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SKELETAL MORPHOLOGY AND LOCOMOTOR CAPABILITIES OF THE ARCHAIC PINNIPED ENALIARCTOS MEALSI

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ABSTRACT—A virtually complete skeleton of the pinniped Enaliarctos mealsi is described from the Pyramid Hill Sandstone Member of the Jewett Sand (late Oligocene or early Miocene) in central California. Skeletal evidence supports the sister group relationship of ursids and pinnipeds and the monophyly of pinnipeds. The structure of the vertebral column, especially the long transverse processes on the lumbar vertebrae and loose-fitting zygapophyses, indicates that the spine was capable of considerable flexion and extension. The limbs, modified as flippers with strongly developed bony processes and expanded areas for muscle attachment, provide evidence of their use in both aquatic and terrestrial locomotion.

INTRODUCTION

Although knowledge of fossil pinnipeds has considerably improved in recent years (see Barnes et al., 1985), for most taxa little postcranial information is available. Discovery of a nearly complete skeleton of the archaic pinniped Enaliarctos mealsi has considerably increased our understanding of the postcranial anatomy and locomotor specializations of the earliest pinnipeds (Berta et al., 1989). The skeleton of Enaliarctos exhibits a mixture of primitive characters that affirm its ursid ancestry and derived characters shared with otariids, odobenids, phocids, and their fossil allies, consistent with its phyletic position as the sister taxon of all other pinnipeds (Wyss, 1987; Berta et al., 1989). The locomotor specializations of Enaliarctos indicate capabilities for swimming, as well as terrestrial locomotion using the fore and hind flippers and the axial skeleton for propulsion. We provide here a detailed description of the skeleton of Enaliarctos and consider its phylogenetic importance and locomotory habits.

Enaliarctos mealsi was originally described by Mitchell and Tedford (1973) on the basis of two partial skulls from late Oligocene or early Miocene rocks at Pyramid Hill in central California. Additional isolated teeth were referred to this taxon and to a second species, E. mitchelli, described from the rostral portions of two skulls (Barnes, 1979), both from different outcrops at Pyramid Hill.

Traditionally, Enaliarctos has been viewed as a transitional form intermediate between ursoids and "otarioids," including otariids, odobenids, and the extinct desmatophocids (Mitchell and Tedford, 1973; Tedford, 1976; Repenning and Tedford, 1977; Barnes, 1979). Wyss (1987) and Berta et al. (1989) presented evidence to support consideration of Enaliarctos as the sister taxon to the remaining pinnipeds, including in addition to the "otarioids" the phocids, which had been allied previously with the musteloids (Tedford, 1976 and references cited therein).

Materials and Methods

The specimen described here is USNM 374272, a virtually complete skeleton of Enaliarctos mealsi found on April 15, 1975, by Douglas Emlong in late Oligocene or early Miocene rocks near Bakersfield, Kern County, California. The specimen was found in the basal part of the Pyramid Hill Sandstone Member of the Jewett Sand at Pyramid Hill. It was recovered from the field in concretionary sandstone blocks separated along weathered joints and bedding planes. The blocks were reassembled in the laboratory (using fiberglass resin, which in part filled natural molds in the matrix) and prepared by A. D. Lewis from both sides to expose the skeleton in death position. It consists of a skull and left jaw fragment, 32 vertebrae (cervical, thoracic, lumbar, sacral, and caudal), 30 ribs, 3 or more sternebrae, parts of both scapulae, right and left forelimb (right forelimb nearly complete), right and left innominate, baculum, and right and left hind limb (Barnes et al., 1985:fig. 5a; Figs. 1, 2 herein).

