On "Retrogression" in the Evolution of the Phocinae and Phylogenetic Affinities of the Monk Seals

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ABSTRACT

The origin of the phocine seals appears to have been associated with a pattern of massive character reversal, particularly as concerns features of the postcranial skeleton. To establish that the primitive features occurring in phocines do in fact represent reversals and not simply retentions from an ancestral phocid condition, a reexamination of the two currently recognized subdivisions of the Phocidae is undertaken. In contrast to the strongly corroborated hypothesis of the monophyly of the Phocinae, it is concluded that the monophyly of the "Monachinae" remains significantly more doubtful. Monk seals have been placed within this latter subfamily in all recent phylogenetic treatments of the Phocidae. Analysis here reveals that this arrangement is less strongly supported than is generally assumed. Moreover, the genus comprising monk seals, "Monachus," does not itself ap-

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pear to be monophyletic. Thus, in the preferred branching arrangement presented here both the "Monachinae" and "*Monachus*" are portrayed as paraphyletic, with the monk seals placed as sequential sister-taxa to the remaining phocids.

Certain aspects of the phocine postcranium, which may be considered primitive, are not primitive for phocids as a whole, and an exceptional series of reversals within the clade comprising the Phocinae must therefore be postulated. This pattern of character transformation is corroborated whether or not "monachine" paraphyly is accepted. Moreover, these reversals can be substantiated whether or not one ascribes to the multiple origin of pinnipeds. Acceptance of either "monachine" paraphyly or pinniped monophyly, however, accentuates the pattern of reversal seen among phocines.

INTRODUCTION

The so-called "true" or "earless" seals of the family Phocidae are undoubtedly among the most highly specialized members of the eutherian order Carnivora. It is well known that in many aspects of the postcranial skeleton members of the phocid subfamily Phocinae differ markedly from other phocids. Hitherto ignored is the observation that many of the features in which phocines depart from the conditions typical of other phocids are decidedly primitive. Also overlooked is the fact that these primitive traits not only set phocines apart from other phocids, but serve as well to distinguish phocines from all other pinnipeds. From a phylogenetic standpoint, then, the situation seen in phocines is compatible with two interpretations; either (1) these characters represent primitive holdovers from the ancestral phocid condition, or (2) they represent reversals to more primitive states that have occurred subsequent to the early diversification of phocids. Preference for one of these transformational hypotheses necessarily depends on the acceptance of a particular notion of phocid phylogeny and thus the remarks presented below are primarily aimed at an examination of some of the more general aspects of the interrelationships of these highly aquatic carnivorans.

The greatly divergent morphology of phocids, coupled with their scant fossil record and a general historical lack of detailed examination, has resulted in both a poor understanding of the origin of the group as a whole and considerable uncertainty regarding the mutual phylogenetic affinites of its members. Higher-level intra-phocid relationships are crucial to deciding between the two alternative sequences of transformation outlined above, and thus form the principal

focus of this paper. If other characters can be recruited to support the placement of phocines as the sister-group of other phocids, it might then become judicious to suggest that the postcranial features of phocines are primitive for phocids. Alternatively, if phocines can be shown to be removed from a sister-group position, then the unusual primitive phocine postcranial attributes may reasonably be interpreted as reversals. The apparently conservative aspects of phocine morphology include features associated with the architecture of the fore- and hind-flippers, and the more proximal appendicular skeleton, as well as a lesser number of soft anatomical and cranial traits.

Phocids are currently divided into the postcranially plesiomorphic Phocinae and the "Monachinae,"[2] which are more typically pinniped in many postcranial aspects. One means of establishing that phocines (assuming for the moment their monophyly) are not the sister-group of other phocids is a demonstration of the paraphyly of the presumed phocine sister-group the "monachines." Therefore I first examine the presumed basal ("monachine"/phocine) phocid dichotomy, dealing specifically with the monophyly of "*Monachus*"—a taxon widely recognized as representing an early offshoot in the evolution of phocids—and a consideration of the affinities of its three Recent species to other phocids. This leads to an evaluation of the evidence bearing on the monophyly of the higher taxonomic group of which "*Mona-*

[2] Because the monophyly of the "Monachinae" and its type genus "*Monachus*" has yet to be securely demonstrated and is in fact called into question by this analysis, these nomena are included in quotes throughout this paper.

chus" is widely held as being a member, the "Monachinae." This phylogenetic framework then permits the central objective of this paper, a more detailed consideration of the occurrence of wide-scale character reversal in the evolution of phocine seals, a possibility suggested above.

The present account is not intended as an exhaustive treatment of intraphocid relationships; it merely represents a preliminary examination of these affinities as they pertain specifically to the questions outlined above. I make no claim to either the originality of any of the observations made or to any of the characters considered. My efforts are aimed simply at putting into a phylogenetic context one particular—and highly peculiar—character distribution.

PHOCID MONOPHYLY AND HISTORICAL CONSIDERATIONS

If any statement about the higher-level relationships among arctoid carnivorans is beyond reasonable doubt, it is that the Phocidae are monophyletic. Advanced features common to members of this highly modified group are many, including: the inability to draw the hind limbs forward during terrestrial locomotion, the lack of a lesser trochanter on the femur, the lack of an alisphenoid canal, a transversely directed basal cochlear whorl, an opening of the cochlear fenestra outside the tympanic cavity to form a cochlear foramen, the lack of an internal auditory meatus and prefacial commissure, strongly everted ilia, a massively developed posterior astragalar process and greatly reduced calcaneal tuber, heavily pachyostotic mastoid region, pterygoids reaching the auditory bulla, pit for insertion of tympanohyal anterior to stylomastoid foramen, greatly inflated heavily ossified caudal entotympanics, and an ilial psoas major insertion (Weber, 1904; Gray, 1905; Fawcett, 1918; Howell, 1929; Kummer and Neiß, 1957; Burns and Fay, 1970; Repenning, 1972; Hunt, 1974; de Muizon, 1981a, 1981b; King, 1983). Features common to phocids that also are approached or matched in *Odobenus,* its close fossil allies, and/or the Miocene allodesmine and dematophocine "otarioids" include: greatly expanded cochlear fenestra, greatly expanded basal whorl of the scala tympani, separation of the entrances of cranial nerves VII and VIII, inguinal testes, dark epidermis, hind limb propulsion, greatly enlarged incus, malleus and epitympanic recess, mortised jugal-squamosal contact, nasals wedging deeply between the frontals, short premaxillary-nasal contact, absence of pinnae, nonmedulated primary hairs, lack of supraorbital processes, lack of fusion between exoccipital and mastoid, and merging of canal for cochlear aqueduct with cochlear fenestra (citations above and Scheffer, 1964; Mitchell, 1966; Barnes, 1972, Fleischer, 1973; Gordon, 1981; Fay, 1982). Most of these and other characters are discussed at length elsewhere (Wyss, 1987). Therein these features are argued to represent evidence of the kinship of phocids to the abovementioned groups (see also remarks below).

Given such an apparently robust diagnosis of the Phocidae, it is not surprising that historically there has been little debate about its genealogical reality. Following Illiger's 1811 recognition of pinnipeds as a group distinct from other aquatic mammals, Gray (1825)

erected the grouping Phocidae to include what would today be regarded as phocids, otariids (sea lions and fur seals), and *Enhydra*. Curiously, Gray's arrangement excluded the walrus, *Odobenus* (=*Trichecus rosmarus*), relegating it instead to isolated familial status within an order encompassing cetaceans and sirenians. It was Brookes (1828) who first recognized the phocid grouping as it is presently conceived. Subsequently, in Allen's (1880) well-known subdivision of the pinnipeds, phocids came to be termed "wrigglers," while their terrestrially more nimble brethren the otariids and *Odobenus* (which maintain the use of their hind limbs in locomoting on land) were dubbed "walkers."

Beyond universal agreement on the question of phocid monophyly, however, there is little consensus regarding other aspects of phocid relationships. Disagreement centers on two areas, identification of a phocid sister-group and the establishment of major phylogenetic subdivisions within the family. With respect to the former, "Which carnivoran lineage is most closely allied to phocids?" there are two widely divergent schools of thought. One view held by many comparative anatomists earlier this century (e.g., Weber, 1904; Winge, 1923, 1941) and shared almost unanimously among molecular and karyological systematists (e.g., Deuel, 1955; Fay et al., 1967; Sarich, 1969a, 1969b; Arnason, 1974, 1977; de Jong, 1982; Arnason and Widegren, 1986), places phocids within a monophyletic Pinnipedia as the sister to a group comprising otariids and odobenids. An alternative view establishes pinnipeds as diphyletic in origin with phocids representing an independently derived aquatic lineage closely allied to mustelids (e.g., McClaren, 1960, Tedford, 1976; de Muizon, 1982a, 1982b). As noted above, evidence has been presented elsewhere (Wyss, 1987) supporting yet a third arrangement, namely that phocids are members of a clade including *Odobenus, Allodesmus,* and *Desmatophoca,* with this grouping in turn embraced within a monophyletic Pinnipedia. *Allodesmus* and *Desmatophoca* traditionally have been allocated to the "Otarioidea"—a group essentially equivalent to Allen's "walkers" plus their subsequently described presumed fossil allies. It should be pointed out, however, that evidence supporting the

"Otarioidea" appears to consist largely of primitive characters, that is, characters of a distribution much more general than simply "otarioids" (e.g., retention of an alisphenoid canal, an internal auditory meatus, and the ability to draw the hind limbs forward during terrestrial locomotion). Thus the morphological basis of the conventionally accepted phylogenetic unity of "otarioids" consists in large measure of the shared absence of the apomorphies common to phocids, leading one to conclude that this collocation has been based largely on the nonphocid status of its constituents. In keeping with this assessment, and on the basis of the features listed above, I have elsewhere presented the admittedly controversial argument that some "otarioids" share a more recent common ancestry with phocids than they do with other supposed "otarioids" (Wyss, 1987).

While higher-level relationships among the major pinniped lineages have attracted much detailed discussion—and are likely to continue to do so as several recent, not always congruent, considerations of the subject indicate (e.g., Flynn et al., 1988; Wozencraft, 1988)—many other interesting phylogenetic problems among pinnipeds remain. The interrelationships among phocids is one area warranting further attention. Naturally the two areas of inquiry, higher-level pinniped relationships and the relationships within one of its subgroups, are to a large degree intertwined.

Before considering relationships among phocids, the phylogenetic position of phocids among other pinnipeds and among other carnivorans must be discussed as this influences decisions about character generality. It is widely recognized that for systematic investigations to yield phylogenetic results (i.e., to reflect genealogy), proposed relationships must be supported on the basis of shared possession of derived attributes (Hennig, 1966). One useful means of establishing character polarity is outgroup comparison. Any analysis should specify its operating assumptions, including the selection of reference taxa. In the present case, the choice of outgroups is inseparable from the question of pinniped monophyly. Although the debate is not settled, space is not taken here to provide a detailed assessment of the dual versus single

origin issue. For the moment it suffices simply to state that the monophyly hypothesis remains by far the least contradicted of presently available alternatives. The present analysis thus proceeds from the premise that otariids and *Odobenus* (and not mustelids) represent appropriate nearest phocid outgroups, with *Odobenus* (among living pinnipeds) being the most immediate sister-group. It should be emphasized, however, that in a certain general sense these assumptions are not critical. For most of the characters examined, the character states in question would be unambiguously regarded as derived even if mustelids were used as an outgroup. Potential conflicts that would arise if mustelids were recognized as the phocid sister-group are noted in the discussion. How the phylogenetic results accepted here would be altered under an assumption of pinniped diphyly, is considered in the conclusions. Reference to the diphyly argument is included to show that the conclusions drawn here are not strictly dependent on the rejection of diphyly. The pattern of primitive character reacquisition identified among phocines, although mildly sensitive in the degree to which it is expressed, holds true whether or not monophyly is assumed.

Historically phocids have been variously divided into two to four major subgroupings. In her insightful 1966 study, King collapsed earlier, more highly split arrangements, advocating instead a two-part division of the Phocidae into the so-called northern (*Erignathus, Cystophora, Halichoerus, Phoca, Pusa, Histriophoca, Pagophilus*) and southern lineages ("*Monachus,*" *Mirounga, Leptonychotes, Lobodon, Hydrurga, Ommatophoca*). At the same time King suggested that *Erignathus* and "*Monachus*" may represent forms linking these two broad groups. This split has been formalized with the recognition of two phocid subfamilies, the "Monachinae" and the Phocinae in numerous subsequent classifications (e.g., King, 1983; de Muizon, 1982a). Presented in figure 1 are what I consider the four most important alternatives for the phylogenetic arrangement of phocids. The most widely held current view of a phocid division into two monophyletic subfamilies (e.g., de Muizon, 1982a) is regarded as a class I hypothesis; this branching scheme admits a monophyletic "*Monachus,*" "Monachinae," and Phocinae. Other arrangements shown in figure 1 are discussed in succeeding sections but are briefly summarized here. Class II hypotheses place "*Monachus*" as the sister-group of other phocids, with the "Monachinae" recognized as paraphyletic. In class III hypotheses "*Monachus*" is recognized as paraphyletic but the monophyly of "monachines" exclusive of "*Monachus*" is preserved. In class IV arrangements only the subfamily Phocinae is recognized as monophyletic with other "monachines" and "*Monachus*" representing successively more distant paraphyletic outgroups.

The "Monachinae" traditionally include (in addition to "*Monachus*" and *Mirounga*) the almost certainly monophyletic tribe Lobodontini, comprising among living forms the Antarctic *Leptonychotes, Lobodon, Hydrurga,* and *Ommatophoca.* As the phylogenetic arrangement of phocids has been interpreted by de Muizon (1982a), *Mirounga* is the sister-group of the lobodontines, with "*Monachus*" in turn representing the outgroup to *Mirounga* + lobodontines. As will be discussed below, however, the monophyly of this subfamily is not as strongly founded as might be desired, particularly as regards the inclusion of "*Monachus.*"

A third phocid subfamily, the "Cystophorinae," was formerly recognized (e.g., Scheffer, 1958) for the two taxa with an inflatable proboscis, *Mirounga* and *Cystophora.* Since King's (1966) contribution, this group is no longer regarded as monophyletic, *Mirounga* being dispatched to the "monachines" and the *Cystophora* to the phocines.

As concerns the status of the genera recognized in this analysis, it is necessary to point out the recommendation that the phocines *Pusa, Histriophoca,* and *Pagophilus* be assigned to subgeneric rank under the genus *Phoca* (Burns and Fay, 1970). Other authors (see de Muizon, 1982a: 188) have also proposed *Pusa* as a subgenus of *Phoca.* I have chosen to sidestep this issue. A matter of more pressing concern is how the various taxa and monophyletic groups of taxa we elect to recognize are interrelated. The monophyly of *Phoca* in the broad sense (including *Pusa, Histriophoca,* and *Pagophilus*) has not been

upheld by one recent study (de Muizon, 1982a). Thus I regard the matter as unsettled and simply recognize all of these four as genera. Similar reasoning applies to the question of the appropriate rank for the group comprising all phocids. This is not an objectively resolvable matter and consequently there exists a considerable diversity of opinion (e.g., Barnes et al., 1985). For the purpose of internal consistency and in the interest of convenience I arbitrarily regard phocids as a family.

