒ 01	(?)
	174	1	0.692	0 → 01	(A)
	174	1	0.692	1 → 01	(D)
	178	1	0.643	1 → 01	(A)
	178	1	0.643	0 → 01	(D)
node 49 → node 48	30	1	0.667	1 → 0	(A)
	40	1	0.500	1 → 0	(A)
	50	1	0.400	1 ⇒ 0	
	*87	1	0.500	1 → 0	(A)
	88	1	0.667	2 ⇒ 9	
	92	1	0.625	2 → 0	(D)
	123	1	0.778	0 ⇒ 1	
	130	1	0.571	0 → 2	(A)
	135	1	0.800	3 → 2	(D)
	163	1	0.667	1 ⇒ 0	
	174	1	0.692	1 → 0	(D)
	175	1	0.750	0 ⇒ 1	
node 48 → *Martes*	17	1	0.250	1 ⇒ 0	
	*18	1	0.455	1 ⇒ 0	
	28	1	0.800	0 → 1	(A)
	30	1	0.667	1 → 0	(D)
	38	1	0.632	2 ⇒ 1	
	40	1	0.500	1 → 0	(D)
	45	1	0.500	0 ⇒ 1	
	47	1	0.333	0 ⇒ 1	
	49	1	0.588	2 → 1	(D)
	74	1	0.625	0 ⇒ 1	
	*77	1	0.833	1 ⇒ 0	
	78	1	0.682	0 → 9	(A)
	78	1	0.682	2 → 9	(D)
	80	1	0.538	0 ⇒ 1	
	83	1	0.800	0 ⇒ 1	
	*87	1	0.500	1 → 0	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	93	1	0.625	0 → 1	(D)
	95	1	0.571	1 ⇒ 9	
	96	1	0.500	0 ⇒ 9	
	97	1	0.500	1 ⇒ 0	(?)
	99	1	0.571	2 ⇒ 0	
	*100	1	0.556	4 ⇒ 0	
	102	1	0.500	1 ⇒ 0	(?)
	113	1	0.375	0 ⇒ 12	
	130	1	0.571	0 → 2	(D)
	157	1	0.765	1 ⇒ 0	
	*158	1	1.000	1 ⇒ 0	
	159	1	0.667	1 → 9	(A)
	159	1	0.667	0 → 9	(D)
	160	1	0.667	0 ⇒ 9	
	172	1	0.625	0 → 1	(D)
	178	1	0.643	0 → 1	(D)
	183	1	0.667	0 ⇒ 1	
Martes (within terminal)	9	1	0.583	1 → 01	(A)
	9	1	0.583	0 → 01	(D)
	10	1	0.647	2 ⇒ 02	(?)
	26	1	0.875	0 → 01	(A)
	26	1	0.875	1 → 01	(D)
	58	1	0.625	1 ⇒ 01	(?)
	66	1	0.667	1 ⇒ 01	(?)
	70	1	0.727	1 ⇒ 12	(?)
	*71	1	0.571	0 ⇒ 01	(?)
	72	2	0.667	9 ⇒ 019	(?)
	113	1	0.375	1 ⇒ 12	(?)
	*125	1	0.333	0 → 01	(A)
	*125	1	0.333	1 → 01	(D)
	126	1	0.579	1 ⇒ 19	(?)
	132	1	0.714	0 ⇒ 01	(?)
	150	1	0.600	1 ⇒ 12	(?)
node 48 → node 47	22	1	0.667	0 → 1	(A)
	24	1	0.571	0 ⇒ 1	
	42	1	0.800	2 ⇒ 0	
	49	1	0.588	1 → 2	(A)
	54	1	1.000	1 ⇒ 0	
	59	1	0.625	0 ⇒ 2	
	73	1	0.750	0 → 1	(A)
	81	1	0.400	2 ⇒ 0	
	84	1	0.400	1 → 0	(A)
	85	1	1.000	1 ⇒ 0	
	91	1	0.556	2 ⇒ 1	
	93	1	0.625	1 → 0	(A)
	110	1	0.500	1 ⇒ 0	
	117	1	0.333	1 → 0	(A)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	128	1	0.667	3 → 2	(A)
	*129	1	0.625	1 ⇒ 0	
	136	1	1.000	3 ⇒ 2	
	149	1	0.667	0 → 1	(A)
	172	1	0.625	1 → 0	(A)
	189	1	0.500	1 → 0	(A)
	190	1	0.750	0 → 1	(A)
node 47 → *Enhydra*	8	1	0.333	0 ⇒ 1	
	9	1	0.583	0 → 1	(D)
	22	1	0.667	0 → 1	(D)
	26	1	0.875	1 → 0	(D)
	28	1	0.800	1 → 0	(D)
	40	1	0.500	0 → 1	(A)
	76	1	0.688	1 ⇒ 2	
	78	1	0.682	2 → 09	(D)
	84	1	0.400	1 → 0	(D)
	*87	1	0.500	1 → 0	(D)
	98	1	0.857	0 ⇒ 1	
	117	1	0.333	1 → 0	(D)
	*125	1	0.333	0 → 1	(A)
	128	1	0.667	3 → 2	(D)
	130	1	0.571	0 → 2	(D)
	135	1	0.800	2 ⇒ 1	
	149	1	0.667	0 → 1	(D)
	165	1	0.500	2 ⇒ 0	
	167	1	0.571	2 ⇒ 1	
	170	1	0.636	0 ⇒ 1	
	178	1	0.643	0 → 1	(D)
	188	1	0.625	0 ⇒ 1	
	189	1	0.500	1 → 0	(D)
Enhydra (within terminal)	4	1	1.000	0 ⇒ 01	(?)
	6	1	0.714	0 ⇒ 01	(?)
	10	1	0.647	2 ⇒ 02	(?)
	20	1	0.733	0 ⇒ 09	(?)
	30	1	0.667	0 → 01	(A)
	30	1	0.667	1 → 01	(D)
	38	1	0.632	2 ⇒ 12	(?)
	49	1	0.588	2 ⇒ 12	(?)
	50	1	0.400	0 ⇒ 01	(?)
	64	1	0.545	0 ⇒ 01	(?)
	65	2	0.545	1 ⇒ 012	(?)
	73	1	0.750	1 → 01	(A)
	73	1	0.750	0 → 01	(D)
	*77	1	0.833	1 ⇒ 01	(?)
	78	1	0.682	0 ⇒ 09	(F)
	79	1	0.727	1 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	95	1	0.571	1 ⇒ 01	(?)
	101	1	0.667	0 ⇒ 01	(?)
	107	1	0.714	0 ⇒ 01	(?)
	119	1	0.786	9 ⇒ 19	(?)
	121	1	0.600	0 ⇒ 01	(?)
	122	1	1.000	0 ⇒ 01	(?)
	133	1	1.000	0 ⇒ 01	(?)
	157	1	0.765	1 ⇒ 12	(?)
	159	1	0.667	1 → 01	(A)
	159	1	0.667	0 → 01	(D)
	190	1	0.750	1 → 01	(A)
	190	1	0.750	0 → 01	(D)
node 47 → node 46	26	1	0.875	0 → 1	(A)
	40	1	0.500	1 → 0	(D)
	44	1	0.636	0 ⇒ 1	
	58	1	0.625	1 → 0	(A)
	62	1	0.556	1 ⇒ 0	
	63	1	0.778	1 ⇒ 0	
	66	1	0.667	1 ⇒ 0	
	*87	1	0.500	0 → 1	(A)
	119	1	0.786	9 ⇒ 0	
	121	1	0.600	0 ⇒ 2	
	*125	1	0.333	1 → 0	(D)
	126	1	0.579	1 → 0	(A)
	130	1	0.571	2 → 0	(A)
	149	1	0.667	1 → 2	(A)
	172	1	0.625	0 → 9	(A)
	178	1	0.643	1 → 0	(A)
	180	1	0.500	2 → 1	(A)
node 46 → *Lutra*	9	1	0.583	0 → 12	(D)
	22	1	0.667	0 → 1	(D)
	30	1	0.667	0 → 1	(A)
	58	1	0.625	0 → 2	(A)
	58	1	0.625	1 → 2	(D)
	73	1	0.750	0 → 1	(D)
	78	1	0.682	0 → 12	(A)
	79	1	0.727	1 ⇒ 0	
	84	1	0.400	1 → 0	(D)
	95	1	0.571	1 ⇒ 0	
	117	1	0.333	1 → 0	(D)
	126	1	0.579	0 → 9	(A)
	126	1	0.579	1 → 9	(D)
	128	1	0.667	2 → 3	(A)
	133	1	1.000	0 ⇒ 1	
	154	1	0.700	0 ⇒ 1	
	159	1	0.667	0 → 1	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	163	1	0.667	0 ⇒ 1	
	165	1	0.500	2 ⇒ 1	
	180	1	0.500	2 → 1	(D)
	189	1	0.500	0 → 1	(A)
	190	1	0.750	0 → 1	(D)
Lutra (within terminal)	3	1	0.800	1 ⇒ 01	(?)
	9	1	0.583	1 ⇒ 12	(?)
	16	1	0.667	0 ⇒ 01	(?)
	*18	1	0.455	1 ⇒ 12	(?)
	20	1	0.733	0 ⇒ 01	(?)
	24	1	0.571	1 ⇒ 01	(?)
	28	1	0.800	0 → 01	(A)
	28	1	0.800	1 → 01	(D)
	42	1	0.800	0 ⇒ 02	(?)
	45	1	0.500	0 ⇒ 01	(?)
	78	1	0.682	1 → 12	(A)
	78	1	0.682	2 → 12	(D)
	*87	1	0.500	1 ⇒ 01	(?)
	88	1	0.667	9 ⇒ 09	(?)
	92	1	0.625	0 ⇒ 01	(?)
	93	1	0.625	0 ⇒ 01	(F)
	98	1	0.857	0 ⇒ 01	(?)
	107	1	0.714	0 ⇒ 01	(?)
	130	1	0.571	0 ⇒ 01	(?)
	132	1	0.714	0 ⇒ 01	(F)
	149	1	0.667	2 → 02	(A)
	149	1	0.667	0 → 02	(D)
	157	1	0.765	1 ⇒ 12	(?)
	*171	1	0.429	1 ⇒ 01	(?)
	172	1	0.625	9 → 09	(A)
	172	1	0.625	0 → 09	(D)
	178	1	0.643	0 ⇒ 01	(F)
	184	1	0.750	1 ⇒ 01	(?)
node 46 → node 45	9	1	0.583	1 → 0	(A)
	14	1	0.538	0 → 9	(A)
	22	1	0.667	1 → 0	(A)
	*27	1	1.000	1 ⇒ 0	
	28	1	0.800	0 ⇒ 9	
	30	1	0.667	1 → 0	(D)
	31	1	0.636	0 → 2	(A)
	*35	1	0.692	9 → 0	(A)
	41	1	0.571	0 → 1	(A)
	58	1	0.625	1 → 0	(D)
	*71	1	0.571	0 ⇒ 1	
	72	1	0.667	9 → 0	(A)
	84	1	0.400	0 → 1	(A)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	86	1	0.500	0 → 1	(A)
	106	1	0.500	0 → 2	(A)
	112	1	0.692	2 ⇒ 0	
	113	1	0.375	0 → 2	(A)
	117	1	0.333	0 → 1	(A)
	126	1	0.579	1 → 0	(D)
	128	1	0.667	3 → 2	(D)
	132	1	0.714	0 → 9	(A)
	137	1	0.700	2 → 0	(A)
	143	1	0.250	0 ⇒ 1	
	144	1	0.600	0 → 1	(A)
	146	1	0.250	1 ⇒ 0	
	149	1	0.667	0 → 2	(D)
	190	1	0.750	0 → 2	(D)
	153	1	0.833	2 → 1	(A)
	161	1	0.333	1 → 0	(A)
	162	1	0.600	1 → 0	(A)
	166	1	0.500	1 → 0	(A)
	167	1	0.571	2 ⇒ 0	
	168	1	0.571	1 ⇒ 0	
	174	1	0.692	0 ⇒ 1	
	177	1	0.400	1 → 0	(A)
	180	1	0.500	1 → 9	(A)
	183	1	0.667	0 → 2	(A)
	188	1	0.625	0 → 2	(A)
	190	1	0.750	1 → 2	(A)
node 45 → node 28	10	1	0.647	2 → 0	(A)
	13	1	1.000	1 ⇒ 0	
	14	1	0.538	0 → 9	(D)
	16	1	0.667	0 ⇒ 1	
	*18	1	0.455	1 → 2	(A)
	41	1	0.571	0 → 1	(D)
	44	1	0.636	1 ⇒ 2	
	45	1	0.500	0 ⇒ 2	
	48	1	0.500	0 ⇒ 1	
	70	1	0.727	1 → 2	(A)
	73	1	0.750	1 → 0	(A)
	82	1	0.500	2 ⇒ 0	
	88	1	0.667	9 → 0	(A)
	89	1	0.500	0 ⇒ 1	
	93	1	0.625	0 ⇒ 1	(F)
	102	1	0.500	1 ⇒ 0	
	106	1	0.500	0 → 2	(D)
	119	1	0.786	0 → 1	(A)
	137	1	0.700	2 → 0	(D)
	144	1	0.600	0 → 1	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	159	1	0.667	0 → 1	(D)
	161	1	0.333	1 → 0	(D)
	166	1	0.500	1 → 0	(D)
	169	1	0.333	1 ⇒ 0	
	*171	1	0.429	1 ⇒ 0	
	172	1	0.625	0 → 9	(D)
	173	1	0.750	2 ⇒ 1	
	188	1	0.625	0 → 2	(D)
node 28 → *Zalophus*	10	1	0.647	2 → 0	(D)
	17	1	0.250	1 ⇒ 0	
	*18	1	0.455	2 → 3	(A)
	*18	1	0.455	1 → 3	(D)
	26	1	0.875	1 ⇒ 2	
	31	1	0.636	0 → 2	(D)
	*32	1	0.643	0 ⇒ 34	
	*33	1	0.667	9 ⇒ 1	
	*34	1	0.750	9 ⇒ 01	
	*35	1	0.692	9 → 0	(D)
	*36	1	0.500	9 ⇒ 1	
	39	1	0.667	0 ⇒ 1	
	43	1	0.545	9 ⇒ 1	
	46	1	0.333	0 ⇒ 1	
	47	1	0.333	0 ⇒ 1	
	50	1	0.400	0 ⇒ 1	
	59	1	0.625	2 ⇒ 0	
	78	1	0.682	2 → 0	(D)
	86	1	0.500	1 → 0	(A)
	88	1	0.667	0 → 2	(A)
	88	1	0.667	9 → 2	(D)
	91	1	0.556	1 ⇒ 2	
	92	1	0.625	0 ⇒ 2	
	97	1	0.500	1 ⇒ 0	
	113	1	0.375	2 → 0	(A)
	117	1	0.333	1 ⇒ 0	(?)
	119	1	0.786	0 → 1	(D)
	123	1	0.778	1 ⇒ 0	
	*125	1	0.333	0 ⇒ 1	
	126	1	0.579	0 ⇒ 3	