The skeleton was compared with terrestrial and aquatic arctoid carnivorans, including ursids (Ursus, Tremarctos, Ailuropoda), mustelids (Enhydra, Lutra), procyonids (Bassariscus, Procyon), and the fossil arctoid Potamotherium Savage, 1957, traditionally regarded as the structural intermediate between otters and phocids (Tedford, 1976). Additional comparisons were made with the fossil otariids Pithanotaria Kellogg, 1925, and Thalassoleon Repenning and Tedford, 1977, the fossil odobenid Imagotaria Mitchell, 1968,
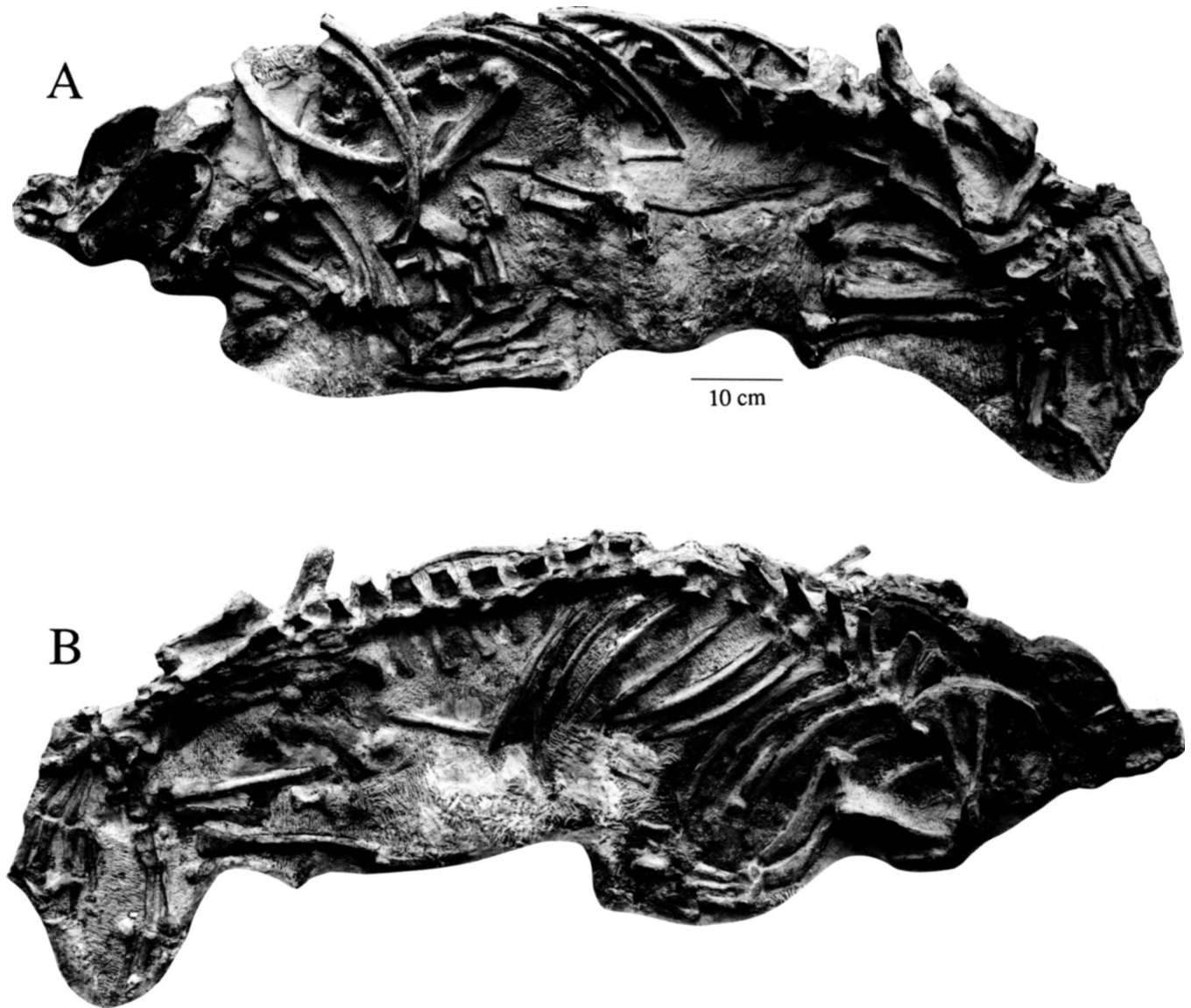
FIGURE 1. *Enaliarctos mealsi,* USNM 374272, skeleton in matrix prepared from left (**A**) and right (**B**) sides. Representative elements identified in Figure 2.

and *Allodesmus* Kellogg, 1922, previously considered a primitive "otarioid" but recently regarded as having closer affinities with odobenids and phocids (Wyss, 1987). Among Recent pinnipeds, we examined otariids (*Zalophus* and *Callorhinus*), phocids (*Monachus* and *Phoca*), and *Odobenus.*

DESCRIPTION

Skull and Jaws—This specimen closely resembles the holotype described and figured by Mitchell and Tedford (1973) and provides additional information on the morphology of the rostrum. The dorsal side of the skull is fairly well preserved, whereas the ventral

side is represented largely by a fiberglass resin cast of the natural mold. All cranial sutures are fused, indicating that the animal was an adult. The skull is broad and low with large orbits, a narrow interorbital region, and a well-developed sagittal crest (Fig. 2). The condylobasal length of the specimen is 223 mm, slightly larger than the holotype.