Most published studies agree on the monophyletic grouping of *Pusa, Histriophoca, Pagophilus, Halichoerus,* and *Phoca,* typically given the tribal designation Phocini (e.g., Burns and Fay, 1970; de Muizon, 1982a), a concept also supported by this analysis.

COMPARATIVE MORPHOLOGY AND PHYLOGENETICS

We are now in a position to attempt a detailed character analysis. First, characters bearing on the question of the placement of "*Monachus*" within the Phocidae will be considered, then features that have been marshalled in support of a "monachine"-phocine division. It will be primarily in review of this second set of characters that the "primitive" attributes of phocines will become apparent. Once the characters have been considered and a phylogenetic framework of phocids established, patterns of character transformation within the phocines will be open to inspection. Detailed consideration is given to the derivation of the proposed phylogeny since such an analysis necessarily forms the backbone of any study of character evolution.

"*Monachus*" Affinities

As currently conceived, the genus "*Monachus*" includes three Recent species, the Hawaiian "*M.*" *schauinslandi,* the Mediterranean "*M.*" *monachus,* and the recently extinct Caribbean "*M.*" *tropicalis.* The question of the mutual affinities of these three seals has attracted only limited attention. However, in view of their singularly important phyletic position as the potential sister-group(s) of other phocids, a consideration of their phylogenetic affinities seems advisable.

Monk seals are said to be among the most conservative members of the Phocidae and to probably represent an early split in the evolution of the group (e.g., Repenning and Ray, 1977; Repenning et al. 1979; de Muizon, 1982a). In their important study of the Hawaiian monk seal, Repenning and Ray (1977) reviewed several lines of evidence suggesting that in many respects species of "*Monachus*" appear to be more primitive than other phocids. Furthermore, these authors highlighted several morphologic differences between the three Recent taxa and noted that "*M.*" *schauinslandi* (ibid.: 684) "appears to be the modern representative of the most ancient of living phocid lineages." Translating these remarks into the terminology of phylogenetic systematics, Repenning and Ray hinted at, but did not advocate explicitly, a phylogeny conforming to a class II or III arrangement of figure 1, where "*M.*" *schauinslandi* represents the sister-taxon of other phocids. Later, however, Repenning et al. (1979: fig. 1) modified this opinion, depicting the "Hawaiian Island Group" as an early offshoot of the monachine (rather than phocid) lineage, thus preserving the traditional monachine-phocine division of the family (a class I hypothesis of fig. 1). If this second interpretation is accepted and if "*M.*" *schauinslandi* is more conservative in several respects than are other phocids, we may infer that the advanced characters of phocids other than the Hawaiian monk seal must have originated at least twice, once within a clade embracing the "monachines" exclusive of "*M.*" *shauinslandi,* and once within phocines. Alternatively, "*M.*" *shauinslandi,* and perhaps other species of "*Monachus,*" may have secondarily reacquired some primitive features not found in other phocids.

Much of the present paper, therefore, is a review of the alternative character transformations implied by these phylogenies. Throughout the discussion that follows, characters are numbered as in tables 1 and 2, where polarity decisions are summarized and the distribution of these features is provided.

CHARACTERS PERTINENT TO THE PLACEMENT OF "*MONACHUS*"

Repenning and Ray (1977) pointed to several features of the "*Monachus*" ear region
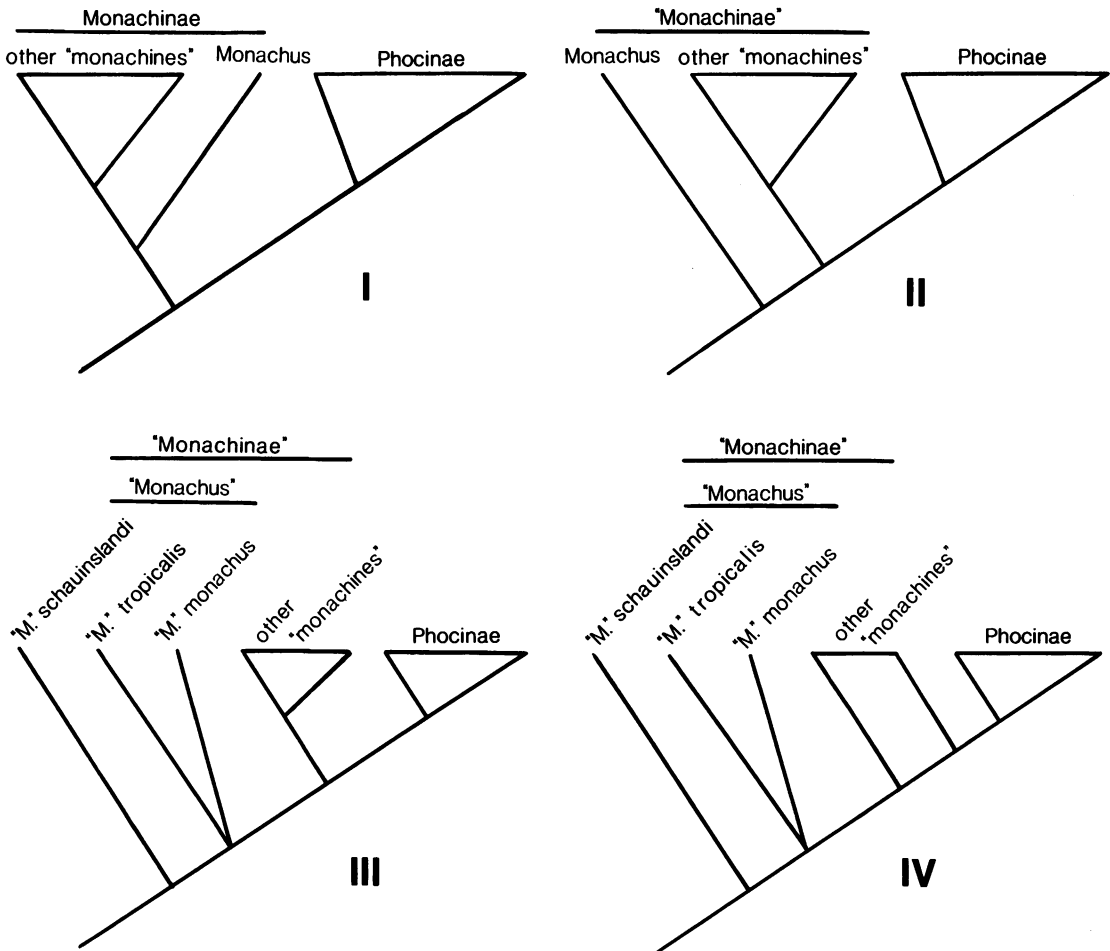
Fig. 1. The four general hypotheses of phocid interrelationships discussed in text. Most commonly debated arrangements represent one of these patterns or slight permutations thereof. These possibilities do not subsume all possible branching arrangements; others include a nonmonophyletic Phocinae, or the placement of phocines as the sister-group of other phocids, but these are not among the most likely alternatives. For example, since King (1966) phocine monophyly has not been questioned. Likewise, the placement of phocines as the sister-group of other phocids has no precedent in the literature nor is such an arrangement given credence by the present analysis.

that are clearly plesiomorphic among phocids. The following five auditory features seem to be primitive (except as noted) among Pinnipedia and their alternative derived conditions may be diagnostic of a monophyletic group of phocids exclusive of "*Monachus.*"

1. "Otarioid"-like distribution of cavernous tissue lining middle ear cavity. The pinniped middle ear cavity is filled by distensible tissue thought to inflate with blood in response to increasing external pressure during

diving (Repenning, 1972). Unlike the other "monachines" and phocines that have been examined, the distribution pattern of this tissue within the epitympanic recesses of "*M.*" *shauinslandi* "appears to parallel that of otarioid pinnipeds" (Repenning and Ray, 1977: 672). They added, however (recognizing that this does not necessarily imply parallelism), that they were inclined to the view that this pattern "reflected some unknown primitive condition" (ibid.). Due to its greater economy I would similarly favor this sec-

TABLE 1
Selected Phocid Features and Polarity Determinations Discussed in Text

Feature	Primitive	Derived
1) tissue lining middle ear cavity	"otarioid"-like	thick near floor and roof
2) dorsal region of petrosal	unexpanded	expanded
3) petrosal apex	unexpanded, pointed	dorsoventrally thickened, blunter in outline
4) internal auditory meatus	remnant of roof present	roof completely absent
5) pericardial plexus	poorly developed	well developed
6) tibia and fibula	unfused proximally	fused proximally
7) innominate, obturator nerve foramen	present	uniformly absent
8) teres major process	caudal scapular angle square	hooklike
9) mastoid swelling	not visible in dorsal view	visible in dorsal view
10) auditory bulla	does not cover petrosal, widely separate from exoccipital	essentially covers petrosal, nearly contacts exoccipital
11) posterior lacerate foramen	circular, basioccipital abuts auditory region	coalesces with petrobasilar fissure medial to auditory region
12) atlas	vertebrarterial foramen visible in posterior view	visible in dorsal view
13) scapular spine	prominent	markedly reduced
14) entepicondylar foramen	absent	present
15) cuneiform	distally projecting ledge absent	present
16) metacarpals I and II, comparative size	I greatly enlarged	approximately equal
17) intermediate phalanx V of carpus	greatly reduced	comparable in size to its counterparts
18) metacarpal head, phalangeal articulations	smooth head, phalanges flat, articulations hingelike	heads with palmar ridges, phalanges round, articulations trochleated
19) ilium	straight, flat	strongly everted, lateral excavation
20) astragalus	sustentacular facet long	facet short
21) metatarsal III, posterior flipper margin	short, margin concave	long, margin straight
22) foreflipper claws	reduced	long
23) hind-flipper claws	long	reduced
24) premaxilla	ascending process visible laterally along entire length	ascending process dips into nasal aperture
25) upper incisors	six	four
26) natal coat	black	gray or white
27) secondary hairs	absent	present
28) molt	cornified tissue and hair do not form sheets	cornified tissue and hair form sheets during molt
29) mystacial whiskers	smooth	beaded
30) mammary teats	four	two
31) chromosomes	$2N = 34$	$2N = 32$
32) upper incisors	round in cross section	compressed laterally
33) carotid canal, posteromedial process of auditory bulla	posterior opening visible in ventral view, process present	not visible in ventral view, process absent
34) interorbital width	least in posterior half of interorbital septum	least in anterior half
35) basioccipital-basisphenoid area	ventral surface strongly concave	flat to convex
36) mastoid lip	does not cover external cochlear foramen	covers or partially covers foramen

TABLE 1—(*Continued*)

Feature	Primitive	Derived
37) humerus, supinator ridge	poorly developed	well developed
38) humerus, deltoid pectoral crest	long, merges with shaft smoothly	short, ends more abruptly
39) post-tibial fossa development	weak	strong

ond interpretation. Regrettably the disposition of this tissue for the other two living species of "*Monachus*" is not known and hence is marked in table 2 by a query. Nevertheless, phocids exclusive of at least "*M.*" *schauinslandi* show a unique (at least among pinnipeds) pattern of distribution of the cavernous tissue lining middle ear wherein it is thickest near the floor and roof of the middle ear cavity, thinning near the eustachian tube, across the tympanic membrane, and in the epitympanic recess (Repenning, 1972).

2. Unexpanded dorsal petrosal region (primitive character distinguishing "*M.*" *schauinslandi* from other phocids). Repenning and Ray (1977) made the important observation that among all known phocids (fossil and Recent) the dorsal part of the petrosal (defined as the region above a horizontal plane extending from the vestibular aqueduct, forward across the cochlear aqueduct to the anterodorsal surface of the petrosal apex) is the least developed among "*M.*" *schauinslandi*. Thus, unlike that in other phocids (including "*M.*" *tropicalis* and "*M.*" *monachus*), the ventral part of the petrosal in "*M.*" *schauinslandi* protrudes medially and apically from beneath the unexpanded dorsal portion. Typically in phocids, the derived expansion of the dorsal part of the petrosal results (in dorsal view) in the ventral portion largely being covered (fig. 2) (see also Repenning and Ray, 1977: pl. 1). Not only is "*M.*" *schauinslandi* the most conservative of living phocids in its relatively unenlarged dorsal petrosal region, it appears to be less advanced than all known fossil phocids as well (ibid.). Also pertinent here is the observation of Repenning and Ray (1977: 675) who noted that the petrosal in "*M.*" *schauinslandi*, by virtue of its relatively small basal cochlear whorl

appears to be "the most primitive of known phocoid seals." The possibility might therefore be considered that other phocids are apomorphically united by a greater enlargement of the basal turn of the cochlea.

3. Unenlarged V-shaped petrosal apex. As has been carefully observed and discussed by Ray (1976) a considerable diversity in the form of the temporal region exists within phocids. Although as Ray noted, the exceedingly complex morphology of the region is not readily broken down into "key" component characters, some potentially systematically useful features do seem to be exhibited. Most conspicuous perhaps is the swelling of the dorsal petrosal surface, resulting in the development of a dense globular mass of bone near the dorsal petrosal apex, a condition seen particularly in phocines (except *Erignathus*) and in *Mirounga* (ibid.). Thus in these forms the highest point on the intracranial surface of the petrosal is on this swollen apex which is seen in anterior view to extend above the level of the entrance of the facial canal.

Another feature of potential significance is the general form—aside from the swelling just noted—of this apical region. Relative to those of other pinnipeds, the petrosal apex of all phocids is massive, but in comparison to those in other members of the family the petrosal apices of all three Recent species of "*Monachus*" remain relatively unexpanded (fig. 2). In carnivorans in general, including otariids and particularly *Odobenus*, the petrosal apex assumes a distinctly V-shaped outline in dorsal view. This appearance is modified somewhat in most phocids either by the apical hypertrophy noted above or by medial and lateral outgrowths near the apical region, both of which contribute to a generally blunter, sometimes almost square, outline (fig. 2). The

TABLE 2

Distribution of Phocid Features Discussed in Text

Features correspond to those listed in table 1. Symbols in the matrix denote the following: + derived character, 0 primitive character, ? not known, * features of phocines which although derived for phocids, are, or approach, the primitive carnivoran (or mammalian) condition.