	132	1	0.714	9 → 0	(A)
	165	1	0.500	2 ⇒ 0	
	177	1	0.400	1 → 0	(D)
	180	1	0.500	9 → 0	(A)
	180	1	0.500	2 → 0	(D)
	183	1	0.667	0 → 2	(D)
Zalophus (within terminal)	20	2	0.733	0 ⇒ 012	(?)
	*32	1	0.643	3 ⇒ 34	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	*34	1	0.750	1 ⇒ 01	(?)
	67	1	0.778	9 ⇒ 19	(?)
	68	1	0.800	9 ⇒ 19	(?)
	70	1	0.727	2 → 12	(A)
	70	1	0.727	1 → 12	(D)
	*71	1	0.571	1 ⇒ 01	(?)
	72	1	0.667	0 → 09	(A)
	72	1	0.667	9 → 09	(D)
	82	1	0.500	0 ⇒ 01	(?)
	130	1	0.571	0 ⇒ 02	(?)
	135	1	0.800	2 ⇒ 23	(?)
	137	1	0.700	0 ⇒ 01	(F)
	138	1	0.636	9 ⇒ 09	(?)
	139	1	0.750	9 ⇒ 19	(?)
	140	1	0.778	9 ⇒ 09	(?)
	149	1	0.667	2 ⇒ 24	(?)
	153	1	0.833	1 → 12	(A)
	153	1	0.833	2 → 12	(D)
	155	1	0.889	0 ⇒ 01	(?)
	157	1	0.765	1 ⇒ 01	(?)
	162	1	0.600	0 → 01	(A)
	162	1	0.600	1 → 01	(D)
	178	1	0.643	0 ⇒ 01	(F)
	184	1	0.750	1 ⇒ 01	(?)
	189	1	0.500	0 → 01	(A)
	189	1	0.500	1 → 01	(D)
	190	1	0.750	2 ⇒ 12	(F)
	192	1	1.000	0 ⇒ 01	(?)
node 28 → *Odobenus*	7	1	0.500	0 ⇒ 1	
	8	1	0.333	0 ⇒ 1	
	9	1	0.583	0 ⇒ 1	(?)
	10	1	0.647	0 → 1	(A)
	10	1	0.647	2 → 1	(D)
	*18	1	0.455	1 → 2	(D)
	20	1	0.733	0 ⇒ 9	
	31	1	0.636	2 → 0	(A)
	*35	1	0.692	0 → 9	(A)
	38	1	0.632	2 ⇒ 19	
	51	1	0.714	2 ⇒ 1	
	60	1	0.750	1 ⇒ 0	
	65	1	0.545	1 ⇒ 2	
	70	1	0.727	1 → 2	(D)
	72	1	0.667	9 → 01	(D)
	78	1	0.682	0 → 29	(A)
	86	1	0.500	0 → 1	(D)
	88	1	0.667	9 → 0	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	113	1	0.375	0 → 2	(D)
	127	1	0.667	3 ⇒ 1	
	128	1	0.667	2 ⇒ 0	
	*129	1	0.625	0 ⇒ 9	
	131	1	0.833	1 ⇒ 9	
	132	1	0.714	0 → 9	(D)
	133	1	1.000	0 ⇒ 9	
	134	1	0.667	0 ⇒ 9	
	135	1	0.800	2 ⇒ 0	
	136	1	1.000	2 ⇒ 0	
	149	1	0.667	2 ⇒ 1	
	150	1	0.600	1 ⇒ 0	
	153	1	0.833	2 → 1	(D)
	162	1	0.600	1 → 0	(D)
	177	1	0.400	0 → 1	(A)
	*179	1	0.333	1 ⇒ 0	
	180	1	0.500	2 → 9	(D)
	183	1	0.667	2 → 0	(A)
	189	1	0.500	1 → 0	(D)
	195	1	0.333	1 ⇒ 0	
Odobenus (within terminal)	6	1	0.714	0 ⇒ 01	(?)
	*27	1	1.000	0 ⇒ 01	(?)
	28	1	0.800	9 ⇒ 19	(?)
	*37	1	0.833	1 ⇒ 01	(?)
	38	1	0.632	1 ⇒ 19	(?)
	52	1	0.692	2 ⇒ 12	(?)
	58	1	0.625	0 ⇒ 01	(?)
	63	1	0.778	0 ⇒ 01	(?)
	72	1	0.667	0 → 01	(A)
	72	1	0.667	1 → 01	(D)
	73	1	0.750	0 ⇒ 01	(F)
	*77	1	0.833	1 ⇒ 01	(?)
	78	1	0.682	2 ⇒ 29	(F)
	83	1	0.800	0 ⇒ 01	(?)
	98	1	0.857	0 ⇒ 01	(?)
	112	2	0.692	0 ⇒ 012	(?)
	119	1	0.786	1 → 01	(A)
	119	1	0.786	0 → 01	(D)
	*124	1	0.692	9 ⇒ 19	(?)
	126	1	0.579	0 ⇒ 09	(F)
	152	1	0.750	0 ⇒ 01	(?)
	164	1	1.000	1 ⇒ 01	(?)
	184	1	0.750	1 ⇒ 01	(?)
	188	1	0.625	2 ⇒ 23	(F)
node 45 → node 44	11	1	0.500	2 ⇒ 0	
	19	1	0.500	0 ⇒ 1	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	*25	1	1.000	1 ⇒ 0	
	26	1	0.875	1 ⇒ 9	
	*32	1	0.643	0 ⇒ 5	
	*33	1	0.667	9 ⇒ 0	
	*34	1	0.750	9 ⇒ 2	
	*36	1	0.500	9 ⇒ 0	
	43	1	0.545	9 ⇒ 0	
	49	1	0.588	2 → 1	(A)
	52	1	0.692	2 → 1	(A)
	*55	1	1.000	0 ⇒ 1	
	56	1	0.636	9 ⇒ 1	
	69	1	0.167	0 → 1	(A)
	72	1	0.667	0 → 1	(A)
	72	1	0.667	9 → 1	(D)
	73	1	0.750	0 → 1	(D)
	81	1	0.400	0 ⇒ 2	
	86	1	0.500	0 → 1	(D)
	108	1	0.429	9 ⇒ 0	
	109	1	0.750	9 ⇒ 2	
	111	1	1.000	1 ⇒ 0	
	113	1	0.375	0 → 2	(D)
	114	1	0.750	0 ⇒ 2	
	115	1	1.000	1 ⇒ 0	
	118	1	1.000	1 ⇒ 0	
	120	1	0.778	2 ⇒ 0	
	123	1	0.778	1 ⇒ 2	
	127	1	0.667	3 → 2	(A)
	130	1	0.571	0 → 2	(A)
	132	1	0.714	0 → 1	(D)
	137	1	0.700	0 → 1	(A)
	137	1	0.700	2 → 1	(D)
	141	1	0.692	9 ⇒ 0	
	142	1	0.750	9 ⇒ 0	
	145	1	0.571	9 ⇒ 1	
	157	1	0.765	1 ⇒ 0	
	159	1	0.667	1 → 0	(A)
	177	1	0.400	1 → 0	(D)
	181	1	1.000	1 ⇒ 0	
	183	1	0.667	0 → 2	(D)
	*185	1	1.000	1 ⇒ 0	
	186	1	1.000	0 ⇒ 1	
	187	1	0.913	9 → 0	(A)
	188	1	0.625	2 → 3	(A)
	188	1	0.625	0 → 3	(D)
	194	1	0.333	0 ⇒ 1	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
node 44 → node 43	6	1	0.714	0 ⇒ 1	
	31	1	0.636	0 → 2	(D)
	*35	1	0.692	0 → 1	(A)
	*35	1	0.692	9 → 1	(D)
	38	1	0.632	2 ⇒ 1	
	41	1	0.571	0 → 1	(D)
	52	1	0.692	2 → 1	(D)
	69	1	0.167	0 → 1	(D)
	74	1	0.625	0 ⇒ 1	
	76	1	0.688	1 → 0	(A)
	79	1	0.727	1 ⇒ 0	
	95	1	0.571	1 ⇒ 0	
	127	1	0.667	3 → 2	(D)
	161	1	0.333	1 → 0	(D)
	162	1	0.600	1 → 0	(D)
	164	1	1.000	1 → 0	(A)
	166	1	0.500	1 → 0	(D)
	175	1	0.750	1 ⇒ 0	
	*179	1	0.333	1 → 0	(A)
	180	1	0.500	2 → 9	(D)
	182	1	0.500	0 → 1	(A)
	187	1	0.913	9 → 0	(D)
	189	1	0.500	1 → 0	(D)
	190	1	0.750	2 → 1	(A)
node 43 → node 42	7	1	0.500	0 ⇒ 9	
	10	1	0.647	2 ⇒ 9	
	12	1	0.333	1 ⇒ 0	
	14	1	0.538	0 → 9	(D)
	20	1	0.733	0 ⇒ 2	
	24	1	0.571	1 → 2	(A)
	*57	1	0.667	1 → 0	(A)
	58	1	0.625	0 → 9	(A)
	59	1	0.625	2 ⇒ 9	
	60	1	0.750	1 → 9	(A)
	61	1	0.600	0 ⇒ 1	
	70	1	0.727	1 ⇒ 2	
	76	1	0.688	1 → 0	(D)
	*87	1	0.500	1 ⇒ 0	(?)
	*105	1	1.000	1 ⇒ 0	
	106	1	0.500	2 ⇒ 9	
	109	1	0.750	2 ⇒ 0	
	119	1	0.786	0 → 1	(A)
	128	1	0.667	2 ⇒ 1	
	130	1	0.571	2 → 0	(A)
	132	1	0.714	1 → 9	(D)
	137	1	0.700	1 → 0	(A)
	141	1	0.692	0 ⇒ 4	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	142	1	0.750	0 → 3	(A)
	144	1	0.600	0 → 1	(D)
	149	1	0.667	2 ⇒ 4	(?)
	150	1	0.600	1 ⇒ 0	
	153	1	0.833	2 → 1	(D)
	172	1	0.625	9 → 0	(A)
	*179	1	0.333	1 → 0	(D)
	192	1	1.000	0 → 1	(A)
	195	1	0.333	1 ⇒ 0	
node 42 → *Mirounga leonina*	6	1	0.714	1 ⇒ 9	
	9	1	0.583	0 ⇒ 9	
	17	1	0.250	1 ⇒ 0	
	*18	1	0.455	1 ⇒ 0	
	24	1	0.571	1 → 2	(D)
	43	1	0.545	0 ⇒ 1	
	44	1	0.636	1 ⇒ 2	
	49	1	0.588	2 → 1	(D)
	63	1	0.778	0 ⇒ 1	
	66	1	0.667	0 ⇒ 1	
	78	1	0.682	2 → 0	(D)
	*124	1	0.692	9 ⇒ 1	
	*129	1	0.625	0 ⇒ 2	
	165	1	0.500	2 ⇒ 1	
	182	1	0.500	1 → 0	(A)
	192	1	1.000	0 → 1	(D)
Mirounga leonina (within terminal)	*34	1	0.750	2 ⇒ 12	(?)
	42	1	0.800	0 ⇒ 01	(?)
	*57	1	0.667	0 → 01	(A)
	*57	1	0.667	1 → 01	(D)
	58	1	0.625	9 → 09	(A)
	58	1	0.625	0 → 09	(D)
	59	2	0.625	9 ⇒ 019	(?)
	60	1	0.750	9 → 19	(A)
	60	1	0.750	1 → 19	(D)
	74	1	0.625	1 ⇒ 01	(?)
	80	2	0.538	0 ⇒ 012	(?)
	97	1	0.500	1 ⇒ 01	(?)
	104	1	1.000	0 ⇒ 01	(?)
	119	1	0.786	1 → 01	(A)
	119	1	0.786	0 → 01	(D)
	123	1	0.778	2 ⇒ 12	(?)
	137	1	0.700	0 → 01	(A)
	137	1	0.700	1 → 01	(D)
	138	1	0.636	9 ⇒ 09	(?)
	139	1	0.750	9 ⇒ 09	(?)
	140	1	0.778	9 ⇒ 09	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	142	3	0.750	3 → 0234	(A)
	142	3	0.750	0 → 0234	(D)
	151	1	0.500	1 ⇒ 01	(?)
	153	1	0.833	1 ⇒ 01	(?)
	154	1	0.700	0 ⇒ 01	(?)
	*156	1	0.833	1 ⇒ 01	(?)
	157	1	0.765	0 ⇒ 09	(?)
	159	1	0.667	0 ⇒ 01	(F)
	164	1	1.000	0 → 01	(A)
	164	1	1.000	1 → 01	(D)
	170	1	0.636	0 ⇒ 01	(?)
	174	1	0.692	1 ⇒ 01	(?)
	183	1	0.667	2 ⇒ 02	(?)
	187	2	0.913	0 ⇒ 013	(?)
	190	1	0.750	1 → 12	(A)
	190	1	0.750	2 → 12	(D)
node 42 → *Mirounga angustirostris*	31	1	0.636	2 ⇒ 1	(?)
	39	1	0.667	0 ⇒ 1	
	49	1	0.588	1 → 2	(A)
	*57	1	0.667	1 → 0	(D)
	58	1	0.625	0 → 9	(D)
	60	1	0.750	1 → 9	(D)
	64	1	0.545	0 ⇒ 1	
	67	1	0.778	9 ⇒ 1	
	68	1	0.800	9 ⇒ 2	
	78	1	0.682	0 → 12	(A)
	91	1	0.556	1 ⇒ 2	
	119	1	0.786	0 → 1	(D)
	126	1	0.579	0 ⇒ 9	(F)
	137	1	0.700	1 → 0	(D)
	142	1	0.750	0 → 3	(D)
	148	1	0.500	0 ⇒ 1	
	182	1	0.500	0 → 1	(D)
	190	1	0.750	2 → 1	(D)
Mirounga angustirostris (within terminal)	24	1	0.571	2 → 12	(A)
	24	1	0.571	1 → 12	(D)
	*34	1	0.750	2 ⇒ 02	(?)
	*35	1	0.692	1 ⇒ 01	(?)
	*36	1	0.500	0 ⇒ 01	(?)
	51	1	0.714	2 ⇒ 12	(?)
	52	1	0.692	1 ⇒ 12	(?)
	78	1	0.682	1 → 12	(A)
	78	1	0.682	2 → 12	(D)
	92	1	0.625	0 ⇒ 01	(?)
	98	1	0.857	0 ⇒ 01	(?)
	120	1	0.778	0 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	131	1	0.833	1 ⇒ 01	(?)
	136	2	1.000	2 ⇒ 123	(?)
	141	1	0.692	4 ⇒ 24	(?)
	*156	1	0.833	1 ⇒ 01	(?)
	157	1	0.765	0 ⇒ 09	(?)
	159	1	0.667	0 ⇒ 01	(F)
	164	1	1.000	0 → 01	(A)
	164	1	1.000	1 → 01	(D)
	165	1	0.500	2 ⇒ 02	(?)
