PINNIPEDS AND CARNIVORES:
PHYLETIC RELATIONSHIPS AND CLASSIFICATION

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Abstract

Shannon, J. S. (Department of Wildlife, Humboldt State University, Arcata, California 95521) 1987. Pinnipeds and carnivores: phyletic relationships and classification. Syst. Zool. xx:xxx-xxx. - Evidence for monophyly and polyphyly of the pinnipeds is summarized and discussed with reference to the classification of the higher subtaxa of the Pinnipedia and the order Carnivora. On the basis of a consensus analysis of data supporting pinniped monophyly, an alternative classification of the Carnivora is proposed. If pinnipeds are demonstrated to be of monophyletic origin, they should be assigned no higher than superfamilial rank (superfamily Pinnipedea new) within the infraorder Arctoidea. If mustelid ancestry for the phocids is firmly established, the classification of Tedford (1976) should be retained. Determination of actual phyletic relationships between pinnipeds and carnivores awaits discovery of additional fossil evidence of proto-phocid and early arctoid forms.

The phyletic relationships of the higher taxonomic groups comprised by the Pinnipedia (Chordata:Mammalia) have posed problems for mammal systematists for over a century. The question of whether the seals (superfamily Phocoidea Smirnov, 1908) and the sea lions and walruses (superfamily Otarioidea Gill, 1866) share an immediate common ancestor remains a topic for debate among taxonomists. At stake is the validity of the widely accepted classifications presently in use. Typically, the superfamilies Otarioidea and Phocoidea are united in the suborder Pinnipedia Illiger, 1811 of the order Carnivora Bowdich, 1821 (Simpson, 1945), although Pinnipedia has also been assigned full ordinal rank (Scheffer, 1958). For the two superfamilies to be legitimately united in their own distinct taxon, however, their descent from a common ancestor (monophyly) must be presumed. Conversely, if a taxon embraces animals which are descendants of different ancestors (polyphyly), then its members are falsely united, and as such, the taxon misrepresents actual phylogenetic patterns. If the taxon Pinnipedia is found to be invalid, then, this has direct implications for the classification of its higher subtaxa, and of the order Carnivora, as well.

W. H. Flower (1869) subdivided the Carnivora into three superfamilies based upon the morphology of the auditory bulla and associated basicranial structures. In a study of these basicranial characters in living pinnipeds, Mivart (1885) described similarities in the auditory bullae of pinnipeds with the carnivores of Flower's superfamily Arctoidea (the families Ursidae, Mustelidae, and Procyonidae). Mivart (1885) concluded that the pinniped family Otariidae was descended from an early ursid-like lineage, while the Phocidae was derived from an early lutrine (otter-like) mustelid lineage. This statement has subsequently become the classical thesis for pinniped polyphyly.

Fossil evidence that could be used to test Mivart's (1885) hypothesis was slow to accumulate, however, because of the poor representation of early pinnipeds in the fossil record. Even today, no proto-phocid fossil form has been discovered. Still, there have been significant fossil discoveries that have helped to fill important gaps in our knowledge of pinniped origins. Much of this evidence has been interpreted as upholding Mivart's (1885) claim for a polyphyletic derivation of the Pinnipedia.

Savage (1957) described the anatomy of an early arctoid lutrine, *Potamotherium valletoni* Geoffroy, 1833 (Figure 1), known from numerous well-preserved specimens collected from late Oligocene lacustrine deposits in central France. In his analysis, Savage (1957) noted a number of resemblances in the cranial, axial, and appendicular skeletons of *Potamotherium* and *Phoca*. Although Savage (1957) did not feel confident enough to propose *Potamotherium* as the ancestor of the phocids, he did believe that the resemblances between *Potamotherium* and *Phoca* were of possible phylogenetic significance.

Savage (1957) also commented on the many similarities between *Potamotherium* and the Pliocene seal-otter *Semantor macrurus* described by Orlov (1931) (Figure 2). *Semantor* is known from a single specimen from the Neogene of western Siberia. Precise systematic placement of *Semantor* is not possible because only the post-lumbar portions of the axial and appendicular skeleton were preserved (Figure 3). Nevertheless, enough remains to reveal a picture of a large, facultatively terrestrial, lutromorphic pinniped. According to Savage (1957):

> ...while *Potamotherium* is a morphological link between *Lutra* and *Phoca,* *Semantor* is a morphological link between *Potamotherium* and *Phoca.*

Because of its Pliocene appearance, however, *Semantor* could not be the *evolutionary* link between *Potamotherium* and the first known early Miocene phocid fossils. *Semantor* probably represented an experiment in incipient phocomorphy in an essentially lutromorphic lineage (Thenius, 1949). However, the real significance of the *Potamotherium-Semantor* series was that phocomorphy had apparently evolved out of lutromorphy. The series further suggested the possibility that a similar but more complete phocomorphic transformation may have taken place in an Oligocene lutrine lineage, thus giving rise to a hypothetical Oligocene/Miocene proto-phocid, and ultimately, the Recent Phocidae.

McLaren (1960) reviewed evidence for polyphyly from anatomical investigations, paleozoogeographical accounts and the fossil record. In a summary scenario of pinniped origins, McLaren (1960) proposed *Potamotherium* as a hypothetical ancestor for the Phocidae. He also concluded that the proto-phocid descendants of *Potamotherium* radiated in the Atlantic-Tethyan region, where most early phocid fossils have been found. The fossil record for early otarioids, though, suggested a contemporaneous North Pacific origin. For both otarioids and phocids, however, a definitive link to an ancestral carnivore lineage remained unknown; that is, until Mitchell and Tedford (1973) described the extinct aquatic carnivore *Enaliarctos mealsi* from the early Miocene of south-central California (Figures 4 and 5).

Enaliarctos was an important discovery, because its skull and dentition were demonstrably transitional between modern otariids and a group of lower Oligocene terrestrial arctoid carnivores, the †subfamily Hemicyoninae Frick, 1926 (specifically *Cephalogale*) (Mitchell and Tedford, 1973). *Enaliarctos* provided tangible affirmation of ursid ancestry for the Otariidae. The precise arctoid origin of the Phocidae, however, remained open to speculation.