	Mona- chus schauins- landi	M. monachus	M. tropicalis	Mirounga	Lepto- nychotes	Lobodon
1) tissue lining middle ear cavity	0	?	?	+	+	+
2) dorsal region of petrosal	0	+	+	+	+	+
3) petrosal apex	0	0	0	+	+	+
4) internal auditory meatus	0	0	0	+	+	+
5) pericardial plexus	0	?	?	+	+	+
6) tibia and fibula	0	+	+	+	+	+
7) innominate, obturator nerve foramen	0	+	+	+	+	+
8) teres major process	0	0	0	0	+	+
9) mastoid swelling	0	0	0	0	0	0
10) auditory bulla	0	0	0	+	+	+
11) posterior lacerate foramen	0	0	0	0	0	0
12) atlas	0	0	0	+	+	+
13) scapular spine	0	0	0	0	+	+
14) entepicondylar foramen	0	0	0	0	0	0
15) cuneiform	0	0	0	0	0	0
16) metacarpals I and II, comparative size	0	0	0	0	0	0
17) intermediate phalanx V of carpus	0	+	0	0	0	0
18) metacarpal head, phalangeal articulations	0	0	0	0	0	0
19) ilium	0	0	0	0	0	0
20) astragalus[c]	0	0	0	0	0	0
21) metatarsal III, posterior flipper margin	+	+	+	+	+	+
22) foreflipper claws	0	0	0	0	0	0
23) hind-flipper claws	+	+	+	+	+	+
24) premaxilla	+	+	0	+	+	+
25) upper incisors	+	+	+	+	+	+
26) natal coat	0	0	0	0	+	+
27) seconary hairs	0	0	0	0	+	+
28) molt	+	?	?	+	0	0
29) mystacial whiskers	0	0	0	+	+	+
30) mammary teats	0	0	0	+	+	+
31) chromosomes	0	0	0	0	0	0
32) upper incisor shape	0	0	0	0	0	0
33) carotid canal, posteromedial process of auditory bulla	0	0	0	0	0	0
34) interorbital width	0	0	0	0	0	0
35) basioccipital-basisphenoid area	0	0	0	0	0	0
36) mastoid lip	0	0	0	0	+	+
37) humerus, supinator ridge	0	0	0	0	0	0
38) humerus, deltoid pectoral crest	0	0	0	0	0	0
39) post-tibial fossa	0	0	0	0	0	0

[a] The phocine scapula more resembles the terrestrial carnivoran form than that of other phocids in its exaggerated hooklike teres major process and strong reduction of the supraspinous fossa.

[b] Very strong scapular spine in phocines.

[c] See text.

[d] Among phocids this feature more closely approaches the primitive carnivoran conditions in phocines.

[e] See text.

TABLE 2—(*Continued*)

Hydrurga	Ommato-phoca	Erig-nathus	Cys-tophora	Phoca	Pusa	Hali-choerus	Histrio-phoca	Pago-philus	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	*a
0	0	+	+	+	+	+	+	+	
+	+	0	0	0	0	0	0	0	
0	0	0	+	+	+	+	+	+	
+	+	0	0	0	0	0	0	0	
+	+	0	0	0	0	0	0	0	*b
0	0	+	+	+	+	+	+	+	*
0	0	+	+	+	+	+	+	+	
0	0	+	+	+	+	+	+	+	*
0	0	+	+	+	+	+	+	+	*
0	0	+	+	+	+	+	+	+	*
0	0	0	+	+	+	+	+	+	
0	0	0	0	0	0	0	0	0	
+	+	0	+	0	0	0	0	0	*d
0	0	+	+	+	+	+	+	+	*
+	+	0	0	0	0	0	0	0	*e
+	+	0	0	0	0	0	+	+	*f
+	+	0	+	0	0	0	0	0	
+	+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	+	*g
0	0	0	0	0	0	0	0	0	
+	+	0	+	+	+	+	+	+	
+	+	0	+	+	+	+	+	+	
0	0	0	0	+	+	+	+	+	
0	0	0	+	+	+	+	+	+	*
0	0	0	+	+	+	+	+	+	
0	0	0	0	+	+	+	+	+	
0	0	+	+	+	+	+	+	+	
+	+	0	0	0	0	0	0	0	
0	0	+	+	+	+	+	+	+	*
0	0	+	+	+	+	+	+	+	*
0	0	+	+	+	+	+	+	+	*

f Although the "monachine" condition is here coded as derived, the condition common to most phocines nevertheless approaches the terrestrial carnivoran form.

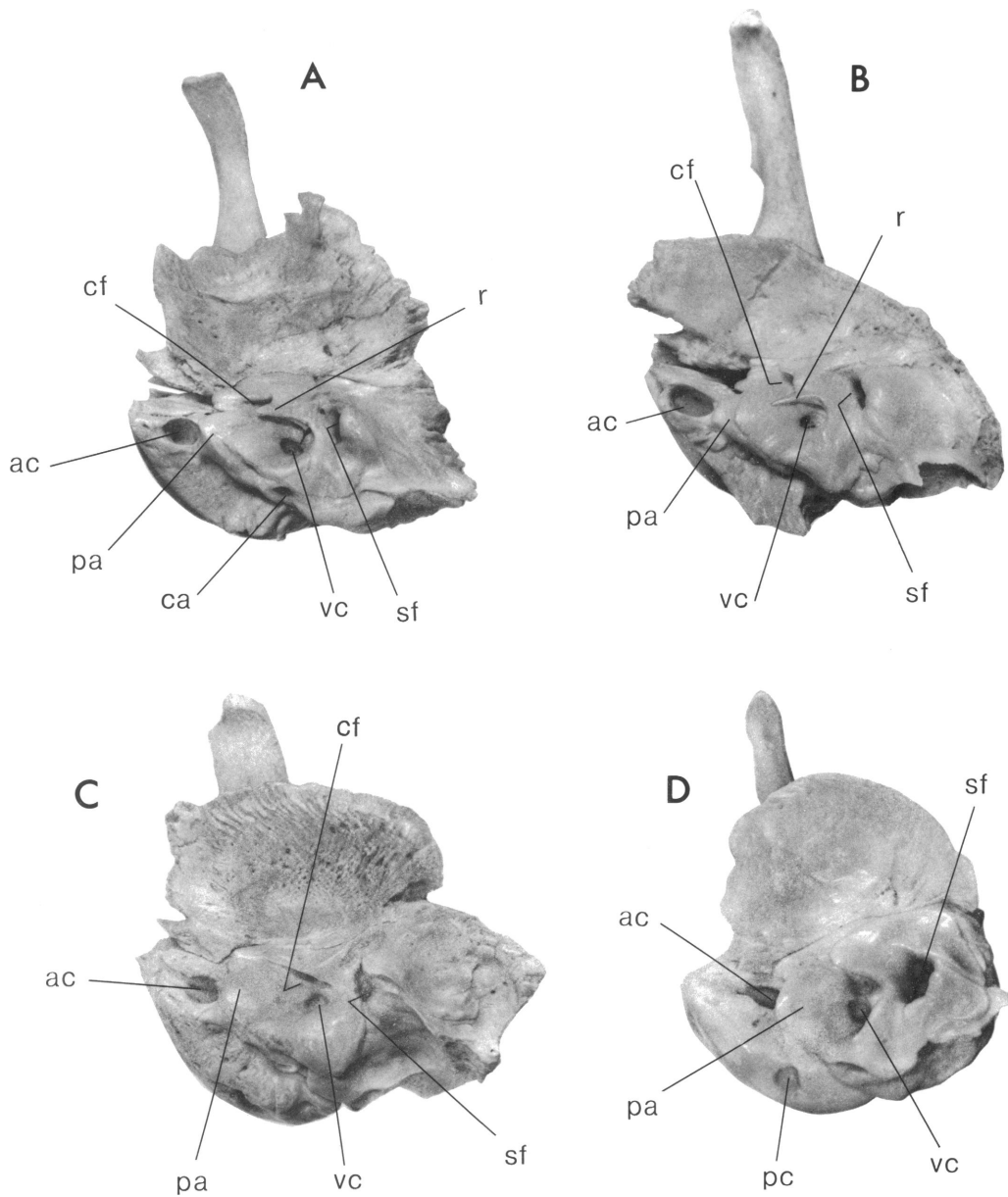*g* As indicated, apparent reversal is not restricted to the Phocinae.

Fig. 2. Dorsomedial views of selected phocid temporal regions (right side, anterior toward left): **A,** "*Monachus*" *schauinslandi*; **B,** "*Monachus*" *tropicalis,* AMNH 35354; **C,** *Lobodon carcinophagus,* AMNH 88535; **D,** *Phoca* sp., AMNH 2195 CA. Note relatively unexpanded dorsal petrosal region in A, the pointed petrosal apices and remnant of the auditory meatal roof in A and B. Abbreviations: **ac,** anterior opening of carotid canal; **ca,** opening of cochlear aqueduct; **cf,** facial (VII) nerve canal; **pa,** petrosal apex; **pc,** posterior carotid foramen; **r,** remnant of roof of internal auditory meatus; **sf,** subarcuate fossa; **vc,** fossa accommodating vestibulocochlear nerve. Scale approximately 0.85× for A, B, D, and 0.70× for C.

exception to this trend is "*Monachus*" wherein the apex remains both dorsoventrally thin and V-shaped in outline.

4. Remnant of roof of internal auditory meatus. All pinnipeds except phocids retain a true mammalian internal auditory meatus.

Typically in mammals this depression on the dorsal (cerebellar) surface of the petrosal is roofed by an anteriorly projecting petrosal lip and serves as the common entrance for the seventh and eighth cranial nerves. In phocids these nerves have separate entrances, a medial fossa accommodating passage of the vestibulocochlear nerve, and a laterally placed canal for the facial nerve (Gray, 1905). In all phocids, therefore, a true internal auditory meatus is lacking and, with the exception of the monk seals, the petrosal lip roofing the internal auditory meatus is completely absent. In all three species of "*Monachus*," vestiges of the former roof of the true meatus can clearly be seen as a thin bony spur projecting dorsally between the vestibulocochlear fossa and the canal for passage for the facial nerve (fig. 2) (see also Repenning and Ray, 1977: pls. 1, 3). Therefore, it stands to reason that the complete absence of the lip roofing the internal auditory meatus may represent a synapomorphy of all living and known fossil phocids exclusive of the three living species of "*Monachus*."

5. Pericardial plexus. The presence of a well-developed pericardial plexus has been reported as typical of phocids but has been found to be absent in "*M.*" *schauinslandi* (Harrison and Tomlinson, 1956; King and Harrison, 1961). Because this venous structure is not known to occur in otariids or *Odobenus* (King, 1977; Fay, 1981), its presence in most phocids is reasonably interpreted as derived. In this connection it is also of interest to note one of the summing remarks offered by King and Harrison (1961: 292) in their important anatomical consideration of "*M.*" *schauinslandi*: "It could be argued that the monk seal shows less vascular (venous) specialization than *Phoca, Mirounga, Leptonychotes, Lobodon, Halichoerus,* and *Hydrurga,* but more than *Zalophus*." The condition of the pericardial plexus in "*M.*" *monachus* and "*M.*" *tropicalis* is known but naturally would be of great interest (distressingly, for the latter such knowledge is now irrevocably lost).

Repenning and Ray (1977) also drew attention to two postcranial features which might imply the remote placement of "*Monachus*" relative to other phocids (numbers 6 and 7 below).

6. Lack of proximal fusion of tibia and fibula. The tibia and fibula fuse proximally in all phocids except "*M.*" *schauinslandi* (Repenning and Ray, 1977). An additional exception was noted by these authors, a then undescribed fossil form from Sacaco, Peru. This taxon remains undescribed but has since been referred to as a small "monachine" from the Pisco formation (de Muizon and Hendey, 1980: 118). The tibia and fibula are proximally fused in all living otariids but unfused in what has been proposed as a sister-taxon of this group, the Miocene form *Thalassoleon mexicanus* (Berta and Deméré, 1986). The condition in *Pithanotaria starri*, another early and cladistically "basal" otariid, may not be unambiguously determined from Kellogg's (1925) description or figures. Nevertheless, the unfused condition in *Thalassoleon mexicanus,* a taxon considered the nearest sister of a group including living otariids plus the Pliocene taxon *Hydrarctos* (Berta and Deméré, 1986) and ancestral to living otariids (Repenning and Tedford, 1977), is well established and likely represents the primitive condition for the group. These elements are only rarely fused in *Odobenus* (King, 1983), unfused in *Allodesmus* (Mitchell, 1966), and unfused in *Enaliarctos* (Berta and Deméré, 1986), a taxon considered the sister-group of all other pinnipeds (Wyss, 1987). Given this distribution in phocid outgroups, proximal fusion of the tibia and fibula is here regarded as an apomorphic resemblance of phocids exclusive of "*M.*" *schauinslandi*. As a result of the condition in *Thalassoleon,* the ancestral otariid condition is considered in this analysis to be unfused; consistent fusion of the tibia and fibula has apparently been independently achieved once within the group encompassing living otariids and once within phocids.

7. Separate foramen for obturator nerve in innominate (fig. 3). In contrast to those of other phocids, the innominate bone of "*M.*" *schauinslandi* presents a separate foramen for passage of the obturator nerve midway between the acetabulum and the obturator fenestra (King and Harrison, 1961; Ray, 1976; Repenning and Ray, 1977). A separate foramen is rarely present in "*M.*" *tropicalis* (e.g., those specimens noted by Repenning and Ray, 1977: 679–680 and AMNH 10421; see fig. 3

Fig. 3. Lateral view of left innominate bones of "*Monachus*" *tropicalis* AMNH 77741 (top) and *Phoca vitulina* AMNH 80195 (bottom), contrasting the general form of the bone in "monachines" plus *Erignathus* and in phocines exclusive of *Erignathus*. Note presence of nearly complete obturator nerve foramen in the Caribbean monk seal and hollowing of anterior ilial region in *Phoca*.

where this foramen is nearly complete). A separate foramen occurs variably among "otarioids" (Repenning and Ray, 1977) appearing most consistently among the arctocephaline otariids. A distinct foramen is present in *Thalassoleon mexicanus* (Repenning and Tedford, 1977) and it appears occasionally in *Odobenus* (bilaterally present in AMNH 73304, unilaterally present in AMNH 90784, 14071) and therefore its absence in phocids (exclusive of "*M.*" *schauinslandi,* where it occurs uniformly) may reasonably be interpreted as apomorphic.

8. Presence of hooklike teres major process (common to all phocids except *Mirounga* and "*Monachus*") (fig. 4). As King (1956) has reported, in "*Monachus*" the posterior and dorsal edges of the scapula meet to form nearly a right angle and thus, in contrast to the condition seen in most phocids, this junction (the caudal angle) is not hook-shaped. Howell (1929: 26) has commented on the essentially primitive form of the scapula in *Mirounga*

(not shown in fig. 3): "[it] is nearly of the form more often encountered in the Otariidae and the supraspinous space is several times as extreme as the infraspinous." The shape of the caudal angle is nearly identical to that seen in "*Monachus*," and agrees closely with the form seen in *Odobenus,* fossil odobenids, otariids, and *Allodesmus* (ibid.; Mitchell, 1966; Repenning and Tedford, 1977; King 1983). Thus it would seem safe to conjecture that the shape of the posterior scapular termination seen in these taxa represents the ancestral phocid configuration and that its more hooklike form in phocids exclusive of "*Monachus*" and *Mirounga* is apomorphic (this hooked form is especially pronounced among the Phocini; see fig. 4F).