The rostrum is short and broad. On the snout anterior to the orbital rim are a pair of deep nasolabialis fossae for insertion of snout muscles (M. quadratus labii). The narial opening is wide, low, and ovoid in anterior view, a feature that distinguishes *Enaliarctos mealsi* from *E. mitchelli* (Barnes, 1979:fig. 16). Supraorbital ridges are weakly developed. The sagittal
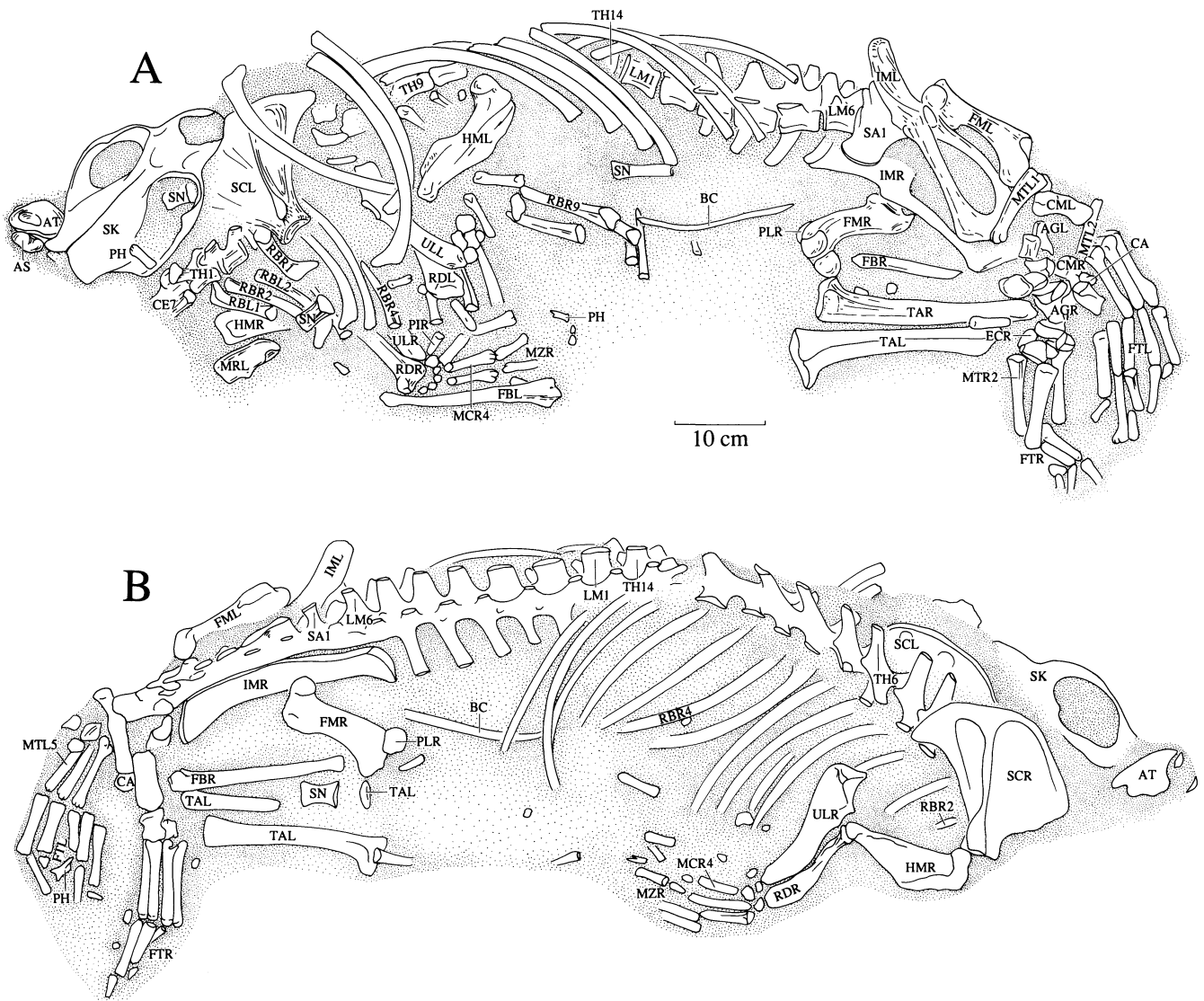
FIGURE 2. *Enaliarctos mealsi,* USNM 374272, diagrammatic representation of skeleton in left (**A**) and right (**B**) lateral aspects, for comparison with Figure 1. Abbreviations: **AG**, astragalus; **AS**, axis; **AT**, atlas; **BC**, baculum; **CA**, caudal vertebra; **CB**, cuboid; **CE**, cervical vertebra; **CM**, calcaneum; **EC**, ectocuneiform; **FB**, fibula; **FM**, femur; **FT**, pes; **HM**, humerus; **IM**, innominate; **LM**, lumbar vertebra; **MC**, metacarpal; **MR**, mandibular ramus; **MT**, metatarsal; **MZ**, manus; **PH**, phalanx; **PI**, pisiform; **PL**, patella; **RB**, rib; **RD**, radius; **SA**, sacral vertebra; **SC**, scapula; **SK**, skull; **SN**, sternum; **TA**, tibia; **TH**, thoracic vertebra; **UL**, ulna. The letters L or R designate left and right paired elements, and numbers refer to serial elements. Virtually all elements have been identified, but only representative ones are labelled.