In a subsequent elaboration of Mivart's (1885) comparative study of basicranial characters, Tedford (1976) presented a case for acceptance of *Potamotherium* as the legitimate intermediate form uniting early mustelids and modern phocids, just as *Enaliarctos* joined the early ursids with the otariids. Tedford (1976) concluded his case for polyphyly by suggesting a new placement of the formerly united pinniped superfamilies in a revised classification of the order Carnivora (Table 1). A cladogram representing Tedford's (1976) classification is shown in Figure 6.

If the Pinnipedia turned out to be monophyletic, of course, the implications for classification would be quite different, and it should be pointed out that some studies of pinniped anatomy have indeed suggested the group shared common ancestry (see McLaren 1960, 1975, for reviews). Overall, however, the bulk of the comparative and historical evidence available to date has been interpreted as upholding a polyphyletic origin for the pinnipeds (McLaren, 1960; Mitchell and Tedford, 1973; Tedford, 1976).

Presented with this seeming weight of evidence in favor of polyphyly, however, there are legitimate reasons for rejecting this hypothesis. The main weakness in the argument for polyphyly remains the inconclusiveness of the fossil evidence cited in support of a mustelid derivation for the Phocidae. Despite Tedford's (1976) appealing case in behalf of *Potamotherium*, for instance, the fact remains that no fossil series is yet known that conclusively links the phocids to any extant or extinct carnivore lineage (Mitchell and Tedford, 1973; Tedford, 1976). Additionally, recently developed biomolecular methodologies for analyzing phylogenetic relationships have provided credible arguments in favor of pinniped monophyly.

Biomolecular techniques estimate taxonomic distances by indexing the amount and rate of immunological interactions between different species' sera. Most comparisons among pinnipeds and carnivores have been made at the protein level (Leone and Wiens 1956; Sarich 1969 a,b), but a recent amino acid sequence study (Miyamoto and Goodman, 1986) has taken the analysis down to the nucleotide level.

Although Leone and Wiens (1956) did not directly address the question of phyletic relations within the Pinnipedia, their study did shed light on the relationship of pinnipeds to fissiped carnivores. Leone and Wiens (1956) compared the sera of six fissiped families with that of otariid pinnipeds. The otariid serum reacted most strongly with the ursid serum, followed in order of reactivity by the mustelid, procyonid, and canid sera. On the basis of this high degree of reactivity between otariid and fissiped sera, Leone and Wiens (1956) believed that subordinal rank for the Pinnipedia was not justified. They suggested the Carnivora be divided into two subordinal groups (not named), one of which combined the superfamily Canoidea Simpson, 1931 (the families Ursidae, Mustelidae, Procyonidae, and Canidae), with the family Otariidae (and presumably the Phocidae; not studied). Thus defined, this Leone and Wiens' (1956) subordinal group was an equivalent taxon to Tedford's (1976) suborder Caniformia Kretzoi, 1945 (Table 1). Leone and Wiens' (1956) prior suggestion was not cited by Tedford (1976), however.

In a study of immunological relationships among fissiped and pinniped albumins, Sarich (1969a) corroborated many of Leone and Wiens' (1956) findings. For example, Sarich (1969a) affirmed the close relationship between pinnipeds and canoids, particularly the ursids. In fact, Sarich (1969a) precisely duplicated the serial order of pinniped-fissiped serum reactivity found by Leone and Wiens (1956): ursid, mustelid, procyonid, canid.

Sarich (1969 a,b), however, developed a further technique of indexing a measure of immunological distance between albumin lineages, which together with the assumed regularity of carnivore albumin evolution, allowed for the use of albumin molecules as evolutionary clocks to quantify broader phylogenetic differences. Because the pinniped families showed less immunological distance among themselves than to the fissipeds, Sarich (1969b) concluded that the Pinnipedia was monophyletic with respect to the other canoid carnivores.

Using amino acid sequence data to construct phylogenetic trees, Miyamoto and Goodman (1986) sought to resolve the higher-level systematics of the infraclass Eutheria (Mammalia). A cladogram depicting the carnivore branch of Miyamoto and Goodman's (1986) eutherian tree is presented in Figure 7. Like Sarich (1969b), Miyamoto and Goodman (1986) upheld the assertion of pinniped monophyly, and the inclusion of the Pinnipedia (at an unspecified rank) within the Canoidea.

The biomolecular evidence in support of pinniped monophyly is apparently unequivocal. Unfortunately, fossil evidence for monophyly has yet to be demonstrated in any form. No known early arctoid lineage can credibly serve as a common ancestor or morphological intermediate for the phocids and otariids (Mitchell and Tedford, 1973). Primarily for this reason, it is unlikely that the question of pinniped monophyly will be resolved until the fossil record of the early arctoid adaptive radiation is more thoroughly revealed (McLaren, 1975).

The fossil gaps that must be closed in order to define the actual phyletic relationships among pinnipeds and carnivores are depicted in Figure 8. As stated previously, the Hemicyoninae-Enaliarctinae-Otariinae series has been convincingly established by Mitchell and Tedford (1973). In the absence of a comparably compelling series in the phocid lineage, the question of alleged affinities between *Potamotherium* and modern phocids (*sensu* McLaren, 1960; Tedford, 1976) takes on central significance. To demonstrate such affinities, an intermediate form from the four-million-year period between the appearance of *Potamotherium* and the earlist known fossil phocids must be found ([1], Figure 8). Despite the preponderence of mustelid characters displayed by *Potamotherium*, however, Tedford (1976) seemed less assured of its alleged mustelid ancestry than were previous authors (e.g. Savage, 1957; McLaren, 1960). Tedford (1976) pointed out, for example, that *Potamotherium* had a more primitive dentition than the earliest known mustelid fossil, the Eocene *?Mustelictis* (Radinsky, 1971), and that its auditory bullae resembled those of early ursids more than those of mustelids (Mitchell and Tedford, 1973; Tedford, 1976). For these reasons, a late Eocene or early Oligocene arctoid form is sought that would unite *Potamotherium* more firmly with proto-mustelid stock ([2], Figure 8). Thus, there are two important fossil gaps that must be filled to conclusively demonstrate a mustelid ancestry for the phocids and, therefore, a polyphyletic relationship among the higher pinniped subtaxa.