	170	1	0.636	0 ⇒ 01	(?)
	*171	1	0.429	1 ⇒ 01	(?)
	172	1	0.625	0 ⇒ 09	(F)
	174	1	0.692	1 ⇒ 01	(?)
	184	1	0.750	1 ⇒ 01	(?)
node 43 → node 41	14	1	0.538	9 → 0	(A)
	45	1	0.500	0 ⇒ 2	
	51	1	0.714	2 ⇒ 1	
	76	1	0.688	0 → 2	(A)
	88	1	0.667	9 ⇒ 0	
	92	1	0.625	0 → 1	(A)
	101	1	0.667	0 ⇒ 1	
	112	1	0.692	0 → 2	(A)
	*125	1	0.333	0 → 1	(A)
	126	1	0.579	0 ⇒ 1	(F)
	132	1	0.714	9 → 1	(A)
	143	1	0.250	1 ⇒ 0	
	144	1	0.600	1 → 0	(A)
	151	1	0.500	1 ⇒ 0	
	153	1	0.833	1 → 0	(A)
	153	1	0.833	2 → 0	(D)
	164	1	1.000	1 → 0	(D)
	*171	1	0.429	1 → 0	(A)
	182	1	0.500	0 → 1	(D)
	196	1	0.500	0 → 1	(A)
node 41 → *Hydrurga*	44	1	0.636	1 ⇒ 2	
	49	1	0.588	1 → 2	(A)
	58	1	0.625	0 ⇒ 12	(?)
	76	1	0.688	1 → 2	(D)
	*77	1	0.833	1 ⇒ 0	
	78	1	0.682	0 → 9	(A)
	78	1	0.682	2 → 9	(D)
	80	1	0.538	0 ⇒ 2	
	81	1	0.400	2 ⇒ 1	
	82	1	0.500	2 ⇒ 0	
	92	1	0.625	1 → 2	(A)
	92	1	0.625	0 → 2	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	98	1	0.857	0 ⇒ 1	
	106	1	0.500	2 → 0	(A)
	112	1	0.692	0 → 2	(D)
	123	1	0.778	2 ⇒ 01	
	*125	1	0.333	0 → 1	(D)
	*129	1	0.625	0 ⇒ 2	
	130	1	0.571	0 → 2	(D)
	138	1	0.636	9 ⇒ 0	
	139	1	0.750	9 ⇒ 0	
	140	1	0.778	9 ⇒ 1	
	169	1	0.333	1 ⇒ 0	
	*171	1	0.429	1 → 0	(D)
	172	1	0.625	0 → 9	(D)
	177	1	0.400	0 ⇒ 1	
	*179	1	0.333	1 → 0	(D)
	190	1	0.750	2 → 1	(D)
	191	1	0.833	1 ⇒ 0	
	196	1	0.500	1 → 2	(A)
	196	1	0.500	0 → 2	(D)
Hydrurga (within terminal)	20	1	0.733	0 ⇒ 01	(?)
	24	1	0.571	1 ⇒ 12	(?)
	31	1	0.636	2 ⇒ 12	(?)
	*35	1	0.692	1 ⇒ 01	(?)
	*37	1	0.833	1 ⇒ 01	(?)
	38	2	0.632	1 ⇒ 019	(?)
	58	1	0.625	1 ⇒ 12	(?)
	61	1	0.600	0 ⇒ 01	(?)
	64	1	0.545	0 ⇒ 01	(?)
	67	1	0.778	9 ⇒ 19	(?)
	68	1	0.800	9 ⇒ 29	(?)
	83	1	0.800	0 ⇒ 01	(?)
	88	1	0.667	0 ⇒ 01	(?)
	123	1	0.778	1 ⇒ 01	(?)
	131	1	0.833	1 ⇒ 01	(?)
	154	1	0.700	0 ⇒ 01	(?)
	155	1	0.889	0 ⇒ 01	(?)
	*156	1	0.833	1 ⇒ 01	(?)
	157	1	0.765	0 ⇒ 09	(?)
	165	1	0.500	2 ⇒ 02	(?)
	187	1	0.913	0 ⇒ 02	(?)
node 41 → node 40	5	1	1.000	0 ⇒ 1	
	17	1	0.250	1 ⇒ 0	
	*18	1	0.455	1 ⇒ 0	
	19	1	0.500	1 ⇒ 0	
	20	1	0.733	0 ⇒ 9	
	*32	1	0.643	5 ⇒ 4	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	*34	1	0.750	2 ⇒ 0	
	49	1	0.588	2 → 1	(D)
	59	1	0.625	2 → 1	(A)
	70	1	0.727	1 ⇒ 0	
	78	1	0.682	2 → 0	(D)
	108	1	0.429	0 ⇒ 1	
	130	1	0.571	2 → 1	(A)
	134	1	0.667	0 ⇒ 1	
	141	1	0.692	0 → 3	(A)
	159	1	0.667	0 ⇒ 1	(F)
	170	1	0.636	0 ⇒ 1	
	*179	1	0.333	0 → 1	(A)
	190	1	0.750	1 → 2	(A)
	196	1	0.500	0 → 1	(D)
node 40 → *Leptonychotes*	11	1	0.500	0 ⇒ 2	
	24	1	0.571	1 ⇒ 0	
	53	1	0.500	0 ⇒ 1	
	59	1	0.625	2 → 1	(D)
	65	1	0.545	1 ⇒ 0	
	69	1	0.167	1 ⇒ 0	
	106	1	0.500	0 → 12	(D)
	107	1	0.714	0 ⇒ 1	
	112	1	0.692	0 → 2	(D)
	*125	1	0.333	0 → 1	(D)
	130	1	0.571	0 → 1	(D)
	137	1	0.700	1 ⇒ 0	(?)
	141	1	0.692	0 → 3	(D)
	142	1	0.750	0 ⇒ 3	
	145	1	0.571	1 ⇒ 2	
	160	1	0.667	0 ⇒ 1	
	*171	1	0.429	0 → 1	(A)
	172	1	0.625	9 → 0	(A)
	180	1	0.500	9 ⇒ 0	
Leptonychotes (within terminal)	10	1	0.647	2 ⇒ 02	(?)
	31	1	0.636	2 ⇒ 12	(?)
	*32	1	0.643	4 ⇒ 34	(?)
	*35	1	0.692	1 ⇒ 01	(?)
	*36	1	0.500	0 ⇒ 01	(?)
	42	1	0.800	0 ⇒ 01	(?)
	61	1	0.600	0 ⇒ 01	(?)
	64	1	0.545	0 ⇒ 01	(?)
	72	1	0.667	1 ⇒ 01	(?)
	76	1	0.688	2 → 12	(A)
	76	1	0.688	1 → 12	(D)
	79	1	0.727	0 ⇒ 01	(?)
	83	1	0.800	0 ⇒ 01	(?)
	88	1	0.667	0 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	92	1	0.625	1 → 01	(A)
	92	1	0.625	0 → 01	(D)
	101	1	0.667	1 ⇒ 01	(?)
	106	1	0.500	2 → 12	(A)
	106	1	0.500	1 → 12	(D)
	114	1	0.750	2 ⇒ 12	(?)
	123	2	0.778	2 ⇒ 012	(?)
	128	1	0.667	2 ⇒ 12	(?)
	*129	1	0.625	0 ⇒ 02	(?)
	132	1	0.714	1 ⇒ 19	(?)
	147	1	0.667	0 ⇒ 01	(?)
	150	1	0.600	1 ⇒ 12	(?)
	154	1	0.700	0 ⇒ 01	(?)
	157	1	0.765	0 ⇒ 01	(?)
	174	1	0.692	1 ⇒ 01	(?)
	175	1	0.750	0 ⇒ 01	(?)
	176	1	0.800	1 ⇒ 01	(?)
	177	1	0.400	0 ⇒ 01	(?)
	178	1	0.643	0 ⇒ 01	(?)
	187	1	0.913	0 ⇒ 03	(?)
	190	1	0.750	2 ⇒ 12	(F)
node 40 → node 39	3	1	0.800	1 ⇒ 0	
	38	1	0.632	1 → 0	(A)
	43	1	0.545	0 ⇒ 1	
	52	1	0.692	1 ⇒ 0	
	82	1	0.500	2 → 1	(A)
	112	1	0.692	2 → 0	(A)
	113	1	0.375	2 → 0	(A)
	*125	1	0.333	1 → 0	(A)
	126	1	0.579	1 ⇒ 9	(F)
	140	1	0.778	9 → 0	(A)
	165	1	0.500	2 ⇒ 0	
node 39 → *Ommatophoca*	6	1	0.714	1 ⇒ 0	
	7	1	0.500	0 ⇒ 9	
	10	1	0.647	2 ⇒ 9	
	12	1	0.333	1 ⇒ 0	
	38	1	0.632	0 → 2	(A)
	38	1	0.632	1 → 2	(D)
	41	1	0.571	1 ⇒ 0	
	45	1	0.500	2 ⇒ 1	
	59	1	0.625	1 → 02	(A)
	62	1	0.556	0 ⇒ 1	
	75	1	0.500	0 ⇒ 1	
	76	1	0.688	2 → 1	(A)
	82	1	0.500	2 → 1	(D)
	106	1	0.500	0 → 2	(D)
	113	1	0.375	2 → 0	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	130	1	0.571	0 → 1	(D)
	141	1	0.692	3 → 0	(A)
	169	1	0.333	1 ⇒ 0	
	*171	1	0.429	1 → 0	(D)
	172	1	0.625	0 → 9	(D)
	*179	1	0.333	1 ⇒ 0	(?)
	187	1	0.913	0 ⇒ 123	
	196	1	0.500	1 ⇒ 2	(?)
Ommatophoca (within terminal)	19	1	0.500	0 ⇒ 01	(?)
	31	1	0.636	2 ⇒ 12	(?)
	54	1	1.000	0 → 01	(A)
	54	1	1.000	0 → 01	(D)
	58	1	0.625	0 ⇒ 01	(?)
	59	1	0.625	0 → 02	(A)
	59	1	0.625	2 → 02	(D)
	63	1	0.778	0 ⇒ 01	(?)
	70	1	0.727	0 ⇒ 01	(?)
	72	1	0.667	1 ⇒ 01	(?)
	74	1	0.625	1 ⇒ 01	(?)
	88	1	0.667	0 ⇒ 01	(?)
	92	1	0.625	1 → 01	(A)
	92	1	0.625	0 → 01	(D)
	104	1	1.000	0 ⇒ 01	(?)
	109	1	0.750	2 ⇒ 02	(?)
	119	1	0.786	0 ⇒ 01	(?)
	121	1	0.600	2 ⇒ 23	(?)
	123	1	0.778	2 ⇒ 12	(?)
	*124	1	0.692	9 ⇒ 19	(?)
	126	1	0.579	9 ⇒ 09	(?)
	137	1	0.700	1 ⇒ 01	(?)
	138	1	0.636	9 ⇒ 09	(?)
	139	1	0.750	9 ⇒ 19	(?)
	140	1	0.778	0 → 09	(A)
	140	1	0.778	9 → 09	(D)
	149	1	0.667	2 ⇒ 23	(?)
	150	2	0.600	1 ⇒ 012	(?)
	154	1	0.700	0 ⇒ 01	(?)
	*156	1	0.833	1 ⇒ 01	(?)
	157	1	0.765	0 ⇒ 09	(?)
	159	1	0.667	1 ⇒ 01	(?)
	176	1	0.800	1 ⇒ 01	(?)
	183	1	0.667	2 ⇒ 12	(?)
	187	2	0.913	1 ⇒ 123	(?)
	191	1	0.833	1 ⇒ 01	(?)
node 39 → node 38	*32	1	0.643	4 ⇒ 2	
	*36	1	0.500	0 → 1	(A)
	59	1	0.625	2 → 1	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	67	1	0.778	9 ⇒ 1	
	68	1	0.800	9 ⇒ 0	
	*71	1	0.571	1 ⇒ 0	
	72	1	0.667	1 ⇒ 9	
	76	1	0.688	1 → 2	(D)
	79	1	0.727	0 ⇒ 1	
	80	1	0.538	0 ⇒ 2	
	92	1	0.625	0 → 1	(D)
	106	1	0.500	2 → 0	(A)
	114	1	0.750	2 → 0	(A)
	130	1	0.571	1 → 0	(A)
	142	1	0.750	0 ⇒ 1	
	174	1	0.692	1 → 0	(A)
	183	1	0.667	2 ⇒ 0	
node 38 → *Lobodon*	14	1	0.538	0 ⇒ 2	
	24	1	0.571	1 ⇒ 0	
	*36	1	0.500	0 → 1	(D)
	38	1	0.632	1 → 02	(D)
	49	1	0.588	1 ⇒ 2	
	50	1	0.400	0 ⇒ 1	
	56	1	0.636	1 ⇒ 0	
	64	1	0.545	0 ⇒ 1	
	65	1	0.545	1 ⇒ 0	
	82	1	0.500	1 → 2	(A)
	99	1	0.571	2 ⇒ 1	
	*100	1	0.556	4 ⇒ 2	
	107	1	0.714	0 ⇒ 1	
	113	1	0.375	0 → 2	(A)
	114	1	0.750	0 → 1	(A)
	114	1	0.750	2 → 1	(D)
	*129	1	0.625	0 ⇒ 2	
	132	1	0.714	1 ⇒ 0	
	137	1	0.700	1 ⇒ 2	(?)
	140	1	0.778	0 → 1	(A)
	140	1	0.778	9 → 1	(D)
	141	1	0.692	3 → 1	(A)
	141	1	0.692	0 → 1	(D)
	148	1	0.500	0 ⇒ 1	
	150	1	0.600	1 ⇒ 0	
	152	1	0.750	0 ⇒ 1	
	*171	1	0.429	0 → 1	(A)
	172	1	0.625	9 → 0	(A)
	176	1	0.800	1 ⇒ 0	
	177	1	0.400	0 ⇒ 1	
	180	1	0.500	9 ⇒ 1	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
Lobodon (within terminal)	3	1	0.800	0 ⇒ 01	(?)
	9	1	0.583	0 ⇒ 01	(?)
	38	1	0.632	0 ⇒ 02	(?)
	39	1	0.667	0 ⇒ 01	(?)
	44	1	0.636	1 ⇒ 12	(?)
	63	1	0.778	0 ⇒ 01	(?)
	92	1	0.625	1 ⇒ 12	(?)
	119	1	0.786	0 ⇒ 01	(?)
	154	1	0.700	0 ⇒ 01	(?)
	164	1	1.000	0 ⇒ 01	(?)
	174	1	0.692	0 → 01	(A)
	174	1	0.692	1 → 01	(D)
	178	1	0.643	0 ⇒ 01	(?)
	183	1	0.667	0 ⇒ 01	(?)
	187	3	0.913	0 ⇒ 0123	(?)
	191	1	0.833	1 ⇒ 01	(?)
node 38 → node 37	11	1	0.500	0 → 2	(A)
	20	1	0.733	9 → 0	(A)
	46	1	0.333	0 → 1	(A)
	58	1	0.625	0 → 1	(A)
	61	1	0.600	0 → 1	(A)
	74	1	0.625	1 ⇒ 2	
	82	1	0.500	2 → 0	(D)
	84	1	0.400	1 ⇒ 0	
	88	1	0.667	0 ⇒ 2	