crest begins just behind the supraorbital ridges and extends posteriorly as a low ridge to the strongly flared lambdoidal crest. The braincase is narrow anteriorly, with squared anterolateral margins becoming wider posteriorly. A pair of deep pseudosylvian sulci are obliquely positioned on the lateral walls of the braincase.

The zygomatic arches are bowed laterally and define large orbits (Fig. 2). The ventral surface of the arch, although not well preserved, appears to have been inclined anterodorsally as in the holotype of *E. mealsi* (see Mitchell and Tedford, 1973:fig. 6; Barnes, 1979:

15). The narrow anterior tip of the zygomatic process of the squamosal contacts the base of the postorbital process of the jugal in a simple splint-like arrangement. The orbital wall is not intact in this specimen; the presence of a lacrimal foramen was noted on the holotype (Mitchell and Tedford, 1973:220).

The ventral side of the skull is poorly preserved. Small posterior palatine processes of the maxilla extend a short distance behind the toothrow. A right lateral incisor, broken near the crown, and a left P^3 are preserved. The premolar is long and medially expanded. It consists of a single central cusp with a strong

lingual cingulum. Although the basicranial region is incomplete, notable is the flask-shaped left tympanic bulla that is slightly inflated medially.

A fragment of the left lower jaw preserves a relatively large, circular canine alveolus and a very fragmentary P_2. The ramus is shallow and robust with a blunt, rounded symphyseal margin.

Vertebrae—The cervical vertebrae are fragmentary. The atlas is represented by the right wing-like transverse process preserved ventrally. A distinct alar notch is developed at the base of the transverse process, a feature *Enaliarctos* shares with most other arctoids (except ursids). A deep fossa on the ventral surface opens into the transverse foramen. Only the neural spine of the axis is preserved. Probably five additional cervical vertebrae were originally present, as is true for terrestrial carnivorans and pinnipeds.

The remaining vertebrae are articulated in natural position and exposed in lateral view (Figs. 1, 2). Large, knob-like mamillary processes (=metapophyses) project dorsally from the transverse processes. Short, heavy anterior ribs are positioned just below the centra of thoracic vertebrae 2 and 4. Thoracic vertebrae 4–14 are for the most part little distorted and present a strongly arched column. The neural spines are high, becoming progressively lower and more recumbent posteriorly.

Six lumbar vertebrae are present; in this feature *Enaliarctos* resembles terrestrial arctoids. With the exception of walruses, all other pinnipeds usually possess five lumbars (King, 1983). The lumbar vertebrae have high, vertical neural spines and long, narrow transverse processes (more than $2\times$ as long as wide) (Figs. 1, 2). The transverse processes are anteriorly directed as in other arctoids (except ursids, where they are transversely oriented) (Davis, 1964:81). Another feature of these vertebrae is the presence of large, loose-fitting zygapophyses (Figs. 1, 2).

The sacrum is composed of three well-fused vertebrae, with the transverse processes fused into a single lateral plate. Sacral vertebrae 2 and 3 have fused neural spines.

Four articulated caudal vertebrae are exposed, and two isolated caudals are positioned near the right pes. Judging from the degree of development of the pre- and post-zygapophyses and ridge-like transverse processes on these vertebrae, probably two or three additional caudals are missing.

Ribs and Sternum—A complete series of ribs, numbering 28, is represented. With the exception of two short, stout anterior ribs, the remainder are long with relatively large vertebral ends. The large capitulum and tubercle are separated by a well-developed neck (Fig. 2).

Three sternebrae are preserved, only one of which is near natural position. These elements are short and broad with rugose articular surfaces.