To demonstrate the pinnipeds' monophyletic descent from the early ursid line, however, as many as four gaps must be filled: a proto-phocid referable to known ursid forms, a North Atlantic ursid form contemporary with the North Pacific *Enaliarctos*, and at least one Eocene or Oligocene proto-ursid form to unite the phocid-otariid-ursid lineages ([3-6], Figure 8).

Interestingly, Mitchell and Tedford (1973) had previously noted a number of morphological similarities between the Miocene contemporaries *Potamotherium* and *Enaliarctos*, and suggested that these similarities might, in fact, reflect a close genetic relationship, and not merely convergence. If *Potamotherium* was actually more closely related to *Enaliarctos* than to other mustelids of its time, then, *Potamotherium* might be eligible to fill the gap for the Miocene North Atlantic "ursid" form. From Figure 8, however, it can be seen that simply moving *Potamotherium* to the ursid line would not necessarily reduce the number of fossil gaps needing to be closed. The shift would also reduce overall explanatory parsimony by increasing the number of *ad hoc* hypotheses required to account for the homoplastic evolution, in the ursid line, of the entire constellation of mustelid characters displayed by *Potamotherium*. Despite its odd mixture of early arctoid features, then, it appears more parsimonious to regard *Potamotherium* as having been more closely related to early mustelids than to ursids (Tedford, 1976).

Although much has been learned about the relationship of pinnipeds and carnivores, workers are left with the uncomfortable fact that the systematics and classification of these mammals remain more a matter of educated opinion than demonstrable taxonomic "truth." Proponents of polyphyly, for example, must necessarily reject the widely recognized mammalian classification of Simpson (1945), which divided the order Carnivora into the suborders Pinnipedia Illiger, 1811 and Fissipeda (=Fissipedia) Blumenbach, 1791. After their discovery of *Enaliarctos*, Mitchell and Tedford (1973) called for placing Simpson's (1945) subordinal taxa in abeyance pending accumulation of additional fossil evidence of the arctoid adaptive radiation. Not only was the monophyly of the Pinnipedia regarded as sufficiently questionable, but because Mitchell and Tedford (1973) demonstrated fissiped ancestry for one of the pinniped superfamilies (the Otarioidea), the Fissipedia was shown to be a paraphyletic taxon - at best a "grade" of Carnivora. Because the validity of both of Simpson's (1945) subordinal taxa was therefore considered dubious, Mitchell and Tedford (1973) suggested an alternate classification of the Carnivora, uniting the families Phocidae and Otariidae in a phyletically unresolved superfamily Canoidea (Table 2).

Other workers, convinced by the evidence for monophyly from biomolecular studies, may wish to adopt a classification that unites the pinnipeds, but which more accurately represents pinniped-fissiped affinities than does Simpson's (1945) classification. Reiterating the conclusions of Leone and Wiens (1956) and Miyamoto and Goodman (1986), the pinnipeds are so closely related serologically to fissiped canoids that to consider the pinnipeds distinct from the fissipeds at the subordinal level (e.g. Simpson, 1945) was deemed unsupportable. Even by proponents of monophyly, then, the pinniped-fissiped dichotomy has become less meaningful taxonomically, at least at the level assumed by Simpson (1945) or Scheffer (1958).

If the phocoids and otarioids do comprise a monophyletic group, then at what taxonomic level can they be legitimately united within the Carnivora? An examination of cladograms generated from data supporting monophyly may prove useful in such a determination. The cladogram of Miyamoto and Goodman (1986) was presented previously in Figure 7. However, neither Leone and Wiens (1956) nor Sarich (1969a,b) constructed a cladogram of this type to express their results. Based upon perceived nested sets of similarities in numerical measurements of immunological distances obtained by Sarich (1969b) (Table 3), the cladistic hypothesis in Figure 9 was generated.

To resolve these cladograms into a unified hypothesis of pinniped monophyly, a consensus analysis must be performed. Normally, consensus analyses make use of numerical algorithms to resolve multiple trees. In this analysis, however, the two cladograms differ only with respect to the position of the pendant node for the Ursidae. Because the topology of Miyamoto and Goodman's (1986) cladogram is contradicted by the known enaliarctid-otariid series, the cladistic hypothesis derived from Sarich (1969b) is favored. A consensus of the biomolecular evidence augmented by a known fossil series, then, suggests a tentative sister-group relationship between the ursids and the presumed monophyletic pinnipeds (Figure 9).

An interim classification of the Carnivora, expressing the phyletic sequence of the cladogram in Figure 9, is presented in Table 4. Using Tedford's (1976) intermediate categorical ranks, the pinnipeds can be united at the superfamily level. The name "Pinnipedea" is suggested for this new arctoid superfamily. If fossil evidence emerges substantiating a true sister-group relationship between the ursids and both pinniped subtaxa, this interim classification should be considered for priority. If the pinnipeds are proven to be polyphyletic - specifically, if mustelid ancestry for the Phocidae is substantiated - the more phyletically-resolved classification of Tedford (1976) should be retained and given priority over the earlier preliminary classification suggested by Mitchell and Tedford (1973). Until the pinnipeds are determined to be monophyletic or not, however, the "Pinnipedia" and "Fissipedia" should be regarded as nominal taxa only.

Finally, questions remain concerning the proper placement of *Potamotherium*, in both an evolutionary and taxonomic sense. I believe that sufficient evidence exists (e.g. Savage, 1957; Kirpichnikov, 1955; Tedford, 1976) to unite *Potamotherium* and *Semantor* in the

†family Semantoridae Orlov, 1931. However, because enough doubt remains about the exact phylogenetic relationship of the Semantoridae, so defined, to the Mustelidae, Ursidae, Phocidae, and Enaliarctidae (Thenius, 1949; Savage, 1957; Chapskii, 1961; Mitchell and Tedford, 1973; Tedford, 1976), the Semantoridae should be removed from the Pinnipedia and referred to an uncertain position *(incertae sedis)* within the Carnivora.