	108	1	0.429	1 → 0	(A)
	114	1	0.750	2 → 0	(D)
	134	1	0.667	1 ⇒ 0	
	138	1	0.636	9 → 0	(A)
	139	1	0.750	9 → 0	(A)
	140	1	0.778	9 → 0	(D)
	146	1	0.250	0 → 1	(A)
	147	1	0.667	0 ⇒ 1	
	149	1	0.667	2 → 3	(A)
	*171	1	0.429	1 → 0	(D)
	172	1	0.625	0 → 9	(D)
	174	1	0.692	1 → 0	(D)
	194	1	0.333	1 ⇒ 0	
	195	1	0.333	1 ⇒ 0	
node 37 → *Monachus monachus*	14	1	0.538	0 ⇒ 9	
	20	1	0.733	9 → 0	(D)
	*36	1	0.500	0 → 1	(D)
	38	1	0.632	0 → 1	(A)
	46	1	0.333	0 → 1	(D)
	47	1	0.333	0 ⇒ 1	
	51	1	0.714	1 ⇒ 2	
	52	1	0.692	0 ⇒ 2	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	61	1	0.600	0 → 1	(D)
	68	1	0.800	0 ⇒ 1	
	70	1	0.727	0 ⇒ 1	
	75	1	0.500	0 ⇒ 1	
	101	1	0.667	1 ⇒ 0	
	108	1	0.429	1 → 0	(D)
	113	1	0.375	0 → 1	(A)
	113	1	0.375	2 → 1	(D)
	*125	1	0.333	0 ⇒ 1	
	126	1	0.579	9 ⇒ 1	
	*129	1	0.625	0 ⇒ 1	
	138	1	0.636	9 → 0	(D)
	139	1	0.750	0 → 1	(A)
	139	1	0.750	9 → 1	(D)
	146	1	0.250	0 → 1	(D)
	149	1	0.667	3 → 4	(A)
	149	1	0.667	2 → 4	(D)
	154	1	0.700	0 ⇒ 1	
	180	1	0.500	9 ⇒ 0	
Monachus monachus (within terminal)	3	1	0.800	0 ⇒ 01	(?)
	11	2	0.500	2 → 012	(A)
	11	2	0.500	0 → 012	(D)
	*32	1	0.643	2 ⇒ 25	(?)
	41	1	0.571	1 ⇒ 01	(?)
	42	1	0.800	0 ⇒ 01	(?)
	58	1	0.625	1 → 01	(A)
	58	1	0.625	0 → 01	(D)
	63	1	0.778	0 ⇒ 01	(?)
	78	1	0.682	0 ⇒ 01	(?)
	79	1	0.727	1 ⇒ 01	(?)
	82	1	0.500	1 → 01	(A)
	82	1	0.500	0 → 01	(D)
	94	1	1.000	0 ⇒ 01	(?)
	95	1	0.571	0 ⇒ 01	(?)
	121	1	0.600	2 ⇒ 12	(?)
	123	1	0.778	2 ⇒ 02	(?)
	133	1	1.000	0 ⇒ 01	(?)
	141	1	0.692	3 → 03	(A)
	141	1	0.692	0 → 03	(D)
	142	1	0.750	1 ⇒ 01	(?)
	152	1	0.750	0 ⇒ 01	(?)
	167	1	0.571	0 ⇒ 01	(?)
	168	1	0.571	0 ⇒ 01	(?)
	183	1	0.667	0 ⇒ 01	(?)
	196	1	0.500	1 ⇒ 12	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
node 37 → node 36	4	1	1.000	0 ⇒ 1	
	11	1	0.500	0 → 2	(D)
	*23	1	0.429	1 → 0	(A)
	24	1	0.571	1 ⇒ 9	
	*36	1	0.500	1 → 0	(A)
	69	1	0.167	1 ⇒ 0	
	80	1	0.538	2 ⇒ 1	
	83	1	0.800	0 ⇒ 1	
	92	1	0.625	1 ⇒ 2	(?)
	113	1	0.375	2 → 0	(D)
	116	1	1.000	0 ⇒ 1	
	123	1	0.778	2 ⇒ 1	
	138	1	0.636	0 → 1	(A)
	141	1	0.692	0 → 3	(D)
	149	1	0.667	2 → 3	(D)
	*156	1	0.833	1 ⇒ 0	
	157	1	0.765	0 ⇒ 9	
	170	1	0.636	1 → 0	(A)
	173	1	0.750	2 → 0	(A)
	178	1	0.643	0 → 1	(A)
	*179	1	0.333	1 → 0	(A)
	182	1	0.500	1 ⇒ 0	
	184	1	0.750	1 ⇒ 0	
node 36 → *Monachus tropicalis*	6	1	0.714	1 ⇒ 0	
	15	1	1.000	0 ⇒ 1	
	*37	1	0.833	1 ⇒ 0	
	38	1	0.632	0 → 9	(A)
	38	1	0.632	1 → 9	(D)
	46	1	0.333	0 → 1	(D)
	49	1	0.588	1 ⇒ 0	
	56	1	0.636	1 ⇒ 2	
	58	1	0.625	0 → 1	(D)
	61	1	0.600	1 → 0	(A)
	64	1	0.545	0 ⇒ 1	
	65	1	0.545	1 ⇒ 0	
	67	1	0.778	1 ⇒ 2	
	82	1	0.500	1 → 0	(A)
	108	1	0.429	0 → 1	(A)
	142	1	0.750	1 ⇒ 3	
	146	1	0.250	1 → 0	(A)
	150	1	0.600	1 ⇒ 0	
	165	1	0.500	0 ⇒ 2	
	173	1	0.750	0 → 1	(A)
	173	1	0.750	2 → 1	(D)
	178	1	0.643	0 → 1	(D)
	*179	1	0.333	1 → 0	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
Monachus tropicalis (within terminal)	5	1	1.000	1 ⇒ 01	(?)
	20	1	0.733	0 → 09	(A)
	20	1	0.733	9 → 09	(D)
	*23	1	0.429	0 → 01	(A)
	*23	1	0.429	1 → 01	(D)
	24	1	0.571	9 ⇒ 09	(?)
	42	1	0.800	0 ⇒ 01	(?)
	44	2	0.636	1 ⇒ 012	(?)
	59	1	0.625	1 ⇒ 12	(?)
	62	1	0.556	0 ⇒ 01	(?)
	74	1	0.625	2 ⇒ 12	(?)
	76	1	0.688	2 ⇒ 12	(?)
	*77	1	0.833	1 ⇒ 01	(?)
	78	1	0.682	0 ⇒ 09	(?)
	84	1	0.400	0 ⇒ 01	(?)
	91	1	0.556	1 ⇒ 12	(?)
	94	1	1.000	0 ⇒ 01	(?)
	*124	1	0.692	9 ⇒ 19	(?)
	*125	1	0.333	0 ⇒ 01	(?)
	126	2	0.579	9 ⇒ 019	(?)
	137	1	0.700	1 ⇒ 01	(?)
	138	1	0.636	1 → 19	(A)
	138	1	0.636	9 → 19	(D)
	139	2	0.750	0 → 019	(A)
	139	2	0.750	9 → 019	(D)
	140	1	0.778	0 ⇒ 09	(?)
	153	1	0.833	0 ⇒ 01	(?)
	155	1	0.889	0 ⇒ 01	(?)
	164	1	1.000	0 ⇒ 01	(?)
	170	1	0.636	0 → 01	(A)
	170	1	0.636	1 → 01	(D)
	183	1	0.667	0 ⇒ 01	(?)
	187	1	0.913	0 ⇒ 02	(?)
	192	1	1.000	0 ⇒ 01	(?)
node 36 → *Monachus schauinslandi*	14	1	0.538	0 ⇒ 1	
	17	1	0.250	0 ⇒ 1	
	*18	1	0.455	0 ⇒ 1	
	*23	1	0.429	1 → 0	(D)
	*32	1	0.643	2 ⇒ 4	
	*34	1	0.750	0 ⇒ 2	
	38	1	0.632	1 → 0	(D)
	41	1	0.571	1 ⇒ 0	
	45	1	0.500	2 ⇒ 1	
	46	1	0.333	1 → 0	(A)
	52	1	0.692	0 ⇒ 1	
	*57	1	0.667	1 ⇒ 0	
	58	1	0.625	1 → 9	(A)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	58	1	0.625	0 → 9	(D)
	59	1	0.625	1 ⇒ 9	
	60	1	0.750	1 ⇒ 9	
	61	1	0.600	0 → 1	(D)
	68	1	0.800	0 ⇒ 2	
	81	1	0.400	2 ⇒ 1	
	82	1	0.500	0 → 1	(D)
	103	1	1.000	0 ⇒ 1	
	106	1	0.500	0 ⇒ 1	
	108	1	0.429	1 → 0	(D)
	121	1	0.600	2 ⇒ 1	
	138	1	0.636	9 → 1	(D)
	139	1	0.750	9 → 0	(D)
	146	1	0.250	0 → 1	(D)
	170	1	0.636	1 → 0	(D)
	173	1	0.750	2 → 0	(D)
Monachus schauinslandi					
(within terminal)	5	1	1.000	1 ⇒ 01	(?)
	20	1	0.733	0 → 09	(A)
	20	1	0.733	9 → 09	(D)
	31	1	0.636	2 ⇒ 12	(?)
	*33	2	0.667	0 ⇒ 012	(?)
	*35	1	0.692	1 ⇒ 01	(?)
	44	1	0.636	1 ⇒ 01	(?)
	62	1	0.556	0 ⇒ 01	(?)
	76	1	0.688	2 ⇒ 12	(?)
	*77	1	0.833	1 ⇒ 01	(?)
	78	1	0.682	0 ⇒ 09	(?)
	91	1	0.556	1 ⇒ 12	(?)
	*124	1	0.692	9 ⇒ 09	(?)
	126	1	0.579	9 ⇒ 09	(?)
	132	1	0.714	1 ⇒ 01	(?)
	133	1	1.000	0 ⇒ 01	(?)
	145	1	0.571	1 ⇒ 12	(?)
	175	1	0.750	0 ⇒ 01	(?)
	178	1	0.643	1 → 01	(A)
	178	1	0.643	0 → 01	(D)
	*179	1	0.333	0 → 01	(A)
	*179	1	0.333	1 → 01	(D)
	180	1	0.500	9 ⇒ 09	(?)
	191	1	0.833	1 ⇒ 01	(?)
node 44 → node 35	3	1	0.800	1 ⇒ 0	
	31	1	0.636	2 → 1	(A)
	31	1	0.636	0 → 1	(D)
	*35	1	0.692	9 → 0	(D)
	41	1	0.571	1 → 0	(A)
	42	1	0.800	0 → 1	(A)
	62	1	0.556	0 ⇒ 1	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	75	1	0.500	0 ⇒ 1	
	78	1	0.682	0 → 1	(A)
	78	1	0.682	2 → 1	(D)
	80	1	0.538	0 ⇒ 2	
	84	1	0.400	1 ⇒ 0	(?)
	99	1	0.571	2 → 0	(A)
	*100	1	0.556	4 → 1	(A)
	121	1	0.600	2 → 1	(A)
	138	1	0.636	9 → 0	(A)
	139	1	0.750	9 → 1	(A)
	140	1	0.778	9 → 0	(A)
	150	1	0.600	1 → 2	(A)
	153	1	0.833	1 → 2	(A)
	154	1	0.700	0 → 1	(A)
	160	1	0.667	0 ⇒ 1	
	161	1	0.333	0 → 1	(A)
	162	1	0.600	0 → 1	(A)
	166	1	0.500	0 → 1	(A)
	170	1	0.636	0 ⇒ 2	
	172	1	0.625	9 ⇒ 2	
	176	1	0.800	1 ⇒ 0	
	178	1	0.643	0 ⇒ 1	(F)
	180	1	0.500	9 → 2	(A)
	187	1	0.913	0 → 3	(A)
	187	1	0.913	9 → 3	(D)
	189	1	0.500	0 → 1	(A)
node 35 → *Cystophora*	7	1	0.500	0 ⇒ 9	
	10	1	0.647	2 ⇒ 9	
	12	1	0.333	1 ⇒ 0	
	14	1	0.538	0 → 29	(D)
	*34	1	0.750	2 ⇒ 1	
	42	1	0.800	0 → 12	(D)
	52	1	0.692	2 → 1	(D)
	56	1	0.636	1 ⇒ 2	
	59	1	0.625	2 ⇒ 0	
	69	1	0.167	0 → 1	(D)
	74	1	0.625	0 ⇒ 2	
	88	1	0.667	9 ⇒ 12	
	92	1	0.625	0 ⇒ 1	
	99	1	0.571	0 → 1	(A)
	99	1	0.571	2 → 1	(D)
	*100	1	0.556	1 → 2	(A)
	*100	1	0.556	4 → 2	(D)
	106	1	0.500	0 → 2	(D)
	121	1	0.600	2 → 1	(D)
	*124	1	0.692	9 ⇒ 1	
	127	1	0.667	3 → 2	(D)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	128	1	0.667	2 ⇒ 1	
	132	1	0.714	1 → 9	(D)
	149	1	0.667	2 ⇒ 4	(?)
	150	1	0.600	1 → 2	(D)
	151	1	0.500	1 ⇒ 0	
Cystophora (within terminal)	14	1	0.538	9 → 29	(A)
	14	1	0.538	2 → 29	(D)
	*25	1	1.000	0 ⇒ 01	(?)
	26	1	0.875	9 ⇒ 09	(?)
	42	1	0.800	1 ⇒ 12	(?)
	49	2	0.588	1 → 012	(A)
	49	2	0.588	2 → 012	(D)
	65	1	0.545	1 ⇒ 12	(?)
	70	1	0.727	1 ⇒ 12	(?)
	88	1	0.667	2 ⇒ 12	(?)
	112	1	0.692	0 ⇒ 01	(?)
	130	2	0.571	2 → 012	(A)
	130	2	0.571	0 → 012	(D)
	137	1	0.700	1 ⇒ 01	(?)
	138	1	0.636	0 → 09	(A)
	138	1	0.636	9 → 09	(D)
	139	1	0.750	1 → 19	(A)
	139	1	0.750	9 → 19	(D)
	140	1	0.778	0 → 09	(A)
	140	1	0.778	9 → 09	(D)
	144	1	0.600	1 → 01	(A)
	144	1	0.600	0 → 01	(D)
	154	1	0.700	1 → 01	(A)
	154	1	0.700	0 → 01	(D)
	163	1	0.667	0 ⇒ 01	(?)
	165	1	0.500	2 ⇒ 02	(?)
	170	1	0.636	2 ⇒ 12	(?)
	172	1	0.625	2 ⇒ 12	(?)
	173	1	0.750	2 ⇒ 12	(?)
	180	1	0.500	2 ⇒ 12	(?)
	184	1	0.750	1 ⇒ 01	(?)
node 35 → node 34	14	1	0.538	9 → 0	(A)
	17	1	0.250	1 ⇒ 0	