Related to the scapular form, it may be mentioned that in "monachines" the supraspinous fossa is generally quite large, most extremely so in *Mirounga* (see also, King, 1969; Piérard, 1971, 1979). King (1956) has noted the square shape of the anterior scapular border in the lobodontines and its short-
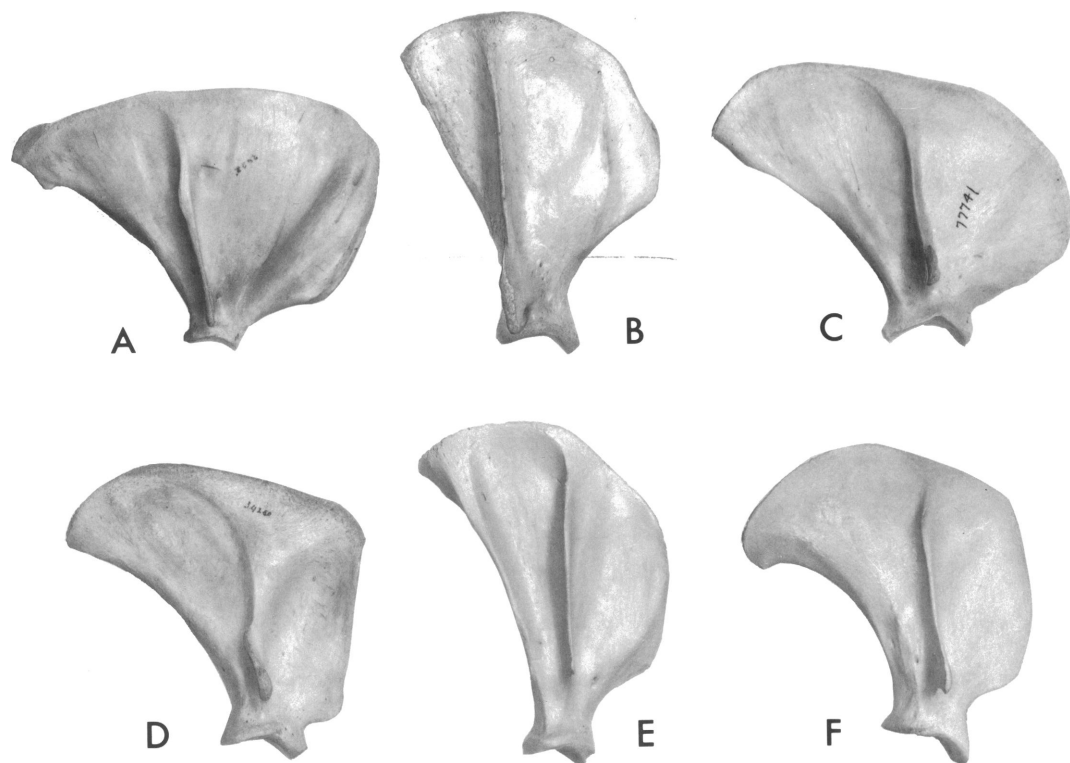
Fig. 4. Lateral views of representative pinniped scapulae: **A,** *Zalophus californicus* AMNH 5039 (reversed); **B,** *Odobenus rosmarus* AMNH 121; **C,** "*Monachus*" *tropicalis* AMNH 77741; **D,** *Leptonychotes weddelli* AMNH 34250; **E,** *Erignathus barbatus* AMNH 19347; **F,** *Phoca vitulina* AMNH 80195. Note particularly the strong hook-shaped teres major process in F, the relatively (for a phocid) large supraspinous fossa in C, and the poor development of the spine in D. Not to scale.

ness in "*Monachus.*" A large supraspinous fossa is a constant feature of otariids, *Odobenus, Allodesmus,* and *Enaliarctos* (Mitchell, 1966; Bisaillon and Piérard, 1981; see fig. 5 of Barnes et al., 1985). In relation to the size of the infraspinous fossa, the supraspinous fossa tends to become substantially reduced, particularly in *Erignathus* and among members of the Phocini. As a result, the scapula of these taxa could be interpreted as showing a closer resemblance to the form typical of terrestrial carnivorans than that of any other pinnipeds. Features of the scapula will be considered further in the discussion of character 13.

AFFINITIES OF THE "MONACHINAE"

From the foregoing tabulation there would appear to be considerable evidence support-

ing the placement of "*Monachus*" as the sister-group of other phocids; this stands in contrast to the currently accepted phylogeny of phocids which incorporates a clean "monachine"/phocine bifurcation. It follows, then, that the characters of the previous section should be considered against those that have been proposed in the past as uniting "*Monachus,*" *Mirounga,* and the lobodontines into a monophyletic "Monachinae." To my knowledge there are only two such data sets, those of King (1966) and de Muizon (1982a).

As has already been discussed, King's (1966) study of the relationships of hooded and elephant seals marked a turning point in the consideration on higher-level relationships among phocids. King listed 17 characters in her study (9–23 below) said to distinguish monachines from phocines: by implication, then, these would argue for

membership of "*Monachus*" in the "Mona-chinae." These features will be briefly re-viewed below—with particular consideration paid to polarity determination.

"MONACHINE" CHARACTERS AND THE "MONACHINE"/PHOCINE DIVISION

9. Mastoid visible in dorsal view of skull. This is almost certainly a derived character occurring by King's accounting in "*Mona-chus*" and in all phocines (and would con-sequently seem to argue against recognition of a "monachine" grouping). The mastoid is generally not visible in dorsal aspect in most mammals including terrestrial carnivorans, otariids, and *Odobenus*. Burns and Fay (1970: 381) reported that the mastoid was in view dorsally in a large percentage of specimens of other "monachines" examined in their study. They emphasized, however, that: "The value of the pars mastoidia as a diagnostic character is its form, which, in the Phocinae . . . is distinctive by reason of the lateral swelling that forms an oblique ridge at an angle of about 60° from the long axis of the mastoid bone as a whole. This ridge is absent or barely discernable in all of the Monachi-nae. . . ." Following this, the lateral swelling of the mastoid visible in dorsal view is re-garded in table 1 as a potential synapomor-phy of the phocines.

10. Petrosal visible in posterior lacerate foramen. Again by King's tabulation, this condition occurs in "*Monachus*" and in the phocines. Since the petrosal is also visible in *Odobenus* and its fossil allies (Repenning and Tedford, 1977), and in what are here consid-ered close phocid allies (desmatophocines + allodesmines) (Berta, personal commun.), this character is most likely primitive at a level higher than the Phocidae. It follows, then, that the petrosal covered completely by the auditory bulla (occurring in *Mirounga* and lobodotines) may plausibly be regarded as a derived attribute. Ray (1976), however, co-gently warned against such a simplistic char-acter demarcation, noting that although the lobodontines and *Mirounga* generally do have little or no petrosal exposure within the pos-terior lacerate foramen, such exposure does occur in some individuals of *Ommatophoca* and *Leptonychotes*. Perhaps of more critical

concern is, as Ray points out, the fact that generally the boundary between the petrosal and the mastoid in this region is highly un-clear if not completely obscured. As a result it becomes exceedingly difficult, if not im-possible, to identify an intrusion into the pos-terior lacerate as definitively "petrosal" or "mastoid" (compare for example figs. 6 and 7 of de Muizon, 1982a). A less arbitrary cri-terion by which the complex morphology of this region may be interpreted might be the posterior extent of the auditory bulla. As Hendey and Repenning (1972) and Ray (1976) have noted, in the lobodontines and *Mirounga* the bulla nearly covers the petrosal and almost contacts the exoccipital, thereby essentially excluding the petromastoid com-plex from contributing to the ventral margin of the posterior lacerate foramen. In table 2, therefore, a bulla essentially covering the pe-trosal and nearly contacting the exoccipital is regarded as a derived attribute; although this condition fails to provide support for a monophyletic "Monachinae," it does poten-tially diagnose at least a subgroup of its mem-bers.

11. Posterior lacerate foramen extending medially to tympanic bulla. Typically in car-nivorans (and mammals in general) the pos-terior lacerate foramen is a roughly circular aperture situated behind the posteromedial corner of the auditory bulla. In pinnipeds this foramen is greatly enlarged but usually main-tains its circular form. In phocines, exclusive of *Erignathus,* the posterior lacerate foramen becomes confluent with a broad petrobasilar fissure, forming a common opening that ex-tends between the basioccipital and the au-ditory complex as far anteriorly as the basi-occipital basisphenoid suture. Thus although this character does not bear directly on the question of "monachine" relations, it is di-agnostic of a phocine subgroup. This condi-tion represents a significant departure from the condition typical of terrestrial carnivo-rans and other pinnipeds wherein the petro-basilar fissure is obliterated during ontogeny and the bullar and basioccipital regions be-come closely appressed. On the basis of this distributional information the condition present in *Cystophora* and the Phocini is here judged to be derived.

12. Atlas, vertebrarterial (=transverse) foramen faces posteriorly. As King (1966) presented only a brief account of this character, I am interpreting it here to mean the direction from which the transverse foramen of the atlas is most clearly visible. King's distributional table shows a posteriorly facing foramen occurring in phocines, and a dorsally facing foramen present in *Mirounga* and the lobodontines. She concluded, however, that the position of the foramen in "*Monachus*" was not convincingly like that of other "monachines." My own observations are in agreement with King's conclusions. Regarding the condition seen in "*Monachus*," I would only add that in "*M.*" *tropicalis* the vertebrarterial foramen is exceptionally large for a phocid, and is therefore at least partially visible in dorsal view (it is, in fact, not dissimilar to the condition found in *Odobenus,* see below). In "*M.*" *monachus* this foramen is much more typical in size and is visible only in posterior view, so that in this respect it much more closely approximates the phocine rather than the *Mirounga* + lobodontine condition. In most terrestrial carnivorans, except canids, the transverse foramen is visible only in posterior view. The same appears to apply to otariids although there is a certain degree of variation. The transverse foramen in *Odobenus,* owing to its extremely large size, is visible in both dorsal and posterior views, therefore not falling neatly into either category; but in the Miocene odobenid *Imagotaria* this foramen is small and clearly faces posteriorly [personal observ. from cast of SBMNH (Santa Barbara Museum of Natural History) 342]. In *Allodesmus* the foramen is also posteriorly directed (see Kellogg, 1931: fig. 10; Mitchell, 1966: pl. 6). From this outgroup information it would appear, then, that of the two conditions occurring in phocids, the condition pertaining to *Mirounga* and lobodontines is more likely the derived one. Thus as concerns the affinities of "*Monachus*" the significance of this character would appear to be moot.

13. Scapular spine reduced, knoblike acromion (fig. 4). These characters have been cited (King, 1966) as common to "monachines." The latter feature may be dealt with easily; a knoblike acromion occurs in ursids

(Davis, 1949, 1964), *Allodesmus* (Mitchell, 1966), *Odobenus* (Bisaillon and Piérard, 1981), and otariids and is therefore likely primitive for pinnipeds. Regarding the condition of the spine, its degree of development is a trait much more difficult to characterize. To my mind three reasonably distinctive patterns of scapular spine development occur among phocids: its strong development among the phocines where it may extend completely to the vertebral scapular border, its extreme reduction to the point of serving as only a support of the acromion process in lobodontines, and a somewhat intermediate condition in "*Monachus*" and *Mirounga* wherein the spine reaches or nearly reaches the scapular margin but is generally less prominently defined than it is in phocines. The degree to which the spine is developed in otariids, *Odobenus,* and *Allodesmus* falls typically somewhere in between the conditions seen in phocines and the monk and elephant seals. Within this spectrum of pinniped scapular spine development, the form seen in the lobodontines (where it is almost entirely absent) is by far the most distinctive. The condition obtaining in "*Monachus*" and *Mirounga* is not sufficiently reduced so as to be closely compared to the unique lobodontine condition and therefore convincingly ally all "monachines." Extreme reduction of the scapular spine is here regarded as a derived condition restricted to the lobodontines; reduction of the acromion may therefore represent a potential synapomorphy of phocines.

14. Humerus, supracondylar (=entepicondylar) foramen present. An entepicondylar foramen is common to phocines; it is unfortunate, however, that interpretation of the polarity of this character among phocids hinges directly on the choice of outgroups. De Muizon (1982a) considered the trend toward absence of this foramen in "monachines" as the apomorphic phocid condition, basing this judgment on his phocid outgroups *Potamotherium* (an enigmatic late Oligocene through Miocene otterlike arctoid) and other mustelids. Given my acceptance of the close alliance of phocids to other pinnipeds and recalling the absence of an entepicondylar foramen in otariids, odobenids, and *Allodesmus,* the presence of this foramen is here

judged to be a potential synapomorphy of phocines; hence its absence in "monachines" is regarded as plesiomorphous. The foramen is also present in some fossil "monachines," e.g., some species of *Monotherium* and *Homiphoca capensis* (formerly *Prionodelphis*) (Hendey and Repenning, 1972; Ray, 1976; de Muizon, 1982a). Additional humeral features will be considered in the discussions of characters 37 and 38.

15. Carpus with distally projecting ledge on cuneiform. A distally projecting process (palmar process) of the cuneiform arcs over the palmar surface of the fifth metacarpal head in all phocines (King, 1966). This broad process is absent in otariids, *Odobenus* [although it is salient in the Miocene odobenid *Imagotaria* (Repenning and Tedford, 1977)], *Allodemus* (Mitchell, 1966), and "monachines" and thus its presence likely represents a synapomorphy for phocines.

16. Metacarpals I and II of approximately equal size (fig. 5). This relationship of metacarpal size occurs among all phocine seals. Although this pattern is undoubtedly primitive for carnivorans, within phocids it must be considered a secondarily derived reversal or, at least, a departure from the typical pinniped condition. This follows from the observation that relative to the second, the first metacarpals of otariids, *Odobenus,* and *Allodesmus* are all greatly elongated and conspicuously more robust. On this basis, therefore, King's ninth character "1st metacarpal noticeably longer and thicker than the others" would appear to be an apomorphic feature, uniting pinnipeds with the exception of phocines where a reversal toward a closer approximation of the primitive carnivoran condition has apparently occurred. The phocine condition may only be regarded as an incomplete reversal, however: although the two elements are of approximately equal size, metacarpal I remains slightly longer than metacarpal II, whereas of course the opposite applies in terrestrial carnivorans.

17. Intermediate phalanx of digit V of foreflipper very reduced (fig. 5). Marked reduction of this phalanx, to the point that it is but a small fraction of the length of its proximal neighbor (e.g., approximately 17%

in *Zalophus*), occurs in "*M.*" *tropicalis,* "*M.*" *schauinslandi, Mirounga,* and the lobodontines. Again, this character is almost certainly primitive for pinnipeds as a group, as it occurs in otariids and *Odobenus* as well. In terrestrial carnivorans the intermediate phalanx forms a significant element of digit V of the manus, being—proportional to digit length—comparable in size to its counterparts on digits II through IV.

Establishment of the polarity of this feature at the level of Phocidae poses some difficulty, however, because of uncertainty regarding the condition in *Allodesmus.* The carpus of the holotype of *A. kelloggi* LACM 4320 (=*A. kernensis* fide Barnes, 1972) depicted in plates 15 and 17 of Mitchell (1966) shows an unreduced intermediate phalanx on digit V, the intermediate element being approximately 70 percent of the length of the proximal (from pl. 15). If Mitchell's reconstruction is correct, and if *Allodesmus* is regarded as the sister-taxon of phocids, this raises a conundrum for establishing the ancestral phocid condition for this character. Until the phylogenetic arrangement of the monk seals is firmly established, the polarity of this feature, at the level of the Phocidae, cannot be unambiguously determined. At present it can equally forcefully be argued that (1) the reduced condition is primitive for phocids and that the resemblance between *Allodesmus,* "*M.*" *monachus,* and the phocines is derived (even if it might be due to convergence), or (2) that the condition seen in *Allodesmus* is primitive and the resemblance seen in "*M.*" *tropicalis,* "*M.*" *schauinslandi, Mirounga,* and the lobodontines is derived.