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TABLE 1. TEDFORD'S (1976) PROVISIONAL REVISION OF THE ORDER CARNIVORA ASSERTING POLYPHYLETIC ARCTOID ORIGINS OF SUB-TAXA COMPRISED BY THE "PINNIPEDIA." A CLADOGRAM EXPRESSING THIS CLASSIFICATION IS DEPICTED IN FIGURE 6.

- Order CARNIVORA Bowdich, 1821 [CV]
  - Suborder Feliformia Kretzoi, 1945 [FE]
  - Suborder Caniformia Kretzoi, 1943 (= Canoidea Simpson, 1931) [CF]
    - Infraorder Cynoidea Flower, 1869 [CA]
    - Infraorder Arctoidea Flower, 1869 [AR]
      - Parvorder Mustelida new [MA]
        - Superfam. Procyonoidea Bonaparte, 1850 [PR]
        - Superfam. Musteloidea Swainson, 1835 [ME]
          - Fam. Mustelidae Swainson, 1835 [MU]
          - Fam. Phocidae Gray, 1825 [PH]
            - †Subfam. Semantorinae Orlov, 1931
      - Parvorder Ursida new [UA]
        - Superfam. Ursoidea Gray, 1825 [UR]
        - Superfam. Otarioidea Gill, 1866 [OT]
          - †Fam. Enaliarctidae Mitchell and Tedford, 1973
          - Fam. Otariidae Gill, 1866 (incl. Odobenidae Allen, 1880)

TABLE 2. MITCHELL AND TEDFORD'S (1973) ALTERNATIVE CLASSIFICATION OF THE ORDER CARNIVORA, REFLECTING THE ABEYANCE CONDITION OF SIMPSON'S (1945) SUBORDINAL TAXA "PINNIPEDIA" AND "FISSIPEDIA."

Order CARNIVORA Bowdich, 1821
- Superfamily Canoidea Simpson, 1931
  - Family Canidae Gray, 1821
  - Family Procyonidae Bonaparte, 1850
  - Family Ursidae Gray, 1825
  - Family Otariidae Gray, 1825, *sensu lato* (= Otarioidea Gill, 1866)
  - Family Mustelidae Swainson, 1835
  - †Family Semantoridae Orlov, 1931
  - Family Phocidae Gray, 1825

TABLE 3. SUMMARIZED DATA FROM SARICH (1969b) OF MEAN IMMUNOLOGICAL DISTANCES BETWEEN PINNIPED AND CANOID ALBUMINS. BRACKETS INDICATE NUMERICAL SUBSETS USED TO CONSTRUCT CLADOGRAM IN FIGURE 9.

Albumin Taxon	Anti-Otariidae	Anti-Phocidae
Otariidae	5	22
Phocidae	25	7
Ursidae	32	38
Mustelidae	41	41
Procyonidae	43	43
Canidae	48	50

TABLE 4. A PROVISIONAL TAXONOMIC REVISION OF THE ORDER CARNIVORA ASSERTING A MONOPHYLETIC ARCTOID ORIGIN OF SUB-TAXA COMPRISED BY THE "PINNIPEDIA." A CLADOGRAM EXPRESSING THIS CLASSIFICATION IS DEPICTED IN FIGURE 9.

Order CARNIVORA Bowdich, 1821 [CV]
- Suborder Feliformia Kretzoi, 1945 [FE]
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  - Infraorder Cynoidea Flower, 1869 [CA]
  - Infraorder Arctoidea Flower, 1869 [AR]
    - Parvorder Mustelida Tedford, 1976 [MA]
      - Superfam. Musteloidea Swainson, 1835 [MU]
      - Superfam. Procyonoidea Bonaparte, 1850 [PR]
    - Parvorder Ursida Tedford, 1976 [UA]
      - Superfam. Ursoidea Gray, 1825 [UR]
      - Superfam. Pinnipedea new [PI]
        - †Fam. Enaliarctidae Mitchell and Tedford, 1973
        - Fam. Otariidae Gill, 1866 [OT]
        - Fam. Odobenidae Allen, 1880
        - Fam. Phocidae Brookes, 1828 [PH]

CARNIVORA *incertae sedis*:
- †Fam. Semantoridae Orlov, 1931

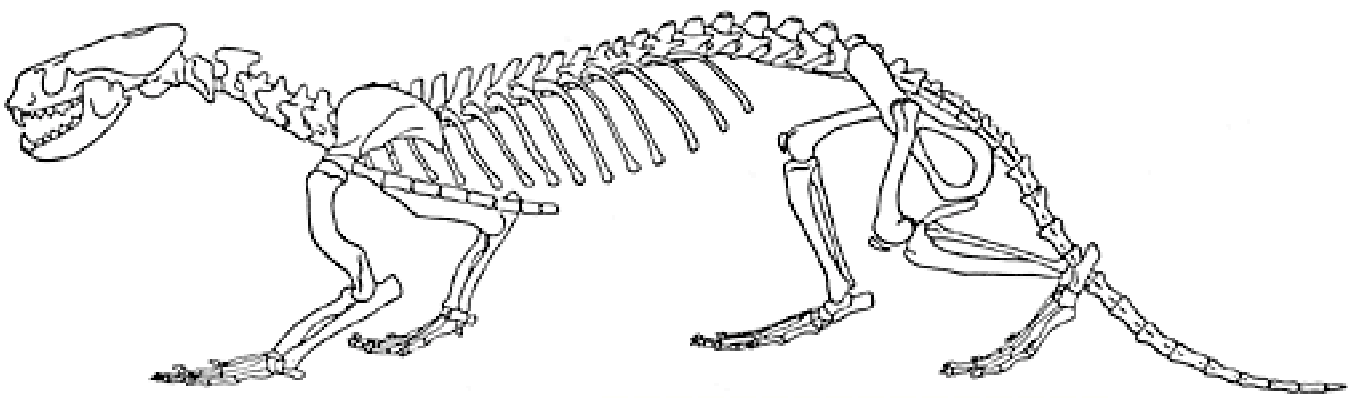

FIG. 1. - Reconstructed skeleton of the Oligocene lutrine *Potamotherium valletoni*. Reproduced from: Savage, R.J.G. 1957. The anatomy of *Potamotherium,* an Oligocene lutrine. Proc. Zool. Soc. Lond. 129:p. 236.