	*18	1	0.455	1 ⇒ 0	
	22	1	0.667	0 → 1	(A)
	*23	1	0.429	1 ⇒ 0	
	24	1	0.571	1 ⇒ 9	
	49	1	0.588	2 → 1	(D)
	52	1	0.692	1 → 2	(A)
	58	1	0.625	0 ⇒ 2	(F)
	64	1	0.545	0 → 1	(A)
	69	1	0.167	1 → 0	(A)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	*87	1	0.500	1 ⇒ 0	(?)
	91	1	0.556	1 ⇒ 2	
	93	1	0.625	0 ⇒ 1	(F)
	99	1	0.571	2 → 0	(D)
	*100	1	0.556	4 → 1	(D)
	106	1	0.500	2 → 0	(A)
	127	1	0.667	2 → 3	(A)
	130	1	0.571	0 → 2	(D)
	132	1	0.714	9 → 1	(A)
	139	1	0.750	9 → 1	(D)
	140	1	0.778	9 → 0	(D)
	141	1	0.692	0 ⇒ 1	
	142	1	0.750	0 ⇒ 1	
	145	1	0.571	1 ⇒ 2	
	154	1	0.700	0 → 1	(D)
	157	1	0.765	0 ⇒ 2	
	167	1	0.571	0 ⇒ 1	
node 34 → *Halichoerus*	8	1	0.333	0 ⇒ 1	
	9	1	0.583	0 ⇒ 1	
	10	1	0.647	2 ⇒ 0	
	14	1	0.538	0 ⇒ 1	(?)
	42	1	0.800	1 → 0	(A)
	56	1	0.636	1 ⇒ 0	
	70	1	0.727	1 ⇒ 0	
	76	1	0.688	1 ⇒ 2	
	79	1	0.727	1 ⇒ 0	
	120	1	0.778	0 ⇒ 1	
	121	1	0.600	2 → 1	(D)
	*125	1	0.333	0 ⇒ 1	
	138	1	0.636	9 → 0	(D)
	144	1	0.600	0 → 1	(D)
	150	1	0.600	1 → 2	(D)
Halichoerus (within terminal)	22	1	0.667	1 → 01	(A)
	22	1	0.667	0 → 01	(D)
	*34	1	0.750	2 ⇒ 12	(?)
	*35	1	0.692	0 ⇒ 01	(?)
	*37	1	0.833	1 ⇒ 01	(?)
	38	1	0.632	2 ⇒ 29	(?)
	41	1	0.571	0 ⇒ 01	(?)
	43	1	0.545	0 ⇒ 01	(?)
	64	1	0.545	1 → 01	(A)
	64	1	0.545	0 → 01	(D)
	*71	1	0.571	1 ⇒ 01	(?)
	72	1	0.667	1 ⇒ 19	(?)
	78	2	0.682	1 ⇒ 012	(?)
	107	1	0.714	0 ⇒ 01	(?)
	123	2	0.778	2 ⇒ 023	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	126	1	0.579	0 ⇒ 02	(?)
	132	1	0.714	1 ⇒ 01	(?)
	141	1	0.692	1 ⇒ 13	(?)
	142	1	0.750	1 ⇒ 13	(?)
	149	1	0.667	2 ⇒ 02	(?)
	157	1	0.765	2 ⇒ 12	(?)
	182	1	0.500	0 ⇒ 01	(?)
	188	1	0.625	3 ⇒ 23	(?)
node 34 → node 33	11	1	0.500	0 ⇒ 2	
	44	1	0.636	1 ⇒ 0	
	72	1	0.667	1 ⇒ 0	
	121	1	0.600	1 → 2	(A)
	138	1	0.636	0 → 1	(A)
	138	1	0.636	9 → 1	(D)
	143	1	0.250	1 ⇒ 0	
	144	1	0.600	1 → 0	(A)
	150	1	0.600	2 → 1	(A)
	155	1	0.889	0 → 1	(A)
	187	1	0.913	3 ⇒ 1	
node 33 → *Phoca largha*	38	1	0.632	2 ⇒ 1	
	49	1	0.588	1 ⇒ 0	
	65	1	0.545	1 ⇒ 0	
	168	1	0.571	0 ⇒ 1	
	178	1	0.643	1 ⇒ 2	
	183	1	0.667	2 ⇒ 1	
	184	1	0.750	1 ⇒ 0	
Phoca largha (within terminal)	20	1	0.733	0 ⇒ 01	(?)
	22	1	0.667	1 → 01	(A)
	22	1	0.667	0 → 01	(D)
	*34	1	0.750	2 ⇒ 02	(?)
	41	1	0.571	0 ⇒ 01	(?)
	42	1	0.800	1 → 01	(A)
	42	1	0.800	0 → 01	(D)
	43	1	0.545	0 ⇒ 01	(?)
	52	1	0.692	2 ⇒ 12	(?)
	62	1	0.556	1 ⇒ 01	(?)
	64	1	0.545	1 → 01	(A)
	64	1	0.545	0 → 01	(D)
	70	1	0.727	1 ⇒ 01	(?)
	76	1	0.688	1 ⇒ 12	(?)
	99	1	0.571	0 ⇒ 01	(?)
	*100	1	0.556	1 ⇒ 12	(?)
	119	1	0.786	0 ⇒ 01	(?)
	*124	1	0.692	9 ⇒ 19	(?)
	126	1	0.579	0 ⇒ 09	(?)
	141	1	0.692	1 ⇒ 13	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	145	1	0.571	2 ⇒ 12	(?)
	155	1	0.889	1 → 01	(A)
	155	1	0.889	0 → 01	(D)
	172	1	0.625	2 ⇒ 12	(?)
node 33 → node 32	42	1	0.800	0 → 1	(D)
	58	1	0.625	2 ⇒ 1	
	64	1	0.545	0 → 1	(D)
	*124	1	0.692	9 ⇒ 0	
	152	1	0.750	0 ⇒ 1	
	155	1	0.889	0 → 1	(D)
	165	1	0.500	2 → 0	(A)
node 32 → *Phoca vitulina*	11	1	0.500	2 ⇒ 01	
	*35	1	0.692	0 ⇒ 1	
	62	1	0.556	1 ⇒ 0	
	64	1	0.545	1 ⇒ 0	
	65	1	0.545	1 ⇒ 0	
	*71	1	0.571	1 ⇒ 0	
	72	1	0.667	0 ⇒ 9	
	76	1	0.688	1 ⇒ 2	
	80	1	0.538	2 ⇒ 01	
	112	1	0.692	0 ⇒ 2	
	130	1	0.571	2 ⇒ 1	
	146	1	0.250	0 ⇒ 1	
	147	1	0.667	0 ⇒ 1	
	165	1	0.500	2 → 0	(D)
	174	1	0.692	1 ⇒ 0	
Phoca vitulina (within terminal)	11	1	0.500	1 ⇒ 01	(?)
	22	1	0.667	1 → 01	(A)
	22	1	0.667	0 → 01	(D)
	31	1	0.636	1 ⇒ 12	(?)
	*34	1	0.750	2 ⇒ 12	(?)
	42	1	0.800	1 ⇒ 12	(?)
	49	1	0.588	1 ⇒ 01	(?)
	52	1	0.692	2 ⇒ 12	(?)
	56	1	0.636	1 ⇒ 01	(?)
	67	1	0.778	9 ⇒ 19	(?)
	68	2	0.800	9 ⇒ 019	(?)
	78	1	0.682	1 ⇒ 12	(?)
	79	1	0.727	1 ⇒ 01	(?)
	80	1	0.538	1 ⇒ 01	(?)
	*87	1	0.500	0 ⇒ 01	(?)
	88	1	0.667	9 ⇒ 09	(?)
	119	1	0.786	0 ⇒ 01	(?)
	123	1	0.778	2 ⇒ 12	(?)
	*124	1	0.692	0 ⇒ 01	(?)
	136	1	1.000	2 ⇒ 23	(?)
	172	1	0.625	2 ⇒ 12	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	187	1	0.913	1 ⇒ 01	(?)
	192	1	1.000	0 ⇒ 01	(?)
node 32 → *Pusa caspica*	9	1	0.583	0 ⇒ 1	
	22	1	0.667	0 → 1	(D)
	43	1	0.545	0 ⇒ 1	
	56	1	0.636	1 ⇒ 2	
	74	1	0.625	0 ⇒ 1	
	78	1	0.682	1 ⇒ 0	
	91	1	0.556	2 ⇒ 0	
	92	1	0.625	0 ⇒ 9	
	93	1	0.625	1 ⇒ 9	
	94	1	1.000	0 ⇒ 9	
	96	1	0.500	0 ⇒ 1	
	*100	1	0.556	1 ⇒ 0	
	121	1	0.600	2 ⇒ 1	
	157	1	0.765	2 ⇒ 1	
	163	1	0.667	0 ⇒ 1	
	165	1	0.500	2 → 0	(D)
	168	1	0.571	0 ⇒ 1	
	188	1	0.625	3 ⇒ 2	
Pusa caspica (within terminal)	14	1	0.538	0 ⇒ 01	(?)
	*37	1	0.833	1 ⇒ 01	(?)
	38	2	0.632	2 ⇒ 129	(?)
	49	1	0.588	1 ⇒ 01	(?)
	59	1	0.625	2 ⇒ 12	(?)
	63	1	0.778	0 ⇒ 01	(?)
	75	1	0.500	1 ⇒ 01	(?)
	107	1	0.714	0 ⇒ 01	(?)
	112	1	0.692	0 ⇒ 02	(?)
	120	1	0.778	0 ⇒ 01	(?)
	*124	1	0.692	0 ⇒ 01	(?)
	131	1	0.833	1 ⇒ 01	(?)
	132	1	0.714	1 ⇒ 01	(?)
	178	1	0.643	1 ⇒ 12	(?)
	184	1	0.750	1 ⇒ 01	(?)
	187	1	0.913	1 ⇒ 12	(?)
node 32 → node 31	10	1	0.647	2 → 1	(A)
	96	1	0.500	0 ⇒ 1	
	107	1	0.714	0 ⇒ 1	
	108	1	0.429	0 → 1	(A)
	123	1	0.778	2 → 1	(A)
	132	1	0.714	1 → 0	(A)
	139	1	0.750	1 → 0	(A)
	155	1	0.889	1 → 0	(A)
	172	1	0.625	2 → 1	(A)
	174	1	0.692	1 ⇒ 0	
	183	1	0.667	2 → 1	(A)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	196	1	0.500	0 ⇒ 1	
node 31 → *Pusa sibirica*	10	1	0.647	2 → 1	(D)
	20	1	0.733	0 ⇒ 9	
	22	1	0.667	0 → 1	(D)
	42	1	0.800	1 ⇒ 0	
	56	1	0.636	1 ⇒ 0	
	63	1	0.778	0 ⇒ 1	
	108	1	0.429	0 → 1	(D)
	109	1	0.750	2 ⇒ 0	
	112	1	0.692	0 ⇒ 1	
	121	1	0.600	2 ⇒ 1	
	*124	1	0.692	0 ⇒ 9	
	126	1	0.579	0 ⇒ 9	
	132	1	0.714	1 → 0	(D)
	139	1	0.750	1 → 0	(D)
	141	1	0.692	1 ⇒ 3	
	155	1	0.889	1 → 0	(D)
	165	1	0.500	0 → 12	(A)
	167	1	0.571	1 ⇒ 0	
	172	1	0.625	2 → 1	(D)
	178	1	0.643	1 ⇒ 2	
	180	1	0.500	2 ⇒ 1	
	183	1	0.667	2 → 1	(D)
	184	1	0.750	1 ⇒ 0	
Pusa sibrica (within terminal)	9	1	0.583	0 ⇒ 01	(?)
	*35	1	0.692	0 ⇒ 01	(?)
	43	1	0.545	0 ⇒ 01	(?)
	51	1	0.714	2 ⇒ 12	(?)
	59	1	0.625	2 ⇒ 12	(?)
	67	1	0.778	9 ⇒ 19	(?)
	68	1	0.800	9 ⇒ 09	(?)
	75	1	0.500	1 ⇒ 01	(?)
	78	1	0.682	1 ⇒ 01	(?)
	91	1	0.556	2 ⇒ 02	(?)
	92	1	0.625	0 ⇒ 09	(?)
	93	1	0.625	1 ⇒ 19	(?)
	94	1	1.000	0 ⇒ 09	(?)
	120	1	0.778	0 ⇒ 01	(?)
	123	1	0.778	1 → 12	(A)
	123	1	0.778	2 → 12	(D)
	130	1	0.571	2 ⇒ 12	(?)
	165	1	0.500	1 → 12	(A)
	165	1	0.500	2 → 12	(D)
	187	2	0.913	1 ⇒ 123	(?)
	191	1	0.833	1 ⇒ 01	(?)
	192	1	1.000	0 ⇒ 01	(?)
	193	1	1.000	0 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
node 31 → *Pusa hispida*	97	1	0.500	1 ⇒ 0	
	123	1	0.778	2 → 1	(D)
	145	1	0.571	2 ⇒ 1	
	165	1	0.500	2 → 0	(D)
Pusa hispida (within terminal)	10	2	0.647	1 → 012	(A)
	10	2	0.647	2 → 012	(D)
	14	1	0.538	0 ⇒ 01	(?)
	22	1	0.667	1 → 01	(A)
	22	1	0.667	0 → 01	(D)
	38	1	0.632	2 ⇒ 12	(?)
	43	1	0.545	0 ⇒ 01	(?)
	49	1	0.588	1 ⇒ 01	(?)
	51	1	0.714	2 ⇒ 12	(?)
	59	1	0.625	2 ⇒ 12	(?)
	65	1	0.545	1 ⇒ 01	(?)
	72	1	0.667	0 ⇒ 01	(?)
	76	1	0.688	1 ⇒ 12	(?)
	108	1	0.429	1 → 01	(A)
	108	1	0.429	0 → 01	(D)
	119	1	0.786	0 ⇒ 01	(?)
	132	1	0.714	0 → 01	(A)
	132	1	0.714	1 → 01	(D)
	139	1	0.750	0 → 01	(A)
	139	1	0.750	1 → 01	(D)
	155	1	0.889	0 → 01	(A)
	155	1	0.889	1 → 01	(D)
	163	1	0.667	0 ⇒ 01	(?)
	172	1	0.625	1 → 12	(A)
	172	1	0.625	2 → 12	(D)
	183	1	0.667	1 → 12	(A)
	183	1	0.667	2 → 12	(D)
node 32 → node 30	10	1	0.647	2 → 0	(A)
	20	1	0.733	0 ⇒ 9	
	22	1	0.667	1 → 0	(A)
	*23	1	0.429	0 → 1	(A)
	24	1	0.571	9 → 0	(A)
	*32	1	0.643	5 → 4	(A)
	52	1	0.692	2 → 1	(A)
	59	1	0.625	2 ⇒ 1	
	72	1	0.667	0 ⇒ 1	
	92	1	0.625	0 ⇒ 1	
	*100	1	0.556	1 → 0	(A)
	120	1	0.778	0 → 1	(A)
	138	1	0.636	1 ⇒ 0	
	165	1	0.500	0 → 2	(A)
	187	1	0.913	1 ⇒ 3	
	196	1	0.500	0 ⇒ 1	