There is, however, reason to question the *Allodesmus* phalangeal arrangement suggested by Mitchell. As is indicated in his discussion, the position of some of the phalanges figured in the plates cited above are uncertain, their placement being based purely on size and curvature. Downs (1956) described the remarkably complete and largely articulated skeleton of *Atopotarus courseni* [=*Allodesmus courseni,* Barnes, 1972] and although he noted the generally poor quality of preservation, gave the lengths of the median and proximal phalanges of digit V as 8.0 and 38.0 mm, respectively (table 1, ibid.). Therefore at least one specimen of *Allodesmus,*
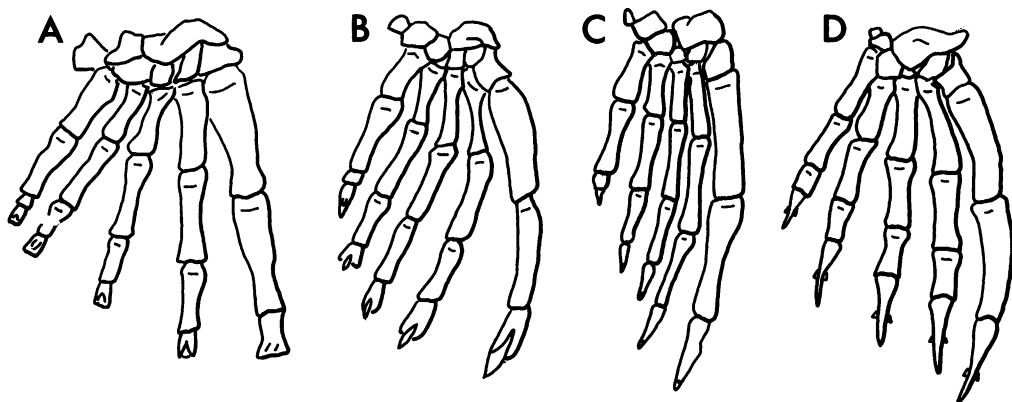
Fig. 5. Dorsal views of walrus and phocid foreflipper osteology: **A,** *Odobenus rosmarus*; **B,** *Monachus tropicalis*; **C,** *Ommatophoca rossi*; **D,** *Phoca vitulina*. The great reduction of intermediate phalanx V is displayed in all but D, the strong disparity in size between metacarpals I and II in A, B, and C (lessened in D), the extremely reduced claws in C, and their very strong development in D. Not to scale.

where the association of phalangeal elements appears to be reasonably certain, demonstrates a strongly reduced fifth medial element.

One additional line of evidence might call into question Mitchell's identification of this element in LACM 4320. Typically, in mammals, including all pinnipeds, there is a decrease in size of the intermediate phalanx from the third digit of the carpus to the fifth. As identified in LACM 4320 (in pl. 15 but not 17, ibid.) the intermediate phalanx of digit V is considerably longer than its counterpart on digit IV, which if true is clearly not what would normally be expected. In short, I presently find it more reasonable to conclude that *Allodesmus* maintained a phalangeal arrangement similar to that found in all pinnipeds exclusive of phocine phocids and the Mediterranean monk seal. From this interpretation it follows that the reduced condition of intermediate phalanx V in "*M.*" *tropicalis,* "*M.*" *schauinslandi, Mirounga,* and the lobodontines should be considered primitive for phocids. But the best that can be said at our current state of knowledge is that the nature of this character in *Allodesmus* remains unsettled. Such being the case, one is forced to examine the next most proximal available outgroups—*Odobenus* and otariids—and as a result, for the moment at least, favor the notion that a reduced intermediate fifth phalanx is primitive for phocids.

Whatever the primitive condition for *Allodesmus* eventually proves to be, and hence whatever polarity of this feature at the level of Phocidae might then be accepted, the condition seen in phocines and "*M.*" *monachus* represents a reversal of an ancestral pinniped condition to a primitive carnivoran (or mammalian) condition. This discussion suggests, therefore, a moderately complex series of transformations of this element during the evolution of phocoids (if *Allodesmus* indeed exhibits the derived condition) and the early diversification of phocids (originating apparently at least twice, once in "*M.*" *monachus* and once in phocines).

18. Metacarpal heads with well-developed palmar ridge (fig. 6). In phocines (as in most terrestrial mammals) a strong longitudinal ridge divides the distal and palmar surface of the metacarpal head, separating the points of articulation of the two sesamoid bones. Coincident with this arrangement, the proximal articulation surfaces of the proximal phalanges are marked by a deep notch on their palmar margins accommodating these metapodial ridges. These features—widespread among terrestrial carnivorans and undoubtedly primitive at a taxonomic level much higher than the Carnivora—do not occur in "monachines" where these ridges are scarcely visible and the proximal surfaces of the proximal phalanges are only weakly indented along

Fig. 6.   Palmar views of phocid phalanges contrasting the trochleated form of interphalangeal articulations in phocines with their more hingelike form in "monachines": **left,** *Phoca vitulina* AMNH 232416 (proximal phalanx II, manus); **right,** *Monachus tropicalis* AMNH 77741 (intermediate phalanx II, manus). Actual lengths: *Phoca,* 29 mm; *Monachus,* 47 mm.

their palmar borders. The metacarpophalangeal and interphalangeal articulations (and their counterparts in the pes) are strongly trochlear in phocines but flatter, broader, and markedly less trochlear in "monachines." Furthermore, the phalangeal bones themselves assume a much more dorsoventrally flattened form in "monachines," which stands in contrast to their primitive, cross-sectionally more rounded form in phocines. Any indication of flattening of these elements in the phocine carpus appears to occur only in the pollex (Howell, 1929) while these bones of the other digits maintain a more typically primitive form. In the phocine pes, flattening is relatively pronounced in the first and fifth proximal and the fifth intermediate phalanges, but otherwise their counterparts are of a more typical mammalian form. As a result of these skeletal modifications, the ball and socket metapodial phalangeal articulations and the strongly trochlear interphalangeal articulations typical of terrestrial carnivorans (and most mammals) are found in "monachines" to be weakly interlocking hinge joints. Importantly, the form of these articulations and the flattened shape of the pha-

langes in "monachines" correspond closely to those seen in otariids, odobenids, and *Allodesmus,* strongly suggesting that the arrangement common to "monachines" represents also the ancestral pinniped condition. Thus the "monachine" condition holds little valence in diagnosing a phocid subgroup; the phocine condition alone represents a derived character (for a pinniped), and so in yet another respect this group appears to have regressed to a more general carnivoran condition.

19. Ilium everted, excavated laterally (fig. 3). Lateral eversion of the ilium is common to all phocids. This lateral twisting of the anterior ilial arm is more markedly developed, however, and is accompanied by a deep lateral excavation in all living phocines save *Erignathus* (King, 1966). Lateral excavation and strong eversion are not present in otariids, *Odobenus, Allodesmus,* or "monachines" and the occurrence of these features may therefore be judged to represent progressive conditions in phocines.

20. Lower astragalus-calcaneum articulation very long. The lower articulation on the plantar astragalar surface (the sustentacular facet) is generally long among members of the Phocini and *Cystophora* (King, 1966). But because this feature seems to display a considerable degree of variation and is difficult to polarize, a few comments are pertinent here. Turning first to a consideration of outgroups, otariids are characterized by a long sustentacular facet which stretches the length of the astragalar neck, contacting proximally the medial tubercle which lies directly internal to the upper (ectal) facet. Thus in otariids the sustentacular and ectal facets nearly meet in this region of the tubercle at the proximointernal angle of the plantar astragalar surface much as they do in most terrestrial carnivorans. A markedly different situation is met in *Odobenus, Allodesmus,* and in phocids where the sustentacular and ectal facets are broadly divided by a deep furrow (interarticular sulcus) running across the length of the distal margin of the ectal facet and extending to the medial margin of the astragalar neck. As a result, the sustentacular facet nowhere closely approaches the medial tubercle or the sustentacular facet but remains broadly iso-

lated; in relation to the condition seen in otariids it would thus be considered "short." King's (1966) categorization of the phocid sustentacular facet as either long or short therefore refers to the subdivision of the arrangement wherein, relative to other carnivorans, the facet is already short. As King noted, the sustentacular facet is generally quite short and a wide gap separates it from the ectal facet in *Mirounga* and the lobodontines. This distribution is not without exceptions, however; for example, I have observed a fairly long condition in some specimens of *Lobodon.* In "*Monachus,*" King pointed out that the articular surface is longer than is usual among "monachines" and is in this respect— as was the case with the atlar character previously mentioned—not assuredly "southern." In fact in "*M.*" *tropicalis* this facet, in addition to being quite long, is extremely broad and is not unlike that seen in *Allodesmus* and *Odobenus.* On the other hand, in "*M.*" *monachus* the long, thin form of the facet is reminiscent of the condition seen in the Phocini. Furthermore, Hendey and Repenning (1972) found the sustentacular to be short in some specimens of *Cystophora* and long in some presumed fossil "monachines" (*Homiphoca* and *Monotherium*). On this basis they questioned the utility of this character at the subfamilial level. In view of the variability observed, a detailed survey of the form and variation of this character in large samples of all phocids is required, a task outside the scope of this paper. Whatever such a study may eventually show, it seems unlikely that this character, given its atypical "southern" manifestations in "*Monachus,*" will ever be used to argue for the monophyletic association of monk seals and other "monachines." Pending such an inquiry I have provisionally coded this character in table 1 as primitive throughout the family. That is not to suggest that all the forms represented in this diversity are necessarily primitive; rather, I do not have sufficient comparative material at hand to reach any broad conclusions. Nevertheless, on the narrower question at hand, my observations indicate that this character does not persuasively unify the "Monachinae."

21. Third metatarsal much shorter than

the others (fig. 7). Based on the observation that the third metatarsal is approximately as long as are its four counterparts in otariids and odobenids, and that it is only slightly shortened in *Allodesmus* (Mitchell, 1966), the development of a marked shortening of this element may plausibly be regarded as a "monachine" synapomorphy. King's (1966: 395) table shows that the length of the third metatarsal, as a percentage of the length of the first metatarsal, ranges between 63.1 and 72.7 in phocines and between 43.2 and 57.7 in "monachines." This table does not include measurements of the third metatarsal of *Cystophora,* however; AMNH 100135 demonstrates surprisingly that the third metatarsal is also relatively short (MT III is approximatley 55% the length of MT I) and that therefore *Cystophora* does not cluster with other phocines as would be expected but rather with "monachines." This raises the possibility that third metatarsal shortening may be viewed as primitive for phocids (judging from what might be construed as the relatively secure placement of "*Monachus*" as the phocid "sister-group"), so that the lengthening in phocines (exclusive of *Cystophora*) might represent another reversal associated with what appears to be the prevailing pattern of character regression associated with the development of the phocine pes. Obviously this assertion is contingent upon the prior acceptance of "*Monachus*" as the sister-group(s) of other phocids. But because this relationship is in fact being tested in the present analysis, this character has been coded in table 1 as a potential "monachine" synapomorphy that has been independently acquired in *Cystophora.*

Naturally, metatarsal shortening is manifest externally in the form of the distal margin of the hind flipper. Although the third digit is also clearly the shortest in members of the Phocini, it tends not to be as short as in "monachines" and *Cystophora.* Thus in "monachines" and *Cystophora* (where the toes are the most highly unequal) there is a strongly concave arrangement of the posterior flipper border. Conversely, the pedal digits in members of the Phocini, although they vary to a certain extent in length, are more uniform than in "monachines" and *Cystophora*: in *Erignathus* the digits of the pes
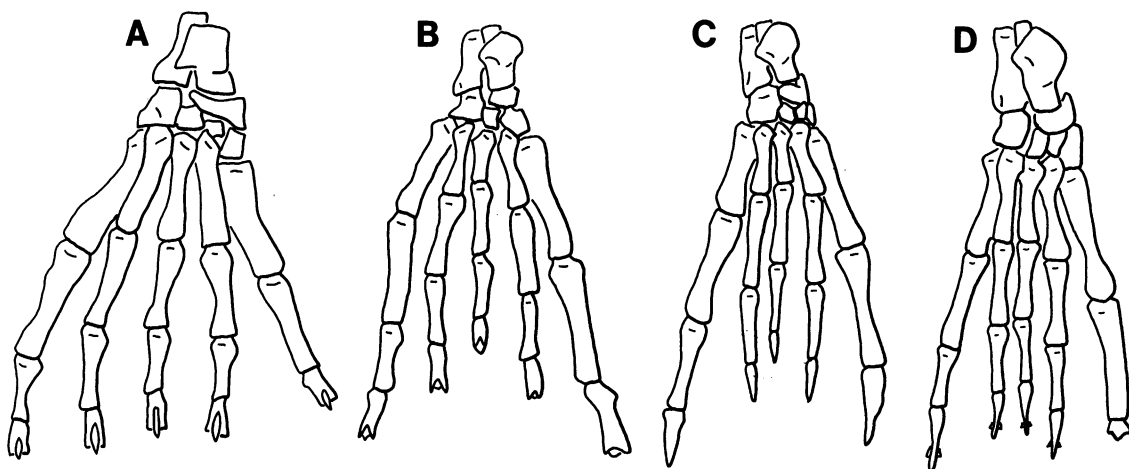
Fig. 7.   Dorsal views of walrus and phocid hind-flipper osteology: **A,** *Odobenus rosmarus*; **B,** *Monachus tropicalis*; **C,** *Ommatophoca rossi*; **D,** *Phoca vitulina.* Note shortening of digit III in B and C, particularly of the metatarsal. With respect to the relative length of digit III, phocines (represented by D) more closely resemble the walrus (A) and otariids (not shown) than they do "monachines." Note also the strong development of ungual processes (indicative of claw size) in D and the lack of same in C. Attention is called to the derived *Odobenus*-phocid similarites of fifth digit enlargement (in particular the fifth metatarsal) and the degree of third digit reduction, conditions not found or expressed to the same degree in otariids. Not to scale.

are of approximately equal length. Thus typically in phocines (excluding *Cystophora*) the posterior flipper margin is more nearly straight than in "monachines." An exception to this generality, as kindly pointed out to me by Fay (personal commun.), is *Histriophoca,* a member of the Phocini with a strongly concave posterior flipper margin. Nevertheless, metatarsal measurements taken from AMNH 180274 indicate that the length of MT III in *Histriophoca,* as a percentage of MT I (63%), falls within the phocine (sans *Cystophora*) range specified by King (1966) (metatarsal length data for this taxon was not presented in her study). In short, the shape of posterior flipper border in the Phocini and *Erignathus* more closely approaches that seen in other pinnipeds than that in other phocids.

22.   Large claws on foreflippers (fig. 5). The fore- and hind flippers of phocines are characterized by the presence of well-developed claws in contrast to "monachines" where claws tend to be more poorly produced. In otariids and *Odobenus* the claws of the manus are reduced to small nodules as they were (if they were present at all) in *Allodesmus* (Mitchell, 1966: 15). Thus the presence of

large claws on the manus may safely be assumed to represent an advanced condition for phocines (if, of course, pinniped monophyly is admitted). Likewise, enlarged claws on the pes must be viewed as derived for phocines (at least for digits I and V, see below) as the outer claws are greatly reduced in the outgroups mentioned. Both of these phocine apomorphies, then, would appear to be reversals from the primitive pinniped condition.