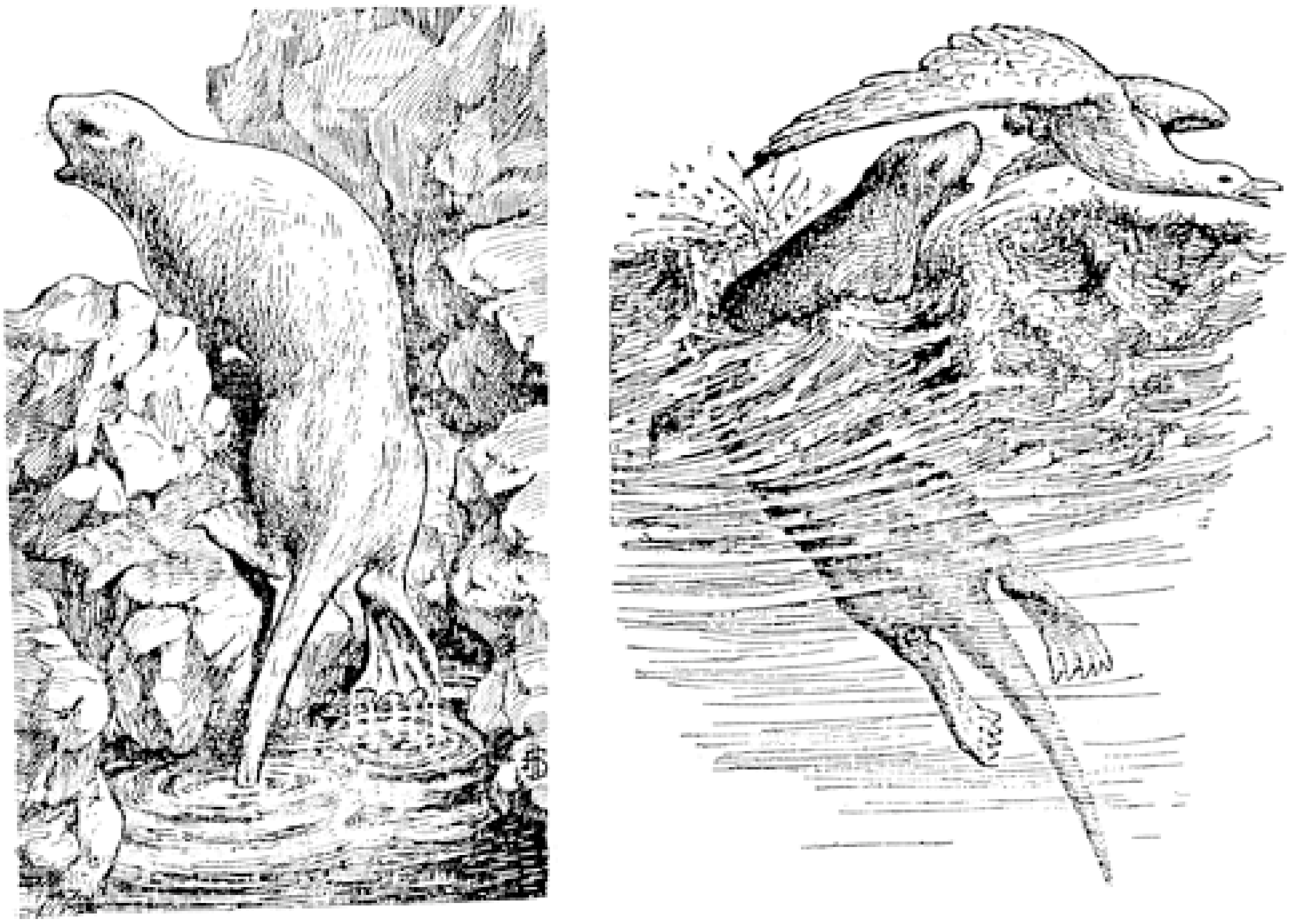

FIG. 2. - Artist's conceptions of *Semantor macrurus* in life. Reproduced from: Orlov, Yu.A. 1933. *Semantor macrurus* (ordo Pinnipedia, fam. Semantoridae fam. nova) aus den Neogen-ablagerungen Westsiberiens. Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 2:p. 249,253.

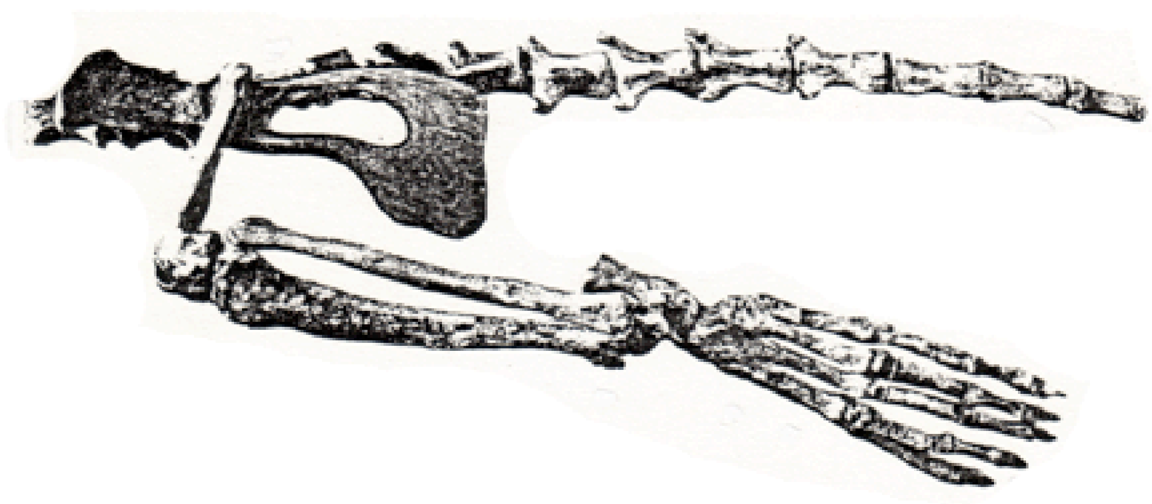

FIG. 3. - Type specimen of the Pliocene carnivore *Semantor macrurus*, an alleged intermediate between terrestrial lutromorphy and aquatic phocomorphy. Reproduced from: Orlov, Yu.A. 1933. *Semantor macrurus* (ordo Pinnipedia, fam. Semantoridae fam. nova) aus den Neogen-ablagerungen Westsiberiens. Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 2:p. XXII.