Appendix E (continued)

Branch	Character	Steps	CI	Change	
node 30 → *Erignathus*	9	1	0.583	0 ⇒ 1	
	17	1	0.250	0 ⇒ 1	
	*18	1	0.455	0 ⇒ 1	
	*23	1	0.429	0 → 1	(D)
	24	1	0.571	9 → 0	(D)
	*32	1	0.643	5 → 234	(D)
	*37	1	0.833	1 ⇒ 0	
	38	1	0.632	2 ⇒ 9	
	44	1	0.636	0 ⇒ 2	
	45	1	0.500	0 ⇒ 1	
	50	1	0.400	0 ⇒ 1	
	52	1	0.692	2 → 1	(D)
	53	1	0.500	0 ⇒ 1	
	62	1	0.556	1 ⇒ 2	
	*87	1	0.500	0 ⇒ 1	
	88	1	0.667	9 ⇒ 01	
	91	1	0.556	2 ⇒ 1	
	95	1	0.571	1 ⇒ 9	
	96	1	0.500	0 ⇒ 9	
	*100	1	0.556	1 → 0	(D)
	101	1	0.667	0 ⇒ 1	
	108	1	0.429	0 ⇒ 1	
	*124	1	0.692	0 ⇒ 9	
	126	1	0.579	0 ⇒ 9	
	130	1	0.571	2 ⇒ 0	
	149	1	0.667	2 ⇒ 0	
	151	1	0.500	1 ⇒ 0	
	168	1	0.571	0 ⇒ 1	
	170	1	0.636	2 ⇒ 01	
	*171	1	0.429	1 ⇒ 0	
	172	1	0.625	2 ⇒ 9	
	180	1	0.500	2 ⇒ 0	
	194	1	0.333	1 ⇒ 0	
Erignathus (within terminal)	10	2	0.647	0 → 012	(A)
	10	2	0.647	2 → 012	(D)
	*32	2	0.643	4 ⇒ 234	(?)
	*34	2	0.750	2 ⇒ 012	(?)
	*35	1	0.692	0 ⇒ 01	(?)
	76	1	0.688	1 ⇒ 12	(?)
	78	1	0.682	1 ⇒ 01	(?)
	79	1	0.727	1 ⇒ 12	(?)
	88	1	0.667	1 ⇒ 01	(?)
	112	1	0.692	0 ⇒ 01	(?)
	119	1	0.786	0 ⇒ 01	(?)
	120	1	0.778	1 → 01	(A)
	120	1	0.778	0 → 01	(D)
	122	1	1.000	0 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	132	1	0.714	1 ⇒ 01	(?)
	157	1	0.765	2 ⇒ 12	(?)
	170	1	0.636	1 ⇒ 01	(?)
	174	1	0.692	1 ⇒ 01	(?)
	176	1	0.800	0 ⇒ 01	(?)
	187	1	0.913	3 ⇒ 23	(?)
	192	1	1.000	0 ⇒ 01	(?)
node 30 → node 29	14	1	0.538	0 → 1	(A)
	42	1	0.800	1 → 0	(A)
	49	1	0.588	1 → 0	(A)
	65	1	0.545	1 ⇒ 2	
	78	1	0.682	1 ⇒ 2	
	80	1	0.538	2 → 0	(A)
	99	1	0.571	0 ⇒ 1	
	*100	1	0.556	0 → 2	(A)
	*100	1	0.556	1 → 2	(D)
	123	1	0.778	2 ⇒ 3	
node 29 → *Pagophilus*	10	1	0.647	2 → 0	(D)
	14	1	0.538	0 → 1	(D)
	*23	1	0.429	1 → 0	(A)
	24	1	0.571	0 → 9	(A)
	31	1	0.636	1 ⇒ 0	
	*32	1	0.643	4 ⇒ 0	
	*33	1	0.667	0 ⇒ 9	
	*34	1	0.750	2 ⇒ 9	
	*35	1	0.692	0 ⇒ 9	
	*36	1	0.500	0 ⇒ 9	
	43	1	0.545	0 ⇒ 9	
	62	1	0.556	1 ⇒ 0	
	64	1	0.545	1 ⇒ 0	
	69	1	0.167	0 ⇒ 1	
	80	1	0.538	2 → 0	(D)
	112	1	0.692	0 ⇒ 2	
	131	1	0.833	1 ⇒ 0	
	145	1	0.571	2 ⇒ 1	
	178	1	0.643	1 ⇒ 2	
Pagophilus (within terminal)	17	1	0.250	0 ⇒ 01	(?)
	*18	1	0.455	0 ⇒ 01	(?)
	22	1	0.667	0 ⇒ 01	(?)
	42	2	0.800	0 → 012	(A)
	42	2	0.800	1 → 012	(D)
	49	1	0.588	0 → 01	(A)
	49	1	0.588	1 → 01	(D)
	51	1	0.714	2 ⇒ 12	(?)
	52	1	0.692	1 → 12	(A)
	52	1	0.692	2 → 12	(D)
	56	1	0.636	1 ⇒ 01	(?)