23.   Reduced claws on hind flippers (fig. 7). Hind flipper claw reduction is common to "monachines." Since claws are present on the central three digits of both otariids and *Odobenus,* on first consideration this character would appear to represent a potential "monachine" synapomorphy. It should be kept in mind, however, that relative to otariids these claws are markedly reduced in *Odobenus.* Judging, therefore, from the apparent prevalence reversal among other characters during the evolution of the phocine flippers, it might reasonably be presumed that phocids were characterized primitively by reduced claws on the hind flippers and that the pho-

cine condition also represents such a reversion. Nevertheless, as with third metatarsal shortening, this hypothetical transformation is necessarily a secondary hypothesis and reduced claws on the hind flippers has been regarded as a potential "monachine" synapomorphy in tables 1 and 2.

De Muizon (1982a) proposed three characters as diagnosing the monophyly of the "Monachinae." One of these, the loss of the entepicondylar foramen, has been discussed above in the coverage of character 14; the remaining two are reviewed as characters 24 and 25 below.

24. Premaxilla-maxilla suture located inside nasal aperture. As Hendey and Repenning (1972) first noted, in lateral view the "monachine" premaxilla is not visible along its entire length as it is in most mammals; rather, it dips along its midsection into the nasal aperture and is therefore obscured by the maxilla. Exceptions to this characterization are "*M.*" *monachus* and *Homiphoca* (ibid., see pl. 3; de Muizon, 1982a) where the primitive condition occurs. In addition, the "monachine" condition of the premaxilla occurs in the phocines *Histriophoca* and *Pagophilus* (de Muizon, 1982a). Despite this variation, among living phocids such an arrangement would appear to be apomorphic for "monachines." It is worth pointing out, however, that *Allodesmus* shows a closely similar condition (Barnes, 1972: 12): "The premaxillary-maxillary suture is only slightly lateral to the margin of the nares, so that unlike the condition in most of the Otariinae [=Otariidae in the sense employed here], very little of the ascending portion of the premaxilla is visible in lateral view . . ." (see Barnes, 1972: fig. 5 and Barnes et al., 1985: fig. 7). Barnes (1987, fig. 1) illustrated a rostrum of *Desmatophoca* which also clearly depicts the "monachine" premaxillary condition described above. It becomes possible to argue, therefore, that the "monachine" configuration of the premaxilla may well be primitive for phocids. Nevertheless, in the interest of conservatism and of giving the proposition of "monachine" monophyly every possible benefit, this character has been scored in tables 1 and 2 as a potential synapomorphy of this assemblage.

25. Tendency toward reduction of the number of upper incisors. Living and fossil "monachines" and the phocine *Cystophora* have only four upper incisors instead of the typical pinniped number of six. Again, judged against living pinnipeds this feature within phocids would appear to represent a potential "monachine" synapomorphy. Taking into account fossils, *Allodesmus packardi* was originally described as having four upper incisors but is now described as having had six (Barnes, 1979: 9). To judge from the cross-sectional area of the incisor alveoli, in *A. kelloggi* the tooth occupying the first position was appreciably reduced, however (see Mitchell, 1966: pl. 2). The only fossil known to stand in exception to the "monachine" pattern is *Monotherium*? *gaudini* from the Italian middle Miocene which retains a full complement of six upper incisors (de Muizon, 1982a). It is relevant to point out, though, that living forms display a considerably degree of variability in this feature. Judging from King's (1956) data, supernumerary incisors are not uncommon among the three Recent species of "*Monachus.*" Burns and Fay (1970) found that four upper incisors occurred in approximately 2 percent of their sample of the phocines *Erignathus*, *Histriophoca*, and *Pagophilus* (in fact, in *Erignathus* the incisor formula 3-3/2-2 occurred in only 60% of their sample) and, as mentioned, *Cystophora* (which is almost assuredly allied to phocines) has only four upper incisors. The dentition of *Odobenus* is highly aberrant and perhaps of little relevance here. Nonetheless it is worth noting that Fay (1982: 84) found the first upper incisor to be present in none of the adults of his sample of 136, and the second upper incisor to be present in less than 50 percent. These observations together with the apparent reduction of the first upper incisor in *Allodesmus* (Barnes et al., 1985: fig. 7) may indicate a trend toward incisor reduction early in phocoid evolution. It is also apparent from these observations that incisor number displays a fair degree of lability among phocids. Nevertheless, four upper incisors is scored as a derived character and is thus considered supportive of, but not unique to, a monophyletic "monachine" grouping.

To the list of characters reviewed above may be added a consideration of several ad-

ditional features well known in the pinniped literature.

26. First pelage color. Monk and elephant seals are born with black pelage (King, 1966; Ling and Button, 1975). This is peculiar among phocids where white natal coats (members of the Phocini) or various shades of gray (Lobodontines, *Erignathus, Cystophora,* some *Phoca;* King, 1983; Fay, personal commun.) are the norm. First coats in otariids are dark brown to black (King, 1983; Ling and Button, 1975) and so the condition seen in "*Monachus*" and *Mirounga* is likely primitive although this assessment is tempered somewhat by the presence of white lanugo in the walrus (Fay, 1982). Granting this qualification, phocids exclusive of these two genera ("*Monachus*" and *Mirounga*) may be considered progressive in having more lightly colored first pelage.

27. Loss of secondary hairs. Although a good deal of information is available, in phylogenetic considerations of the Pinnipedia, aspects of the morphology and distribution of hair have been used only to a limited extent. Nonetheless, some variation of hair pattern has proven to be of systematic importance (e.g., Ling, 1978) and these data would seem to invite further consideration. Generally in carnivorans, hairs are arranged in groups (units) consisting of a central coarse primary hair surrounded by a number of finer secondary hairs. These individual hair units assume what appear to be rather conservative patterns of spacing (de Meijere, 1894). Noteworthy of phocids is the absence of a pith or medulla of the primary hairs, an apparently derived condition known to occur elsewhere in the Carnivora only in *Odobenus* (Scheffer, 1964). Of further interest is the absence of secondary hairs in some pinnipeds. Secondary hairs occur in all otariids and the majority of phocids but are virtually absent (occurring in about 1 of every 50 units) in "*Monachus*" *schauinslandi, Mirounga angustirostris* (ibid.), and (in about 1 out of 10 units) *Odobenus* (Fay, 1982). The occurrence or nonoccurrence of secondary hairs in the other species of "*Monachus*" has not previously been reported. On the several skins housed in the AMNH of "*M.*" *monachus* and "*M.*" *tropicalis* I have examined, however, secondary

hairs appear to be almost totally absent. Ling and Bryden (1981) have reported the absence of secondary hairs in *Mirounga leonina.*

Regarding the systematic interpretation of this character, then, it could be suggested that the presence of secondary hairs is primitive for phocids and that loss occurs at least three times within pinniped phylogeny, once in *Odobenus,* once in "*Monachus*" (assuming its monophyly), and once in *Mirounga.* Depending on the phylogenetic arrangement of these taxa specified by other characters, it may equally be argued (with the potential savings of a minimum of one evolutionary step) that the lack of secondary hairs is primitive for the group *Odobenus* + phocids and that these hairs have been regained by the lobodontines and phocines. Obviously neither interpretation is entirely compelling but in the context of the phylogeny advocated here (fig. 9) the hypothesis of single loss and single regain is more economical. Acceptance of pinniped diphyly would noticeably change the interpretation offered above. With mustelids placed as the phocid sister-group, the sparse secondary hair in "*Monachus*" and *Mirounga* would be viewed as apomorphic (and therefore supportive of the pairing of these taxa, a relationship that to my knowledge is without precedent and likely, in my estimation, to remain so) with the condition in *Odobenus* considered an independent loss.

28. Cornified layer and hair form sheets during molting. Associated perhaps with this loss of secondary hairs is an unusual pattern of molting that occurs in *Mirounga,* and the single species of "*Monachus*" so far examined, "*M.*" *schauinslandi.* In both the northern and southern elephant seals and the Hawaiian monk seal the primary hairs become fused to the stratum corneum so that when the pelage is shed it forms large continuous patches held together by this thin layer of cornified epidermal tissue (Kenyon and Rice, 1959; Ling and Thomas, 1967). This pattern has not been reported elsewhere among pinnipeds and is therefore provisionally coded as derived for these two taxa in tables 1 and 2. From the topology of the phylogeny derived from other characters considered in this analysis (see systematic conclusions section), the cohesion of hair and the

cornified layer during molting could be interpreted as a primitive phocid feature which is lost at the node Lobodontini plus Phocinae. Clearly, however, the validity of this interpretation is dependent upon prior acceptance of a cladogram similar in geometry to the one presented in figure 9.

29. Beaded mystacial whiskers. Beaded mystacial whiskers occur in all phocids except "*Monachus*" and *Erignathus* (King, 1956, 1983). Inasmuch as these whiskers are smooth in otariids, *Odobenus*, and other carnivorans it stands to reason that the peculiar beaded condition typical of the majority of phocids may reasonably be regarded as apomorphic. In this way, beaded mystacial whiskers may serve to diagnose a group of phocids exclusive of "*Monachus*" with an apparent retention of, or reversion to, the primitive smooth conditions occurring in *Erignathus*.

30. Mammary teats. Otariids and *Odobenus* have two pairs of nipples situated near the umbilicus, a condition taken here to be primitive for pinnipeds. By contrast, all phocids except (in a distribution mimicking that of the previous character) "*Monachus*" and *Erignathus* retain only the two nipples thought to correspond to the posterior pair of other pinnipeds, an evidently advanced condition. "*Monachus*" and *Erignathus* maintain the primitive full pinniped complement of four nipples (King, 1983; see also references in Kenyon, 1981).

31. Chromosomes. Pinnipeds (as do other groups of marine mammals) display, in relation to comparably diverse terrestrial groups, a remarkable karyotypic uniformity. Otariids are characterized by karyotypes of $2N = 36$ and the walrus $2N = 32$ (Fay et al., 1967; Arnason, 1974, 1977). It is well established that members of the Phocini (*Phoca, Pusa, Halichoerus, Histriophoca,* and *Pagophilus*) have karyotypes of $2N = 32$ whereas all other phocids have karyotypes of $2N = 34$ (ibid.). Further, it has been determined through G- and C-band studies, that the m1 chromosome, characteristic of the 32 chromosome karyotype of the Phocini, has arisen from a fusion between the short arm of the t chromosome and the small satellite of the sat chromosome of the 34 chromosome com-

plement (Arnason, 1974, 1977). There exists direct evidence, then, that the 32 chromosome karyotype of the Phocini is apomorphic and that the 34 chromosome condition of "monachines," *Erignathus,* and *Cystophora* is (for phocids) plesiomorphic.

It should also be noted that *Erignathus* displays several karyotypic features not found elsewhere in the Phocidae (ibid.). Arnason concluded that the *Erignathus* karyotype probably represents a separate line of phocid chromosomal evolution which effectively bars it from being ancestral to the 32 chromosome type. This statement, however, is equivalent to the observation that the *Erignathus* karyotype is autapomorphic. This in no way influences the acceptance of the $2N = 32$ karyotype as an apomorphy diagnostic of the Phocini; while this information fails to support a phocine placement of *Erignathus,* it does not contradict it either.

In their consideration of the phylogenetic placement of *Histriophoca,* Burns and Fay (1970) provided a thorough distributional analysis of cranial characters previously used for the diagnosis of subfamilial and tribal phocid groupings. This consideration included an appraisal of characters discussed by Chapski (1955) and Scheffer (1958) as pertaining to the tribe Phocini; two of these are briefly reviewed below under characters 32 and 33.

32. Compression of upper incisor roots. The roots of the upper incisors, particularly of the first two, are generally extremely transversely compressed among carnivorans (including otariids). Judging from the condition seen in "monachines" and *Erignathus,* phocids would appear to have been characterized primitively by roots that are much rounder in cross section. Burns and Fay (1970) reported the strong lateral compression of the upper incisors of *Halichoerus, Pusa, Phoca, Pagophilus, Cystophora,* and (in 94% of their sample) *Histriophoca.* Thus in this respect most phocines display the more generalized carnivoran condition that is likely not primitive for phocids.

33. "Process from posteromedial edge of the bulla absent" (Burns and Fay, 1970). The hallmark feature of arctoid carnivorans is a

canal formed of caudal entotympanic which transmits the medial branch of the internal cartoid artery within the medial auditory bullar wall. In ventral aspect the posterior opening of this canal is generally clearly visible, and in otariids, *Odobenus,* and most phocids from the dorsal and/or medial margin of the aperture a bony shelf may be seen to project toward the posterior lacerate foramen. Due primarily to prominent bullar inflation, in phocines the posterior opening is not visible in ventral view and, as Burns and Fay have noted, the aperture is smooth and the process near its border absent. This would appear to represent an advanced condition common to the Phocini and *Cystophora,* occurring only rarely in *Erignathus* (Burns and Fay, 1970).

34. "Least interorbital width of adults in the anterior half of the interorbital septum." Burns and Fay (1970: 383) have noted this character as being common to members of the Phocini and *Cystophora,* occurring occasionally in *Erignathus* (in 17% of the their sample). Primitively the narrowest point in the pinniped interorbital region occurs in its posteriormost section (e.g., in "monachines," otariids, and *Odobenus*).

35. Basioccipital-basisphenoid area flat to convex. Burns and Fay (1970) also have commented on the flat to convex ventral surface of the basioccipital-basisphenoid region in all phocines. In marked contrast, this region is strongly concave in "monachines," otariids, and *Odobenus,* particularly in the areas of insertion of the rectus capitus musculature, a condition taken here to be primitive.

36. Mastoid lip. Several authors have commented on the unique presence among the Lobodontini of a mastoid lip overlapping the posterior bullar wall (Repenning and Ray, 1977; de Muizon and Hendey, 1980; de Muizon, 1982a). There is little doubt that this lip (covering ventrally the cochlear foramen in these forms) represents a derived condition (typically in phocids the cochlear foramen remains exposed ventrally). As it stands, then, this character does not play a role in a "monachine"-phocine demarcation, although it is of interest for potentially diagnosing a subgroup of the former.

The humerus has already been considered

in relation to the presence or absence of the entepicondylar foramen (character 14). Several additional "monachine"/phocine distinctions discussed below reside on the humerus.

37. King (1966) noted the tendency for greater development of the supinator ridge in phocines than in "monachines." My own observations are in agreement with her suggested distinction; the supinator "ridge" in southern phocids is invariably only faintly developed, occurring as a low rounded eminence. This condition stands in clear contrast to the long, sharply defined ridge found in phocines (fig. 8). This ridge is generally strongly developed in terrestrial carnivorans but is absent in otariids, *Odobenus,* fossil odobenids, and *Allodesmus* (Repenning and Tedford, 1977; Mitchell, 1966, from pls. 15 and 16; and personal observ.). Accordingly the lack of this ridge may be securely considered primitive for pinnipeds. Thus the presence of a supinator crest in a phocid represents an advanced condition, even though the character is undoubtedly primitive at a much more general level, perhaps Carnivora. It follows that the appearance of a strong supinator crest in phocines is likely just one more example of a reversion in this group to a more primitive terrestrial carnivoran condition.