Scapula—Both scapulae are preserved laterally, although much of the left scapula is represented as a fiberglass cast from the natural mold. In overall shape this element is similar to that in otariids with a supraspinous fossa that is nearly twice as large as the infraspinous fossa (Howell, 1929) (Figs. 2, 3). The scapula resembles that of the fossil otariid *Thalassoleon,* in which the cranial and vertebral borders form one long continuous arc rather than having a straight cranial border as in living otariids (Repenning and Tedford, 1977). As in modern otariids and to a lesser extent odobenids, the posterovertebral border (caudal scapular angle of English, 1977) is expanded.

The scapular spine is reduced proximally, and it terminates in a large, thick, knob-like acromion process (Figs. 2, 3). The metacromion process is indistinct. In these features *Enaliarctos* is more similar to ursids (Davis, 1949, 1964) than to other arctoids. Mustelids possess a strong flange-like metacromion (Tedford, 1976; e.g., *Potamotherium* Savage, 1957:fig. 21). Poor preservation of the lateral surface of the teres process does not allow confirmation of the presence or absence of a postscapular fossa.

The coracoid process is large and hook-like and extends below the glenoid cavity.

The right forelimb is nearly complete and is preserved in articulation in natural position.

Humerus—The humerus is short and robust. The deltopectoral crest is prominent and extends from the greater tuberosity for nearly three-fourths the length of the shaft, a feature characteristic of all pinnipeds except phocines and *Leptonychotes* (Wyss, 1988b; pers. observ.) (Figs. 3, 4). The rugose margin of the crest is reflected ventrally. *Potamotherium* is the only fissiped with a comparably developed deltopectoral crest (Savage, 1957).

The head is offset posteriorly on the shaft, rather than lying nearly on top of the shaft as it is in *Ursus* and *Tremarctos* (Davis, 1964) (Figs. 3, 4). The greater tuberosity, although enlarged, differs from that of otariids and odobenids in not being elevated above the head (Figs. 3, 4). The lesser tuberosity is large and rounded and lies slightly below the level of the head.

The lateral supracondylar ridge is well developed as a wing-like extension on the posterolateral surface of the shaft. The medial epicondyle is a large subtriangular projection that sweeps in a low curve from the shaft (Fig. 4). The entepicondylar (=supracondylar) foramen is absent.

The distal articulation consists of a narrow, deep trochlea and a cylindrical capitulum. Above the trochlea is a shallow olecranon fossa, a feature characteristic of all pinnipeds and *Potamotherium* (Savage, 1957). Most terrestrial arctoids differ in having a deep olecranon fossa.