Appendix E (continued)

Branch	Character	Steps	CI	Change	
	58	1	0.625	1 ⇒ 12	(?)
	76	1	0.688	1 ⇒ 12	(?)
	*87	1	0.500	0 ⇒ 01	(?)
	88	1	0.667	9 ⇒ 09	(?)
	120	1	0.778	1 → 01	(A)
	120	1	0.778	0 → 01	(D)
	141	1	0.692	1 ⇒ 13	(?)
	163	1	0.667	0 ⇒ 01	(?)
	165	1	0.500	2 ⇒ 02	(?)
	167	1	0.571	1 ⇒ 01	(?)
	168	1	0.571	0 ⇒ 01	(?)
	180	1	0.500	2 ⇒ 12	(?)
	184	1	0.750	1 ⇒ 01	(?)
	187	3	0.913	3 ⇒ 0123	(?)
node 29 → *Histriophoca*	*23	1	0.429	0 → 1	(D)
	24	1	0.571	9 → 0	(D)
	38	1	0.632	2 ⇒ 1	
	42	1	0.800	1 → 0	(D)
	49	1	0.588	1 → 0	(D)
	67	1	0.778	9 ⇒ 01	
	68	1	0.800	9 ⇒ 0	
	119	1	0.786	0 ⇒ 1	
	120	1	0.778	0 → 1	(D)
	141	1	0.692	1 ⇒ 0	
	188	1	0.625	3 ⇒ 2	
Histriophoca (within terminal)	6	1	0.714	0 ⇒ 01	(?)
	10	1	0.647	0 → 02	(A)
	10	1	0.647	2 → 02	(D)
	14	1	0.538	1 → 01	(A)
	14	1	0.538	0 → 01	(D)
	*32	1	0.643	4 → 45	(A)
	*32	1	0.643	5 → 45	(D)
	*34	1	0.750	2 ⇒ 12	(?)
	52	1	0.692	1 → 12	(A)
	52	1	0.692	2 → 12	(D)
	56	2	0.636	1 ⇒ 012	(?)
	67	1	0.778	1 ⇒ 01	(?)
	70	1	0.727	1 ⇒ 01	(?)
	76	1	0.688	1 ⇒ 12	(?)
	80	2	0.538	0 → 012	(A)
	80	2	0.538	2 → 012	(D)
	92	1	0.625	1 ⇒ 12	(?)
	121	1	0.600	2 ⇒ 23	(?)
	130	1	0.571	2 ⇒ 12	(?)
	142	1	0.750	1 ⇒ 14	(?)
	149	1	0.667	2 ⇒ 02	(?)
	155	1	0.889	1 ⇒ 01	(?)
	174	1	0.692	1 ⇒ 01	(?)