38. Hendey and Repenning (1972) have discussed some additional points further differentiating the "monachine" and phocine humerus. In general, pinniped humeri show a distinct resemblance in the strong development of the deltoid/pectoral crest (Howell, 1929) but in the details of construction there exist notable "monachine" and phocine distinctions (Hendey and Repenning, 1972). According to these authors, generally in "monachines" insertion of the pectoralis is extended distally down the shaft terminating just proximal to the distal articulation (although this pattern of insertion does not apply to "*M.*" *schauinslandi*; Fay, personal commun.). The deltoid crest also is expanded two-thirds to three-quarters the length of the shaft, at which point the crest and shaft merge smoothly (fig. 8). In this respect the monachine humerus resembles that of otariids, odobenids, and *Allodesmus,* where a similar elongation of pec-

toral insertion and the deltoid crest occurs (Hendey and Repenning, 1972; Repenning and Tedford, 1977; Mitchell, 1966). Strengthening of the pectoralis insertion in phocines is accomplished in quite a different manner. Insertion does not extend nearly as far distally; the deltoid crest stretches less than one-half the length of the shaft, where it ends abruptly, forming a near overhang of the shaft in lateral view. From the distributional information indicated above, I conclude that the short deltoid crest and proximally restricted pectoralis insertion very likely represent derived phocine attributes whereas the condition characterizing "monachines" is essentially primitive.

The Pliocene phocid *Homiphoca* is of considerable interest with respect to the features of the humerus just mentioned. By all published accounts *Homiphoca* is allied, at least in a general sense, to the Antarctic lobodontines and has therefore traditionally been confidently placed within the "Monachinae." However, the humerus of this taxon bears a striking resemblance to that of phocines, a fact called to attention explicitly by its original describers (Hendey and Repenning, 1972). Both an entepicondylar foramen and strongly developed supinator ridge are present, as is a long deltoid pectoral crest, a character otherwise typical of "monachines" and other pinnipeds. Hendey and Repenning (ibid.) did not view the phocine resemblances of the humerus as necessarily contradicting the "monachine" allocation of *Homiphoca*, concluding instead that King's (1966) criteria for distinguishing phocine and "monachine" humeri (the presence of an entepicondylar foramen and a well-developed supinator ridge) appear to apply to modern species only. These authors judged the pattern of insertion of the pectoral muscle to be a character of greater validity in classifying phocids than the two criteria offered by King.

Leaving aside the question of justification for the latter decision, a more general issue concerning the treatment of fossil data may be raised. While it may be tempting to argue from an operational standpoint that certain characters appear to be valid only among living forms, the fact is that character conflicts remain character conflicts whether they occur in fossils or not. Suggestions that a particular character does not apply to a fossil taxon amounts to little more than an argument for convergence (or reversal), or for the multiple independent appearance of the alternate state of that character among that fossil's living allies. In other words, suggestions of this kind do not more than underscore the discordant distribution of the character in question. Such reasoning, as far as it goes, is of course perfectly plausible provided that it is substantiated by the distribution of other characters.

Returning to the character at issue here, de Muizon and Hendey (1980) confronted the apparent problem of the phocine resemblances of the *Homiphoca* humerus by suggesting that they are primitive. Indeed an entepicondylar foramen and strongly developed supinator ridge do occur in *Potamotherium* and for that matter most other arctoids, and from a diphyletic perspective of pinniped origins, de Muizon and Hendey's (1980: 116) conclusion that these two characters are "evidently primitive features" is, in a restricted sense, fully justified. A point seemingly overlooked in this interpretation, however, is that the establishment of a character as primitive at one level—for example, as de Muizon and Hendey would argue, the primitive presence of an entepicondylar foramen at the level of Phocidae—does not imply that it is necessarily primitive at some less inclusive level, e.g., the Lobodontini. Just as the absence of limbs is primitive for the group Vertebrata, the lack of limbs in a group of tetrapods such as snakes is derived. Similarly if one wishes to argue that the presence of an entepicondylar foramen is primitive for phocids, the appearance of these features in a lobodontine—the taxonomic placement of *Homiphoca* favored by de Muizon and Hendey (1980) and de Muizon (1982a)—which are characterized by the lack of an entepicondylar foramen, cannot be dismissed on the ground that it is primitive.

Considering this problem from the perspective of a single pinniped origin favored here, presence of an entepicondylar foramen and strong supinator ridge in *Homiphoca* represent advanced features (at a level inside the Phocidae). Similarly, acceptance of pinniped monophyly calls into question the presence of a long deltoid/pectoral crest as representing a derived condition among phocids. In
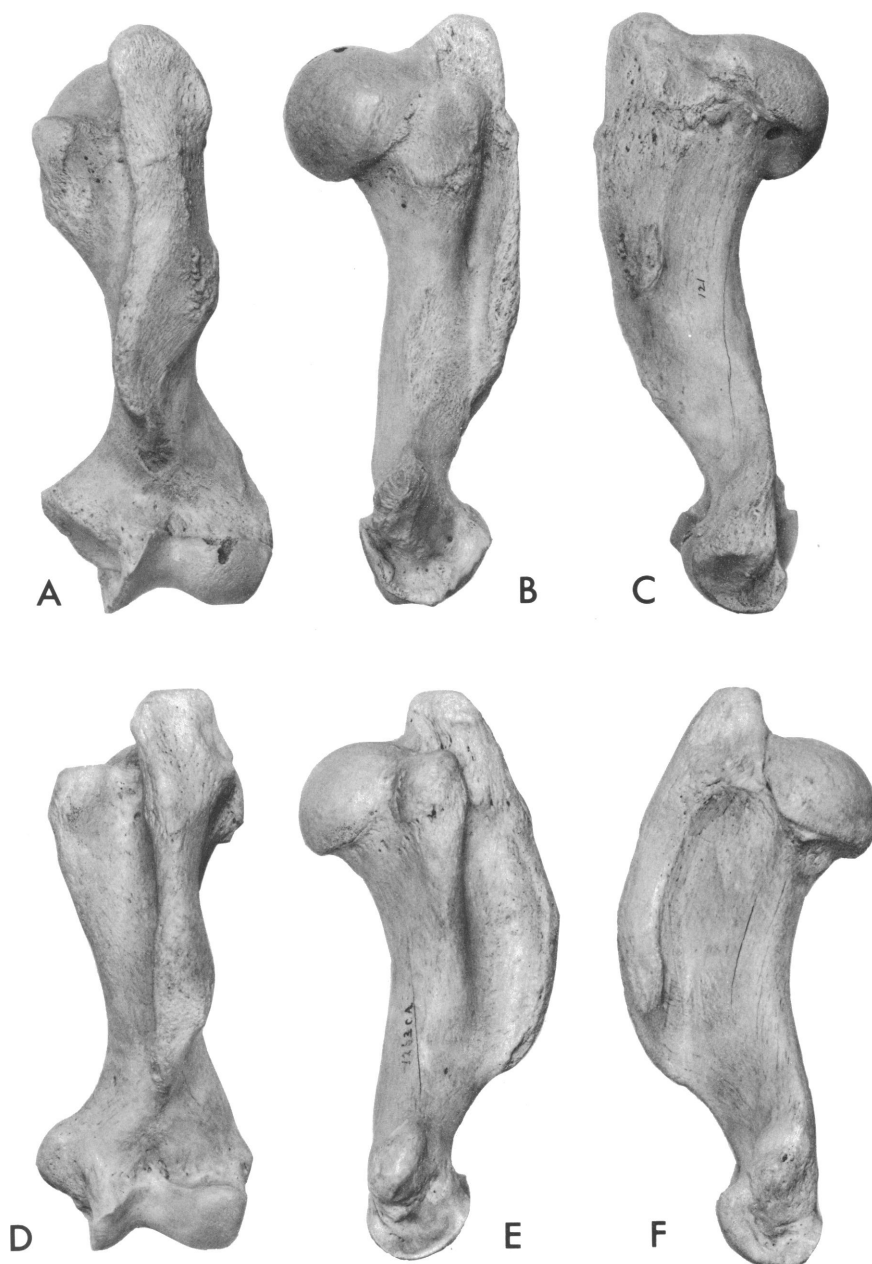
Fig. 8. Representative "monachine," phocine, walrus, and otariid humeri. Anterior (A, D, G. J), medial (B, E, H, K), and lateral (C, F, I, L) views of: *Odobenus rosmarus* AMNH 121 (A, B, C); *Zalophus californicus* AMNH 1263 CA (D, E, F); "*Monachus*" *tropicalis* AMNH 10421 (G, H, I); *Erignathus barbatus* AMNH 19347 (J, K, L). Attention is called to the long deltoid/pectoral crest in all except *Erignathus*. Note also the presence of an entepicondylar foramen and strongly pronounced supinator ridge in *Erignathus*. Abbreviations: **dpc,** deltoid/pectoral crest; **sr,** supinator ridge; **ef,** entepicondylar foramen. Not to scale.

view of its widespread appearance in pinnipeds, this last mentioned feature speaks neither to the monophyly of the "Monachinae" nor to the placement of *Homiphoca* within it.

From the foregoing it should be apparent

Fig. 8. *Continued.*

that rather than arguing for monachine affinity (by virtue of one primitive character), the humerus of *Homiphoca* shows advanced features in which it resembles phocines. That is not to say, however, that I necessarily espouse a phocine placement of *Homiphoca*; there is, in fact, evidence to the contrary (Hendey and Repenning, 1972; Repenning and Ray, 1977; de Muizon and Hendey, 1980). I have raised the subject simply to point out that if monachines are monophyletic, and if on other evidence *Homiphoca* can be referred to this group, its humerus offers a curious instance of character conflict. In the context of either pinniped monophyly, or the inclusion of *Homiphoca* within a

monophyletic "Monachinae" or Lobodon-
tini, the phocine resemblances of the *Hom-
iphoca* humerus may not simply be regarded
as primitive but must be considered synap-
omorphic or homoplastic.

39. Tibia. King (1966) noted that the post-
tibial (=intercondyloid) fossa is more pro-
nounced among the Phocinae than in the
"Monachinae." Howell (1929: 39) indicated
that the post-tibial fossa is much more deeply
developed in *Pusa* than it is in *Zalophus.*
Similarly the post-tibial fossa achieves only
shallow development in other otariids, *Odo-
benus,* and most terrestrial carnivorans (per-
sonal observ.), and Mitchell (1966) has re-
ported a similar shallow condition in
Allodesmus. From this it may be concluded
that the phocine condition is most probably
derived. *Homiphoca,* as Hendey and Repen-
ning (1972) have pointed out, is remarkable
for its "development of pronounced fossae
on the posterior and antero-lateral surfaces"
of this element (see also de Muizon and Hen-
dey, 1980). Thus, as with the humerus, the
tibia of *Homiphoca* displays an unusual oth-
erwise "phocine" attribute.

Two additional characters exhibit what ap-
pear to be trends toward primitive character
reversion in phocines, particularly among the
Phocini. These are not sufficiently constant
to be treated across all taxa considered and
therefore do not consistently differentiate all
phocines; nevertheless a general pattern of
reversal is revealed by their distribution.

As suggested by Burns and Fay (1970) the
major palatine foramen is normally situated
anterior to the maxillary-palatine suture
among "monachines" while among phocines
it typically rests on or behind this suture. This
foramen is situated far anterior of the suture
in otariids, and less extremely so in *Odo-
benus,* but it occurs on the suture in ursids,
canids, felids, and most mustelids. This dis-
tribution would argue, therefore, that the
condition typical of phocines represents a re-
versal of the primitive pinniped condition.

Phocines differ from other phocids, as well
as from other pinnipeds, in their marked ten-
dency to develop a distinct trochanteric fossa
of the femur (King, 1966). This fossa is ex-
tremely pronounced among members of the
Phocinae and occurs, but apparently not as

strongly, in the "monachines" *Lobodon* and
Homiphoca (de Muizon and Hendey, 1980).
This fossa, which is otherwise widespread
among the Carnivora, is not known to occur
elsewhere in the Pinnipedia.

SYSTEMATIC CONCLUSIONS AND IMPLIED PATTERNS OF CHARACTER EVOLUTION

What phylogenetic implications may be
gleaned from the evidence here considered?
Using table 2, questions of monophyly for a
number of groups may be addressed: First,
is *"Monachus"* monophyletic? Second, are
the "Monachinae" monophyletic? Third, are
the Phocinae monophyletic? And finally, if
some or all of these points of inquiry can be
answered with any degree of confidence, any
recurring patterns of character evolution
within the Phocidae may be considered.

The monophyly of a taxonomic group is a
scientific hypothesis, a notion open to testing.
Shared derived characters are potentially in-
dicative of relationships and achieve synap-
omorphic status (and therefore phylogenetic
significance) only when they are found to be
congruent with other derived characters in-
dicating similar relationships. The phyloge-
netic status of a character is never known
with certainty but is itself an hypothesis sup-
ported largely on the basis of its relationship
to other features. As character information is
increased or improved, concepts of relation-
ship are altered, resulting in turn in a mod-
ification of previously accepted notions of
character support for given phylogenetic
groupings. Thus phylogenetic concepts re-
main in a constant state of flux, a context in
which the present analysis should be viewed.

The data of table 2 were analyzed using
Swofford's (1985) PAUP (Phylogenetic Anal-
ysis Using Parsimony) software package. Ini-
tial runs were conducted using the mulpars
global branch swapping procedures; these
yielded over 100 maximally parsimonious
trees, with most variants simply representing
rotations within polytomous branchpoints.
On subsequent runs, groups of taxa with in-
variant character distributions (i.e., members
of the Phocini and Lobodontini) were col-
lapsed to single terminal taxa and the result-
ing data matrix then run on the exhaustive

search option branch and bound. Three equally most parsimonious trees were obtained and these were reduced to the consensus branching arrangement depicted in figure 9 (where the "redundant" taxa have been reinserted) using the CONTREE (strict) subroutine of PAUP.

Returning to the specific questions posed above it may be said, respecting "*Monachus*" monophyly, that the characters reviewed here tend not to support the naturalness of this grouping as "*M.*" *monachus* and "*M.*" *tropicalis* seem more closely related to other phocids than to "*M.*" *schauinslandi*. Several features, most of which were addressed by Repenning and Ray (1977), indicate such a remote placement of "*M.*" *schauinslandi* relative to other members of the family (see below). Confidence in this placement could be significantly enhanced with knowledge of several structures of the "soft" anatomy currently unavailable for the other two species of the "genus." Most helpful in this regard would be information concerning the pattern of the distensible tissue of the middle ear and the development of the pericardial plexus in "*M.*" *monachus*. Even in the absence of these data, however, a few skeletal characters for which the distribution naturally is well known [such as (2) the unexpanded dorsal petrosal region, (6) lack of proximal tibia and fibula fusion, and (7) invariable presence of obturator nerve foramen in the innominate] point to several important plesiomorphic aspects of the Hawaiian species.

This result raises a nomenclatural concern: if monk seals are indeed paraphyletic it would seem desirable to recognize this circumstance in their binomial appellations. At this point, however, I think it premature to propose new generic assignments for members of "*Monachus*." Although such action would seem justified, at least in the case of "*M.*" *schauinslandi,* until such time as the mutual relationships of the other two species are more satisfactorily understood, the proposal of new names would be premature. Meanwhile I think it preferable to place "*Monachus*" within quotation marks to emphasize the questionable status of its monophyly.