Ulna—The ulna is short, robust, and anteroposteriorly compressed, although less so than in other pinnipeds. This element differs from all other pinnipeds in having an olecranon process that is heavy and knob-like with a nearly straight posterior margin and a deeply concave lateral surface (Figs. 3, 4); in this feature it resembles ursids. Other arctoids differ in having the olecranon flattened and slenderly proportioned (e.g.,
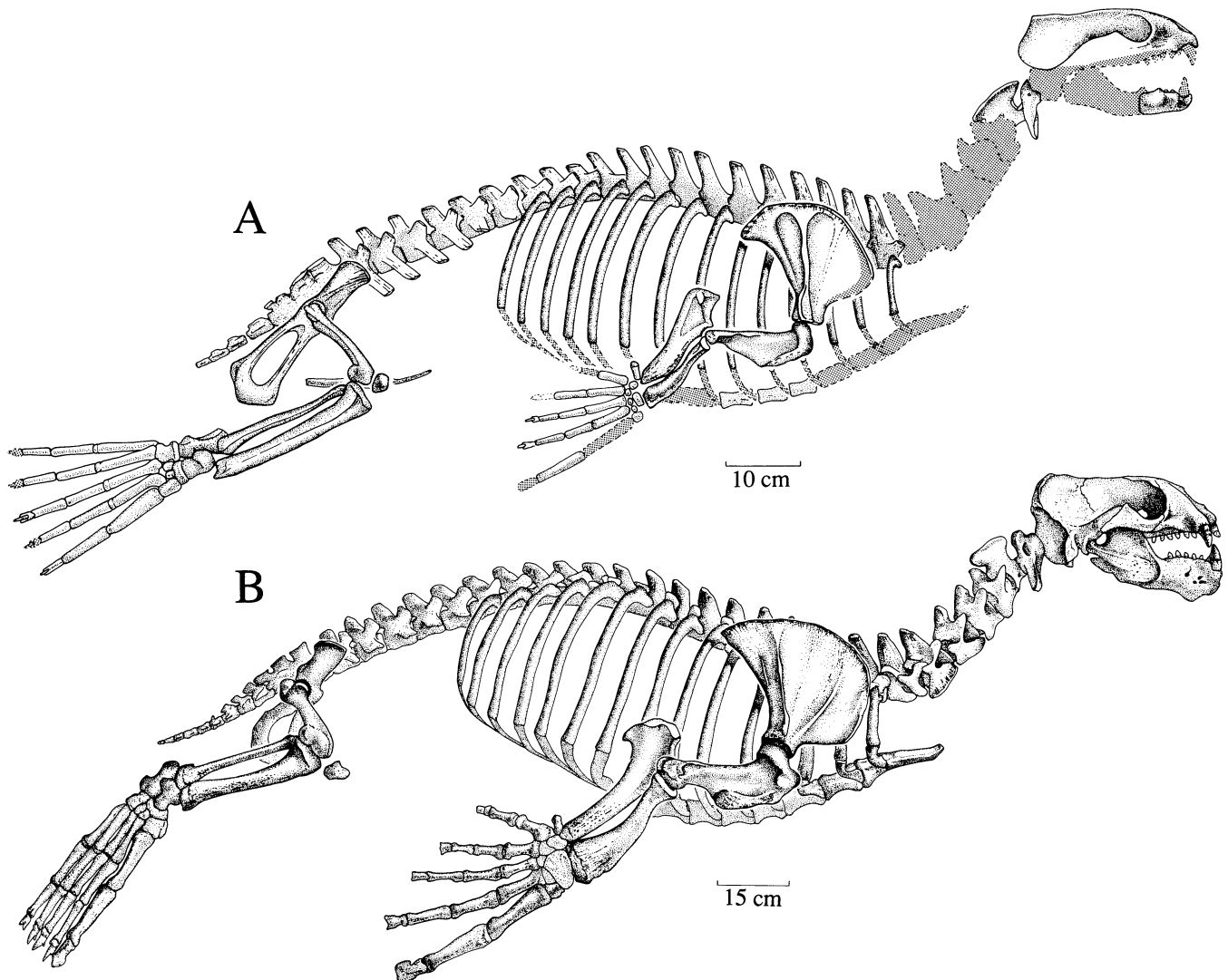
FIGURE 3. A reconstruction of *Enaliarctos mealsi* (**A**), USNM 374272 (missing elements stippled), compared with the Southern Sea Lion, *Otaria flavescens* (**B**) (redrawn from Blainville, 1839–1864). Skeletons represented at similar estimated length of vertebral column. Note: For *Enaliarctos* the thoracic vertebral count is 14 instead of 15 as illustrated by Berta et al. (1989:fig. 1).

Potamotherium Savage, 1957:fig. 23). Other pinnipeds possess a strongly compressed, posteriorly expanded, hook-like olecranon process.

At the elbow, the articular surfaces of *Enaliarctos* are more similar to those of pinnipeds than of terrestrial carnivorans. The lateral portion of the ulnar articular surface is weakly developed, and the medial portion forms an expanded trough for the radial head. In terrestrial arctoids the opposite is true, and only the lateral portion of this articular surface is developed. The coronoid process forms a prominent medial border rather than an articular surface. In addition, the anconeal process is more strongly developed in terrestrial arctoids than in pinnipeds, including *Enaliarctos*.

Along the radial border of the shaft is located a roughened area for attachment of the interosseous ligament. Distally, the shaft broadens and terminates in a peg-like styloid process.

Radius—The radius is short and heavy. The bicipital tuberosity is prominent on the short neck. The shaft is nearly straight and lacks the marked distal flattening and expansion along the radial border, typical of all other pinnipeds (Figs. 3, 4).

At the distal end, the blunt styloid process projects farther distally than in modern pinnipeds. The articular surface for the scapholunar is long anteroposteriorly and narrow transversely as in terrestrial arctoids, rather than short and wide as in other pinnipeds.

Carpus and Manus—The right manus is exposed dorsally and ventrally in articulation with the radius

and ulna (Fig. 2). The carpals are very weathered. Although the scapholunar is fragmentary, as judged from the radial articular surface, it is broad and ovate with a strongly sloped lateral portion. The pisiform is large, with a rounded distal end that diverges laterally away from the styloid process. The cuneiform with its large, rounded palmar tuberosity articulates with the styloid process of the ulna, the radius, and metacarpal V.

On the right side, the first to fifth digits are represented by metacarpals I, II, III, IV, and V, proximal phalanges I, II, III, and IV and medial phalanges II, III, and IV. Two ungual phalanges were identified. The digits are flattened but not as extensively as in extant pinnipeds.