APPENDIX F

Character Diagnostics (unweighted)

The information contained in this appendix applies to the overall (consensus) solution presented in Fig.5B. Note that steps are listed as the number of changes in state for each character (= unweighted steps). Excluded characters are preceded by an asterisk.

Charac. No.	Min. Steps	Tree Steps	Max. Steps	CI	HI	RI	RC
*1	-	-	-	-	-	-	-
*2	-	-	-	-	-	-	-
3	4	5	4	0.800	0.800	0.900	0.720
4	3	3	4	1.000	0.667	1.000	1.000
5	3	3	6	1.000	0.667	1.000	1.000
6	5	7	10	0.714	0.714	0.600	0.429
7	2	4	5	0.500	0.500	0.333	0.167
8	1	3	3	0.333	0.667	0.000	0.000
9	7	12	12	0.583	0.750	0.000	0.000
10	11	17	18	0.647	0.824	0.143	0.092
11	4	8	11	0.500	0.750	0.429	0.214
12	1	3	4	0.333	0.667	0.333	0.111
13	1	1	2	1.000	0.000	1.000	1.000
14	7	13	15	0.538	0.769	0.250	0.135
15	1	1	1	1.000	0.000	0/0	0/0
16	2	3	4	0.667	0.667	0.500	0.333
17	2	8	12	0.250	0.875	0.400	0.100
*18	5	11	14	0.455	0.727	0.333	0.152
19	2	4	13	0.500	0.750	0.818	0.409
20	11	15	20	0.733	0.800	0.556	0.407
21	1	1	2	1.000	0.000	1.000	1.000
22	6	9	9	0.667	0.889	0.000	0.000
*23	3	7	11	0.429	0.857	0.500	0.214
24	8	14	21	0.571	0.786	0.538	0.308
*25	2	2	9	1.000	0.500	1.000	1.000
26	7	8	12	0.875	0.625	0.800	0.700
*27	2	2	7	1.000	0.500	1.000	1.000
28	4	5	8	0.800	0.600	0.750	0.600
29	1	1	1	1.000	0.000	0/0	0/0
30	2	3	5	0.667	0.667	0.667	0.444
31	7	11	17	0.636	0.818	0.600	0.382
*32	9	14	21	0.643	0.714	0.583	0.375
*33	4	6	10	0.667	0.500	0.667	0.444
*34	12	16	24	0.750	0.812	0.667	0.500
*35	9	13	20	0.692	0.846	0.636	0.441
*36	4	8	12	0.500	0.750	0.500	0.250
*37	5	6	6	0.833	0.833	0.000	0.000
38	12	19	21	0.632	0.842	0.222	0.140

Appendix F (continued)

Charac. No.	Min. Steps	Tree Steps	Max. Steps	CI	HI	RI	RC
39	2	3	3	0.667	0.667	0.000	0.000
40	1	2	4	0.500	0.500	0.667	0.333
41	4	7	11	0.571	0.857	0.571	0.327
42	12	15	19	0.800	0.867	0.571	0.457
43	6	11	19	0.545	0.818	0.615	0.336
44	7	11	18	0.636	0.818	0.636	0.405
45	4	8	13	0.500	0.750	0.556	0.278
46	1	3	3	0.333	0.667	0.000	0.000
47	1	3	3	0.333	0.667	0.000	0.000
48	1	2	4	0.500	0.500	0.667	0.333
49	10	17	19	0.588	0.882	0.222	0.131
50	2	5	7	0.400	0.800	0.400	0.160
51	5	7	11	0.714	0.857	0.667	0.476
52	9	13	16	0.692	0.846	0.429	0.297
53	1	2	2	0.500	0.500	0.000	0.000
54	2	2	5	1.000	0.500	1.000	1.000
*55	1	1	8	1.000	0.000	1.000	1.000
56	7	11	18	0.636	0.727	0.636	0.405
*57	2	3	3	0.667	0.667	0.000	0.000
58	10	16	19	0.625	0.812	0.333	0.208
59	10	16	21	0.625	0.812	0.455	0.284
60	3	4	4	0.750	0.500	0.000	0.000
61	3	5	6	0.600	0.800	0.333	0.200
62	5	9	15	0.556	0.778	0.600	0.333
63	7	9	12	0.778	0.889	0.600	0.467
64	6	11	13	0.545	0.909	0.286	0.156
65	6	11	12	0.545	0.818	0.167	0.091
66	2	3	6	0.667	0.667	0.750	0.500
67	7	9	11	0.778	0.667	0.500	0.389
68	8	10	11	0.800	0.700	0.333	0.267
69	1	6	9	0.167	0.833	0.375	0.062
70	8	11	14	0.727	0.818	0.500	0.364
*71	4	7	12	0.571	0.857	0.625	0.357
72	10	15	21	0.667	0.867	0.545	0.364
73	3	4	7	0.750	0.750	0.750	0.562
74	5	8	13	0.625	0.750	0.625	0.391
75	3	6	13	0.500	0.833	0.700	0.350
76	11	16	18	0.688	0.875	0.286	0.196
*77	5	6	6	0.833	0.833	0.000	0.000
78	15	22	26	0.682	0.864	0.364	0.248
79	8	11	13	0.727	0.818	0.400	0.291
80	7	13	19	0.538	0.846	0.500	0.269
81	2	5	7	0.400	0.600	0.400	0.160
82	4	8	10	0.500	0.750	0.333	0.167

Appendix F (continued)

Charac. No.	Min. Steps	Tree Steps	Max. Steps	CI	HI	RI	RC
83	4	5	6	0.800	0.800	0.500	0.400
84	2	5	13	0.400	0.800	0.727	0.291
85	1	1	4	1.000	0.000	1.000	1.000
86	1	2	3	0.500	0.500	0.500	0.250
*87	4	8	13	0.500	0.875	0.556	0.278
88	12	18	24	0.667	0.833	0.500	0.333
89	1	2	3	0.500	0.500	0.500	0.250
*90	-	-	-	-	-	-	-
91	5	9	15	0.556	0.778	0.600	0.333
92	10	16	21	0.625	0.812	0.455	0.284
93	5	8	16	0.625	0.750	0.727	0.455
94	4	4	4	1.000	0.500	0/0	0/0
95	4	7	14	0.571	0.714	0.700	0.400
96	2	4	5	0.500	0.500	0.333	0.167
97	3	6	6	0.500	0.667	0.000	0.000
98	6	7	7	0.857	0.714	0.000	0.000
99	4	7	14	0.571	0.571	0.700	0.400
*100	5	9	14	0.556	0.556	0.556	0.309
101	4	6	9	0.667	0.667	0.600	0.400
102	2	4	5	0.500	0.500	0.333	0.167
103	2	2	2	1.000	0.000	0/0	0/0
104	4	4	4	1.000	0.500	0/0	0/0
*105	1	1	2	1.000	0.000	1.000	1.000
106	4	8	11	0.500	0.625	0.429	0.214
107	5	7	8	0.714	0.857	0.333	0.238
108	3	7	15	0.429	0.714	0.667	0.286
109	3	4	12	0.750	0.500	0.889	0.667
110	1	2	3	0.500	0.500	0.500	0.250
111	1	1	8	1.000	0.000	1.000	1.000
112	9	13	17	0.692	0.846	0.500	0.346
113	3	8	10	0.375	0.750	0.286	0.107
114	3	4	13	0.750	0.500	0.900	0.675
115	1	1	8	1.000	0.000	1.000	1.000
116	1	1	2	1.000	0.000	1.000	1.000
117	1	3	3	0.333	0.667	0.000	0.000
118	1	1	8	1.000	0.000	1.000	1.000
119	11	14	17	0.786	0.857	0.500	0.393
120	7	9	14	0.778	0.778	0.714	0.556
121	6	10	14	0.600	0.700	0.500	0.300
122	3	3	4	1.000	0.667	1.000	1.000
123	14	18	23	0.778	0.833	0.556	0.432
*124	9	13	15	0.692	0.846	0.333	0.231
*125	3	9	10	0.333	0.889	0.143	0.048

Appendix F (continued)

Charac. No.	Min. Steps	Tree Steps	Max. Steps	CI	HI	RI	RC
126	11	19	21	0.579	0.789	0.200	0.116
127	2	3	11	0.667	0.333	0.889	0.593
128	4	6	10	0.667	0.500	0.667	0.444
*129	5	8	11	0.625	0.625	0.500	0.312
130	8	14	19	0.571	0.857	0.455	0.260
131	5	6	6	0.833	0.667	0.000	0.000
132	10	14	19	0.714	0.857	0.556	0.397
133	5	5	5	1.000	0.600	0/0	0/0
134	2	3	4	0.667	0.333	0.500	0.333
135	4	5	5	0.800	0.400	0.000	0.000
136	8	8	9	1.000	0.500	1.000	1.000
137	7	10	15	0.700	0.800	0.625	0.438
138	7	11	17	0.636	0.818	0.600	0.382
139	9	12	19	0.750	0.833	0.700	0.525
140	7	9	16	0.778	0.778	0.778	0.605
141	9	13	24	0.692	0.615	0.733	0.508
142	9	12	21	0.750	0.583	0.750	0.562
143	1	4	7	0.250	0.750	0.500	0.125
144	3	5	7	0.600	0.800	0.500	0.300
145	4	7	17	0.571	0.714	0.769	0.440
146	1	4	9	0.250	0.750	0.625	0.156
147	2	3	5	0.667	0.667	0.667	0.444
148	1	2	2	0.500	0.500	0.000	0.000
149	10	15	18	0.667	0.733	0.375	0.250
150	6	10	11	0.600	0.800	0.200	0.120
151	2	4	10	0.500	0.750	0.750	0.375
152	3	4	10	0.750	0.750	0.857	0.643
153	5	6	13	0.833	0.667	0.875	0.729
154	7	10	15	0.700	0.900	0.625	0.438
155	8	9	11	0.889	0.889	0.667	0.593
*156	5	6	7	0.833	0.833	0.500	0.417
157	13	17	26	0.765	0.824	0.692	0.529
*158	1	1	1	1.000	0.000	0/0	0/0
159	6	9	14	0.667	0.778	0.625	0.417
160	2	3	12	0.667	0.333	0.900	0.600
161	1	3	13	0.333	0.667	0.833	0.278
162	3	5	13	0.600	0.800	0.800	0.480
163	4	6	8	0.667	0.833	0.500	0.333
164	6	6	10	1.000	0.833	1.000	1.000
165	7	14	16	0.500	0.857	0.222	0.111
166	1	2	11	0.500	0.500	0.900	0.450
167	4	7	15	0.571	0.714	0.727	0.416
168	4	7	11	0.571	0.714	0.571	0.327
169	1	3	4	0.333	0.667	0.333	0.111
170	7	11	20	0.636	0.818	0.692	0.441

Appendix F (continued)

Charac. No.	Min. Steps	Tree Steps	Max. Steps	CI	HI	RI	RC
*171	3	7	10	0.429	0.857	0.429	0.184
172	10	16	24	0.625	0.812	0.571	0.357
173	3	4	5	0.750	0.500	0.500	0.375
174	9	13	17	0.692	0.923	0.500	0.346
175	3	4	12	0.750	0.750	0.889	0.667
176	4	5	13	0.800	0.800	0.889	0.711
177	2	5	10	0.400	0.800	0.625	0.250
178	9	14	18	0.643	0.857	0.444	0.286
*179	2	6	7	0.333	0.833	0.200	0.067
180	6	12	17	0.500	0.750	0.455	0.227
181	1	1	8	1.000	0.000	1.000	1.000
182	2	4	7	0.500	0.750	0.600	0.300
183	8	12	19	0.667	0.833	0.636	0.424
184	9	12	13	0.750	0.917	0.250	0.188
*185	1	1	8	1.000	0.000	1.000	1.000
186	1	1	8	1.000	0.000	1.000	1.000
187	21	23	35	0.913	0.826	0.857	0.783
188	5	8	11	0.625	0.625	0.500	0.312
189	2	4	12	0.500	0.750	0.800	0.400
190	6	8	12	0.750	0.750	0.667	0.500
191	5	6	6	0.833	0.833	0.000	0.000
192	6	6	6	1.000	0.833	0/0	0/0
193	1	1	1	1.000	0.000	0/0	0/0
194	1	3	12	0.333	0.667	0.818	0.273
195	1	3	6	0.333	0.667	0.600	0.200
196	3	6	13	0.500	0.667	0.700	0.350

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