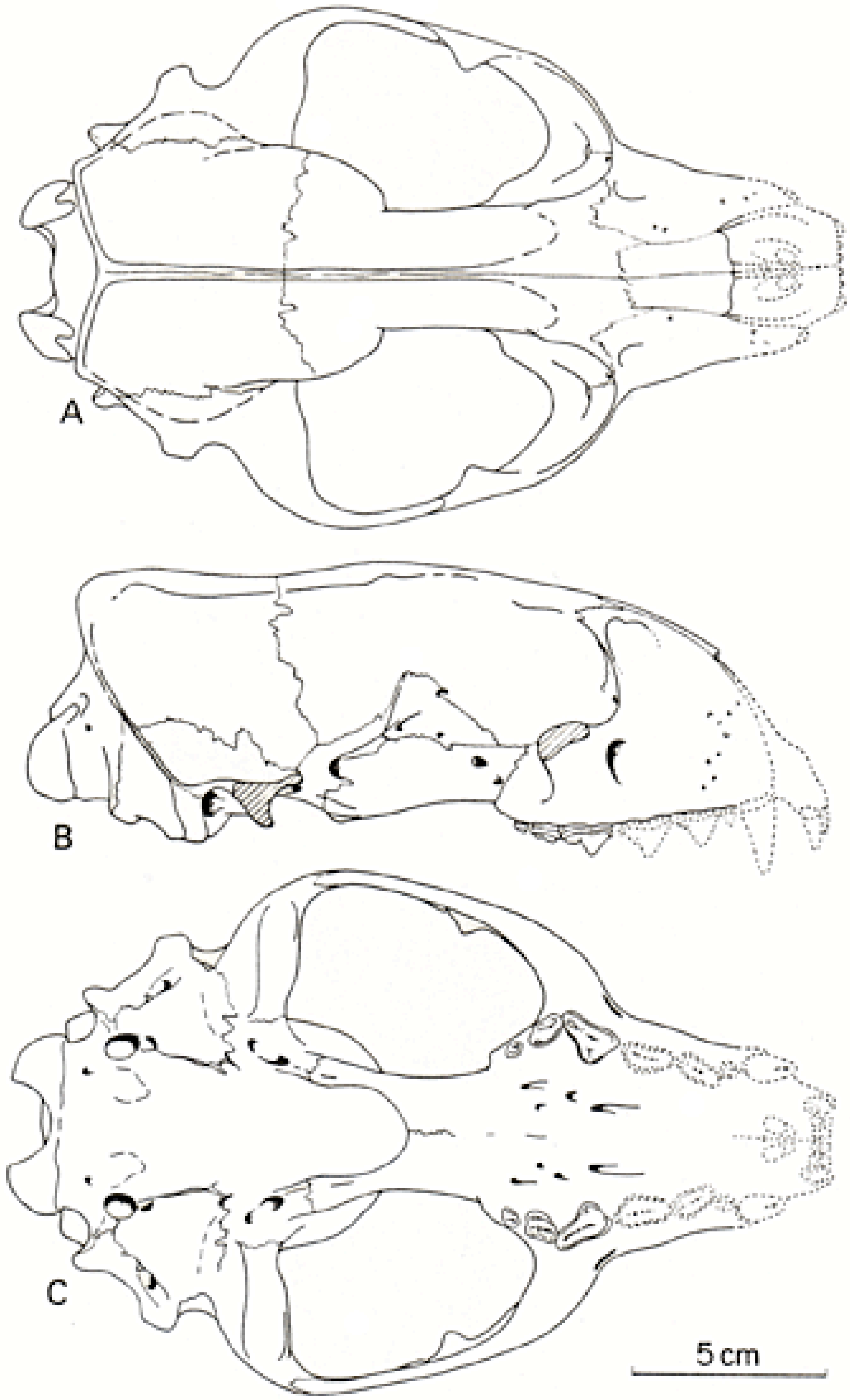

FIG. 4. - Reconstruction of the skull of the Miocene carnivore *Enaliarctos mealsi*, the presumed intermediate form between primitive terrestrial ursids and fully aquatic otariids. Reproduced from: Mitchell, E.D., and Tedford, R.H. 1973. The Enaliarctinae, a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bull. Amer. Mus. Nat. Hist. 151:p.244.

FIG. 5. - Artist's conception of *Enaliarctos mealsi* in life. Reproduced from: Mitchell, E.D., and Tedford, R.H. 1973. The Enaliarctinae, a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bull. Amer. Mus. Nat. Hist. 151:p.277.