Digits II, III, IV, and V are progressively shorter, a trait *Enaliarctos* shared with all other pinnipeds. The metacarpals of *Enaliarctos* differ from those of all other pinnipeds except phocines (Wyss, 1988b) in having relatively shorter metapodial shafts that are rounder in cross section with keeled heads and associated trochleated phalangeal articulations (Fig. 3). The phalanges are rounded in cross section with strongly trochleated interphalangeal articulations. Proximal phalanges are nearly equal in length and slightly larger than the medial phalanges. The ungual phalanges are short with a large ungual process projecting from the dorsal surface and a relatively flat, broad ventral surface, onto which were probably developed cartilaginous extensions.

Baculum—The baculum is approximately 217 mm in length, slender, and ventrally curved. The shaft flattens distally. The distal end or apex is distinctly flared but lacks development of ventral and dorsal knobs characteristic of adult otariid bacula (Morejohn, 1975; Wyss, 1987).

Pelvis—The pelvis resembles that of extant pinnipeds in having a short ilium relative to the length of the ischium and pubis (Table 1).

The ilia are blade-like and lie in a sagittal plane (Fig. 2). Their anterior portions are curved laterally. The dorsolateral surface of the ilium is delimited by a strongly developed crest that is much less prominent in other pinnipeds. A second equally well-developed crest partitions the ventrolateral surface of the ilium. On the medial surface, the iliopectineal eminence is a knob-like process that projects from the body of the ilium as in otariids (Howell, 1929).

The pubis and ischium are flat and thick and enclose a large obturator foramen. Although the innominates are separate, it is clear from their extensive articular surfaces that the pubic symphysis formed a fully ossified union; in this feature *Enaliarctos* resembles terrestrial arctoids rather than pinnipeds. The auricular surfaces of the ilia are strongly joined to the sacrum at the sacroiliac articulation.

Femur—The femora are near natural position in articulation with the pelvic girdle. The femur is short, broad, and strongly flattened. The greater trochanter is at nearly the same level as the head; it is distinctly separate from the lateral border, rather than being broadly continuous with it as in modern pinnipeds. It
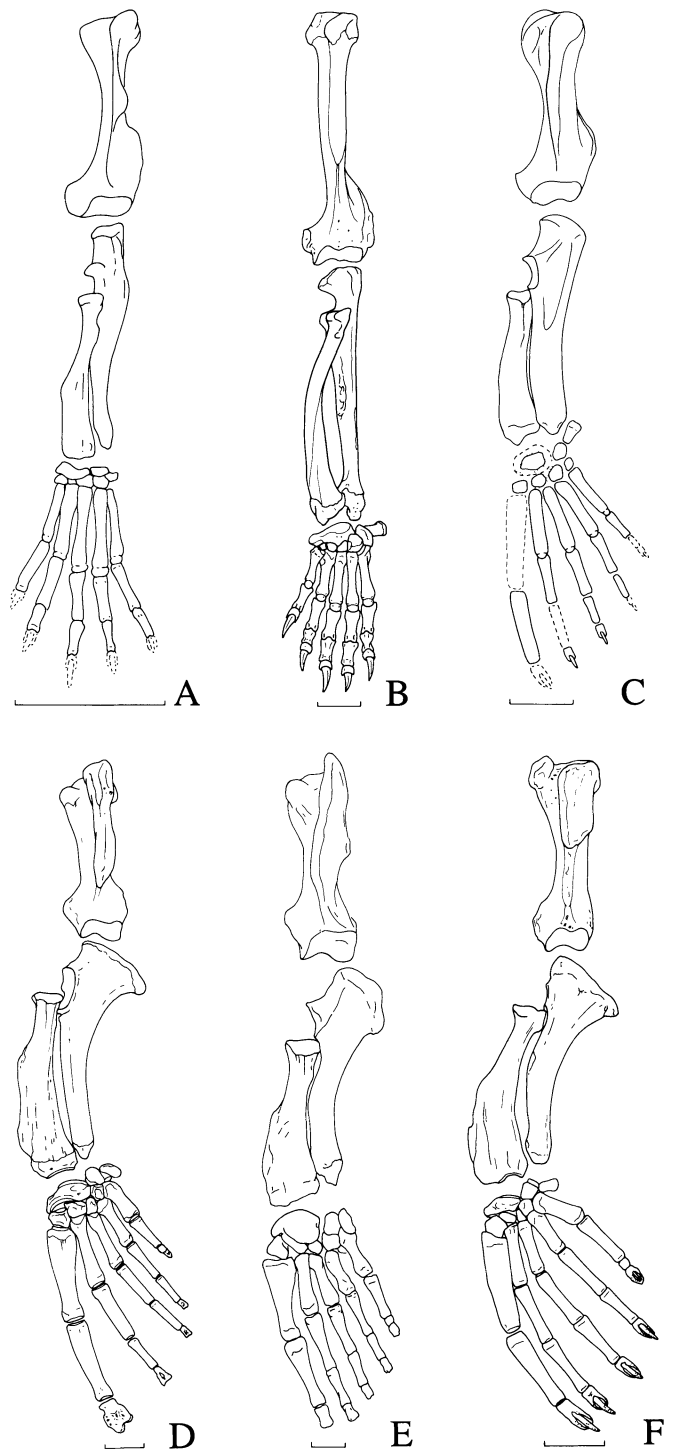