If the paraphyly of monk seals and the sister-group position of "*M.*" *schauinslandi* to other phocids are accepted, then the "Mon-

achinae" are necessarily not monophyletic. For the sake of argument, though, the problems associated with "*Monachus*" monophyly may be ignored for the moment and an assessment of the relative strength of the morphological evidence favoring a monophyletic as opposed to a paraphyletic "Monachinae" may be carried out independently. At first inspection several derived characters seem to support the monophyletic integrity of the "monachine" grouping. These include: (21) shortening of the third metatarsal, (23) reduced claws on the pes, (24) configuration of the premaxilla, and (25) reduced upper incisor number. As detailed in the discussions of characters, most of these features have shortcomings. Of the four, only 23 (reduced hind-flipper claws) occurs uniquely among "monachines." In addition to problems previously mentioned, the derived condition of 25 (four upper incisors) occurs also in *Cystophora*. Notwithstanding the possibility that the "monachine" premaxillary configuration (considered the derived state for character 24) is in fact primitive for phocids, this feature does not occur in some "monachines" and is present in some phocines (see above).

These four potential "monachine" characters stand in opposition to those which indicate the exclusion of "*Monachus*" from a group including all other phocids, for example: (3) enlargement of the petrosal apex, (4) complete loss of the roof of the auditory meatus, (8) hooklike teres major process, (26 and 27) features of the pelage and molt, and (30) the presence of four mammary teats [(30) occurs also in *Erignathus* and (26 and 27) serve equally to set *Mirounga* apart from other phocids].

Preference for one of these two alternatives, if considered strictly, is based on a relatively slim character margin. If the character base is broadened, however, to include those pertinent to the question of "*Monachus*" monophyly, then support swings decidedly in favor of a nonmonophyletic "Monachinae" (fig. 1, II–IV). Consequently, one would opt, on the basis of parsimony, for the hypothesis that the "monachine" configuration of the premaxilla, reduced claws on the pes, four upper incisors, and third metatarsal shortening are all characters primitive for the
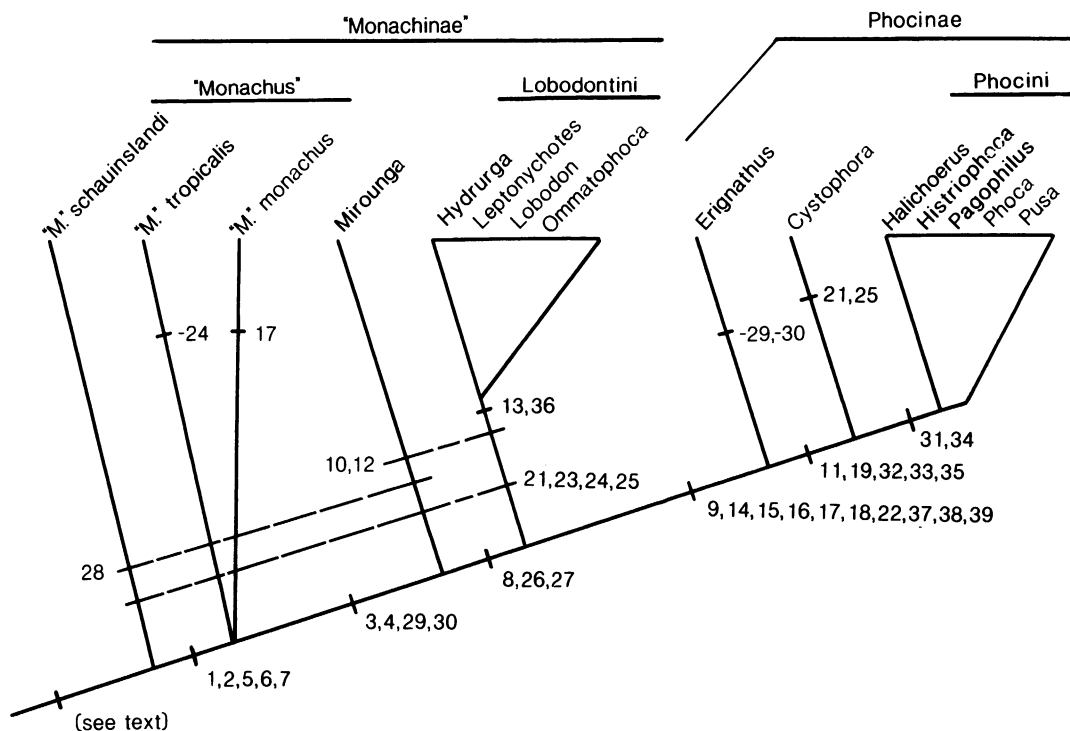
Fig. 9.   Cladogram depicting consensus results of PAUP for Recent phocid genera: intratribal relationships of the Lobodontini and Phocini left unresolved. Numbers identify characters discussed in text and listed in tables 1 and 2. Minus symbols indicate postulated reversals. Broken lines identify the most severe instances of character conflict: (upper) apomorphies common to *Mirounga* and the Lobodontini; (middle) a character shared by "*Monachus*" and *Mirounga*; (lower) characters that potentially diagnose a monophyletic Monachinae. Note, however, that none of these relationships is upheld within the context of overall parsimony and the characters involved are best regarded as homoplastic. In the scheme presented, characters 21, 23, 24, and 25, for example, are more efficiently interpreted as primitive phocid features which reverse at the level of the Phocinae. In addition to these four, postulated reversals (or partial reversals) from more generalized pinniped conditions occurring at the phocine node include: 14, 16, 17, 18, 22, 37, 38, 39, and perhaps 13 (see text). Tribal designations for "*Monachus*," *Mirounga*, *Erignathus*, and *Cystophora* are unspecified. Some character distributions have equally parsimonious alternative interpretations (e.g., 21 and 25 may be primitive for phocids and have been lost independently in *Erignathus* and the Phocini) but these do not influence cladogram topography. Presence of characters 2 and 5 in "*M.*" *tropicalis* and "*M.*" *monachus* is conjectural.

Phocidae that have been secondarily modified within the Phocinae. The feasibility of this proposal (which might seem rather untenable at first) will be more apparent following a consideration of the "northern" subfamily.

In answer to the third question posed above, it seems that the monophyly of the Phocinae (*Erignathus* + *Cystophora* + the tribe Phocini) is indeed very securely founded. The following are characters common to the group: (9) mastoid visible in dorsal view, (14) entepicondylar foramen present, (15) plantar process on cuneiform, (16) metacarpals I and II nearly equal in size, (17) fifth intermediate phalanx on manus not reduced, (18) metacarpal heads with strong palmar ridge, phalanges not flat, (22) large claws on manus and pes, (37) well-developed supinator ridge on humerus, (38) deltoid crest short, ends abruptly above humeral shaft, and (39) deep post-tibial fossa.

Within this phocine grouping may be diagnosed a pairing of *Cystophora* and the Phocini on the basis of their shared possession of the following characters: (11) petrobasilar

fissure and posterior lacerate foramen merge to isolate bulla medially, (19) strongly everted ilium with lateral excavation, (33) posterior opening of carotid canal not visible in ventral view and absence of process from the posteromedial edge of the auditory bulla, and (35) ventral surface of basioccipital/basisphenoid region flat to convex. Many of these phocine and *Cystophora* + Phocini features are uniquely derived, but these two sets of characters include some that might easily be mistaken as primitive (e.g.: 14, presence of entepicondylar foramen; 16, metacarpals I and II not greatly disparate in size; 17, typical fifth intermediate phalanx on manus; 18, trochleated interphalangeal articulations; 22, long foreflipper claws; 32, upper incisors flat in cross section; 37, well-developed supinator ridge; 38, relatively short deltoid pectoral crest; 39, strongly developed post-tibial fossa). In this category would be placed also the tendency among phocines to develop a trochanteric fossa of the femur, reduction of the supraspinous fossa of the scapula, and a posterior position of the palatine foramen. For reasons discussed earlier, these characters, while representing general carnivoran or mammalian features, may not be considered primitive for pinnipeds (assuming monophyly). Suggesting otherwise implies that phocines are the sister-group of all other pinnipeds, a proposal which seems hardly credible in the face of overwhelming evidence supporting phocid monophyly. These seemingly "primitive" phocine characters must therefore have originated within the Pinnipedia, more precisely within the Phocidae, and necessarily represent reversals.

To reject the proposal advanced here that the numerous "primitive" features seen in phocines are in fact reversals, one must simultaneously accept both pinniped diphyly and "monachine" monophyly. Employing mustelids as the phocid sister-group (leaving aside the doubtful nature of this assumption) strengthens the evidence for "monachine" monophyly, shifting (14) the absence of an entepicondylar foramen in its favor and removing doubt about the possible primitiveness of (24) the "monachine" premaxilla configuration. Nevertheless, admittance of mustelids as close phocid allies does not sufficiently redistribute the overall character

balance to disrupt the case for "monachine" paraphyly. Acceptance of the diphyly notion alone, therefore, does not convincingly overturn the reversal interpretation.

Rejection of the reversal hypothesis demands also the demonstrably insecure assumption of "monachine" monophyly. Furthermore, an argument against the reversal hypothesis requires yet a third unlikely proposition, namely that the derived resemblances of "monachines" and other pinnipeds (such as the reduction of the fifth intermediate phalanx on the carpus, the tremendous enlargement of the first metacarpal, and flattened phalanges lacking trochleated articulations, to name but a few) are the result of convergence. In summary, the possibility that the character distribution among phocines considered here represents anything but a suite of reversals is exceedingly unlikely.

It is curious to note how reversals are particularly evident in flipper structure. Here they have occurred to such an extent that in many respects [e.g.: reduction in size of metacarpal I (16), enlargement of intermediate phalanx V in the carpus (17), metacarpal heads with palmar ridges, phalanges round in cross section, and trochleated interphalangeal articulations (18), and large claws on manus (22)] these seals have reverted to, or approached, the primitive carnivoran (not simply pinniped) character states. If the "Monachinae" are viewed as paraphyletic, then this pattern of character reversal within the flippers also encompasses lengthening of the third metatarsal (21) and the gain of claws on the pes (23). Reversals are by no means limited to flippers but include features of the humerus [presence of entepicondylar foramen (14), strong supinator ridge and short abruptly terminating pectoral crest (37 and 38)], the dentition [six (25) laterally compressed incisors (32)], tibia (presence of a strong post-tibial fossa) and perhaps the premaxillary configuration (24) as well.

By way of a general conclusion, I offer one brief remark regarding the higher-level relationships within the Phocidae. As is often the case in systematics, when a well-defined monophyletic grouping is subtracted from another more inclusive group (in the case examined here, the Phocinae from other Phocidae), agglomerating the "leftovers" (here the

Fig. 10. Lateral view of *Phoca vitulina* skeleton illustrating distinctive phocine features discussed in text. Originally published as lithograph in de Blainville (1839–64), leaders have been purposely omitted so as not to compromise integrity of the original figure. Characters listed below refer to features depicted. Numbers preceding character descriptions agree with those used in text and tables 1 and 2. Asterisks indicate postulated reversals in the corresponding character, i.e., expressions of characters that although derived for pinnipeds, represent, or at least approach, a more generalized carnivoran condition. Characters shown include: (8) strong teres major process on scapula*; (13) strong scapular spine*; (16) metacarpal I not greatly more massive than metacarpal II*; (17) nonreduced intermediate phalanx V*; (18) trochleated metatarsal-phalangeal and interphalangeal articulations*; (19) strongly everted ilium; (21) metatarsal III not extremely shortened, posterior flipper margin only moderately convex*; (22) strong foreflipper claws*; (23) strong hind-flipper claws*; (24) premaxillary configuration (see text); (37) strong humeral supinator ridge*; (38) short (for a pinniped) deltoid pectoral crest*.

"Monachinae") usually yields a nonmono-phyletic result. In such instances, cohesion of the residual taxa is more often based simply on the mutual exclusion of its members from the more restricted monophyletic subdivision, than it is on features intrinsic to those taxa. While the "monachine"-phocine split may be convenient for discussing biogeography (as popularity of the locutions "northern" and "southern" indicates), this dichotomy receives less than persuasive support from comparative morphology. Whatever the merits or pitfalls of the phylogeny depicted in figure 9, this analysis raises serious doubts about seemingly unquestioned validity of this widely accepted basal phocid dichotomy. The possibility of phylogenies conformable with class III and IV hypotheses of figure 1 need to be considered. Rather than continue to force living and fossil taxa into a traditional but very likely unnatural classificatory scheme, alternatives might profitably be entertained.

In the conclusion of his classic "Contribution to the comparative anatomy of the eared and earless seals," Howell (1929) puzzled over his observation that in several respects such as details of the myology, the greater tendency toward flattening of the phalanges of the pes, and the cartilaginous extensions of the digits, *Zalophus* has "traveled farther from the typical terrestrial carnivore" than has *Pusa.* The lack of these skeletal modifications struck Howell as particularly vexing given that such structures would seem far more "useful" to the hind-limb swimming phocids—which, moreover, are generally regarded as the most highly aquatic of the pinnipeds—than to the otherwise seemingly less aquatically specialized otariids. Likewise he found perplexing the presence of certain specializations of the forelimb in *Pusa* that appear to be of no "real use." Thus as related to the evolution of what are generally regarded as the two major groups of pinnipeds, otariids (including odobenids) and phocids (for contrary view see Wyss, 1987), Howell entertained (but remained far from convinced of) the possibility that this unexpected morphology was attributable to a pattern of retrogressive evolution.

To be sure, this proposition amounts to little more than a descriptor, yet I think it aptly delineates some of the character transformations that likely occurred during the early evolution of phocids as a group, and in large measure many of the character transformations during the evolution of its various subgroups, particularly the phocines. Whatever developmental mechanisms underlie such wide-scale character reversal, that such "retrogression" has occurred appears, at this point, difficult to refute.

The evolution of the limbs of the Phocinae affords a well-founded example of broad-based character reversal. The difficulty typically posed in cases where the appearance of atavistic characters or heterochronic ontogenetic modifications such as neoteny are suspected, is finding sufficient additional characters independent of such processes for "correctly" placing a given taxon within a phylogeny. In highly transformed taxa, reversals may be so pervasive as to erase most or all derived characters which might otherwise have been indicative of more highly resolved cladistic placement. The almost certain monophyly of the Phocinae and their membership within an unquestionably monophyletic Phocidae provides a rigorously supported phylogenetic hypothesis, the essential element of any demonstration of character reversal. Phocine seals, therefore, present a rare opportunity for the study of extensive character reversion. This phenomenon is normally extremely difficult to identify, and in the case of "adaptively unified functional complexes" (such as pinniped flippers) is sometimes claimed not to occur.

Finally, results presented here counter the seemingly logical notion held by most workers (e.g., Laws, 1959; King, 1964) that phocids have undergone a phylogenetic trend toward increasing flipper "specialization" from a structurally conservative phocine arrangement to an ostensibly more highly "advanced" "monachine" form. It seems, however, that phocid flipper evolution has progressed in a direction exactly opposite this expectation, culminating in a pattern looking deceptively primitive phylogenetically but being in fact only secondarily so.

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