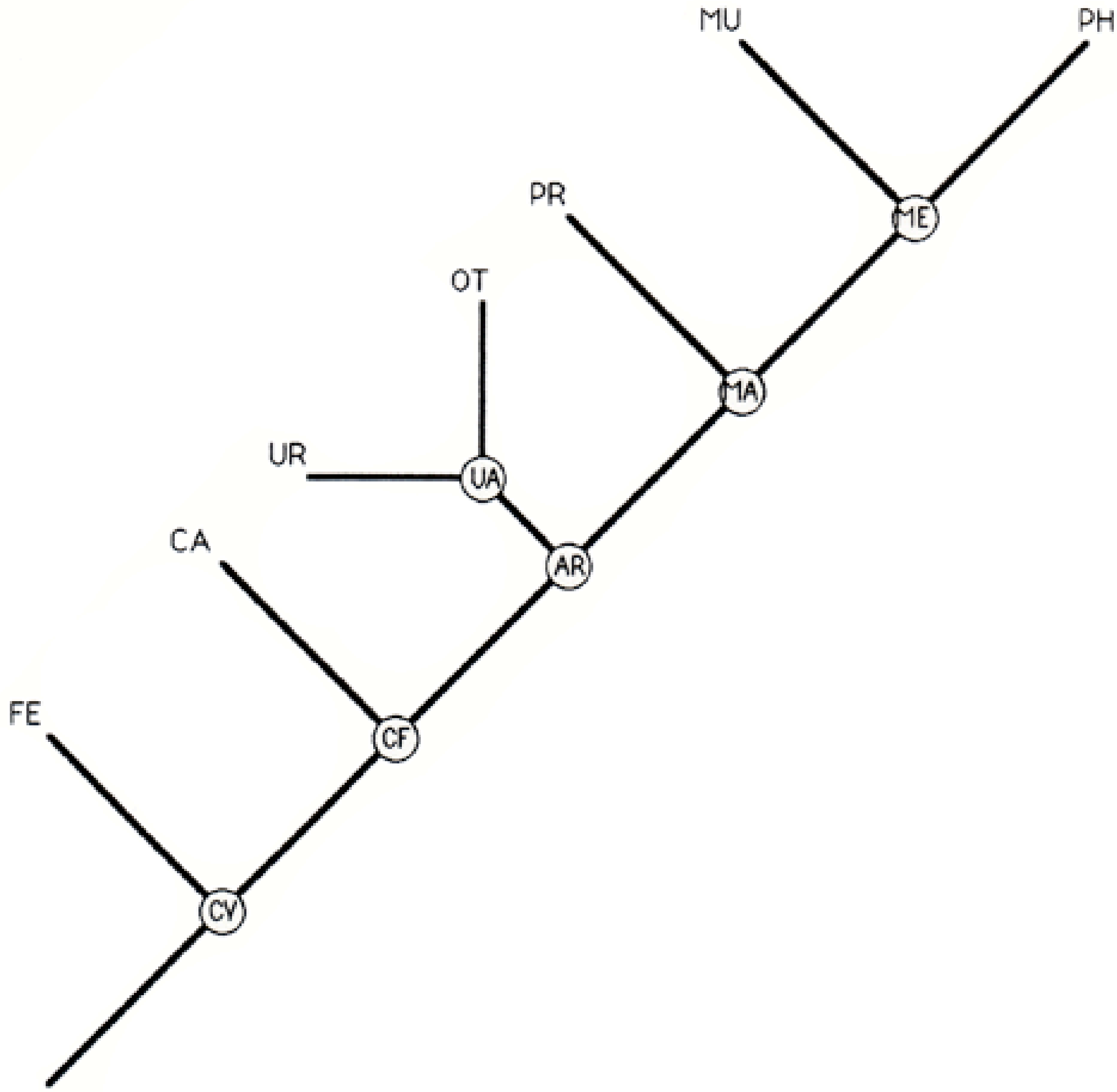

FIG. 6. - Simplified cladogram adapted from Tedford (1976) expressing the hypothesis of pinniped polyphyly in which a mustelid origin for the Phocidae is asserted. Tedford's (1976) suggested classification of the order Carnivora based upon the phyletic sequence expressed in this cladogram is given in Table 1. Node abbreviations are also defined in Table 1.

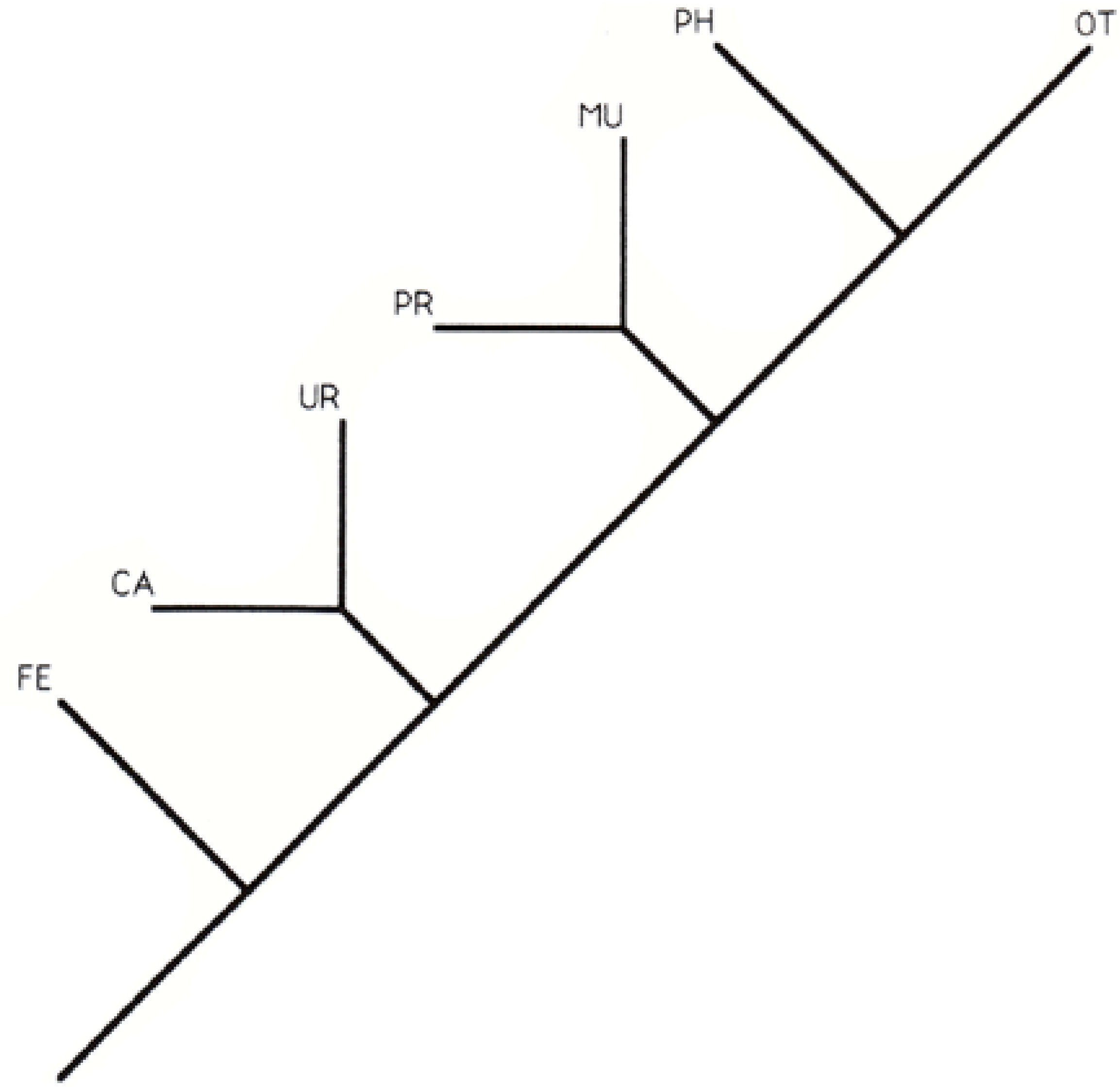

FIG. 7. - Cladogram of the carnivore branch of Miyamoto and Goodman's (1986) eutherian tree. Monophyly for the Pinnipedia is expressed. Topology was determined by comparisons of protein amino acid sequences as a measure of species' relative taxonomic distances.

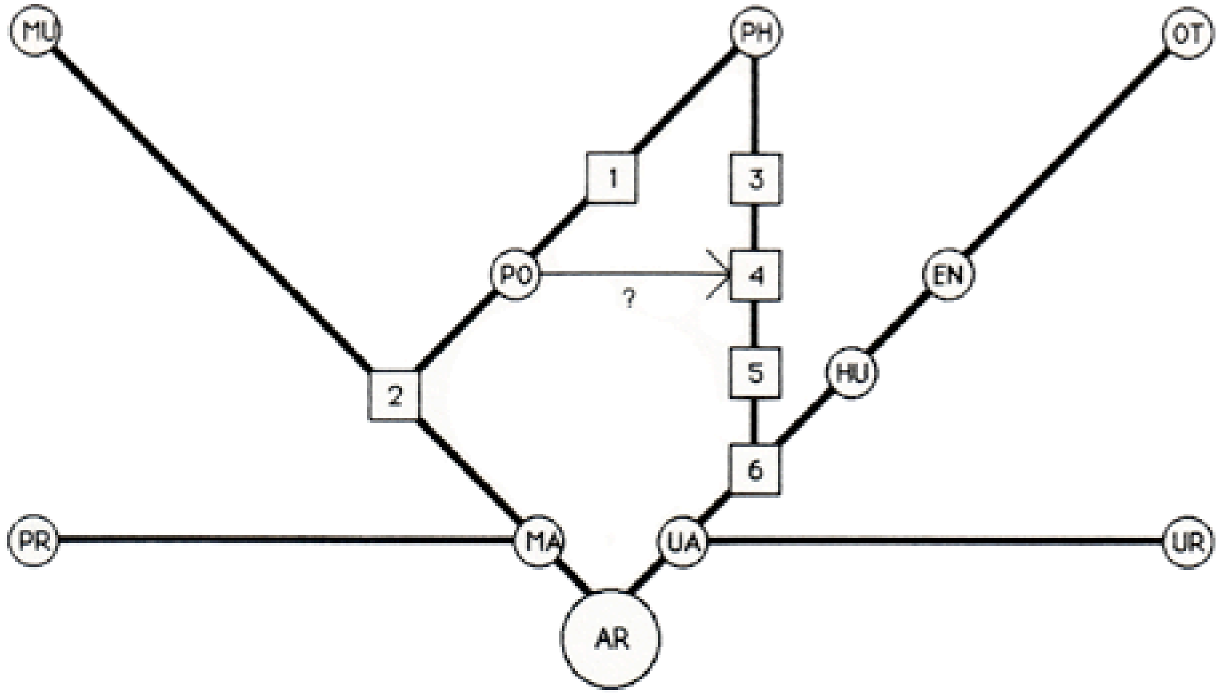

FIG. 8. - Cladogram illustrating gaps in fossil record which must be closed to determine actual phyletic relationships among arctoid carnivores and pinnipeds. Fossil gaps are represented by numbered squares. For the phocids to be derivable from the Mustelida (MA), a proto-phocid intermediate [1] between *Potamotherium* and known Miocene phocids must be found. Also, a late Eocene/early Oligocene arctoid form [2] is sought which would more firmly unite *Potamotherium* with proto-mustelid stock. To demonstrate a phocid origin from the Ursida (UA), an ursid proto-phocid [3] and a North Atlantic form [4] contemporary with *Enaliarctos* are needed. In addition, at least one Eocene or Oligocene proto-ursid form ([5], or preferably [6]) must be found in order to unite the phocid and otariid lines in a monophyletic relationship. If *Potamotherium* does share a close genetic relationship with *Enaliarctos* (*sensu* Mitchell and Tedford, 1973), *Potamotherium* may be eligible to fill gap [4] (indicated by arrow). This shift alone, however, does not necessarily reduce the number of fossil gaps needed to be closed, nor does it increase parsimony in any currently-advanced hypothesis of relationships among early arctoids (see text).

Node abbreviations are defined in Table 1. (HU) represents the Oligocene proto-ursid subfamily Hemicyoninae. The position of *Potamotherium* (PO) follows suggestions by Tedford (1976). The positions of the pendant nodes for the Procyonoidea and Ursoidea are not intended to represent temporally accurate branching events.

FIG. 9. - Hypothetical cladogram generated from immunological distance data of Sarich (1969b). This cladogram also represents the consensus condition of pinniped monophyly, incorporating results from Leone and Wiens (1956), Sarich (1969b), and Miyamoto and Goodman (1986), as resolved by the enaliarctid-otariid fossil series (Mitchell and Tedford, 1976) (see text). A suggested classification of the order Carnivora based upon the phyletic sequence expressed in this cladogram is described in Table 4. Node abbreviations are also defined in Table 4.