FIGURE 4.   Left forelimb of representative pinnipeds and generalized terrestrial carnivores in dorsal view. **A**, *Potamotherium valletoni* (redrawn from Savage, 1957); **B**, *Ursus americanus*; **C**, *Enaliarctos mealsi*; **D**, *Zalophus californianus*; **E**, *Odobenus rosmarus*; **F**, *Monachus tropicalis*. Scale bars = 5 cm.
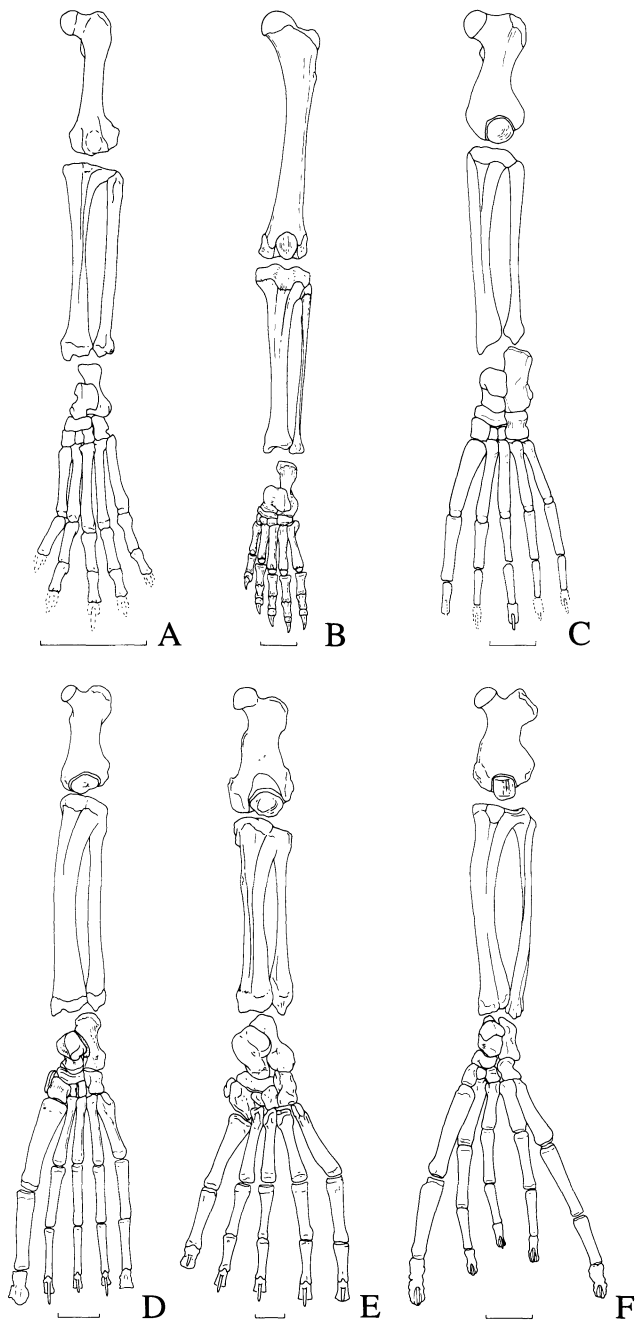
FIGURE 5. Left hind limb of representative pinnipeds and generalized terrestrial carnivores in dorsal view. **A**, *Potamotherium valletoni* (redrawn from Savage, 1957); **B**, *Ursus americanus*; **C**, *Enaliarctos mealsi*; **D**, *Zalophus californianus*; **E**, *Odobenus rosmarus*; **F**, *Monachus tropicalis*. Scale bars = 5 cm.

further differs in the development of a shallow fossa on the anterior surface, just below the greater trochanter near the lateral margin (Fig. 5).

There is a well-defined pit on the cylindrical head for the teres femoris ligament; in other pinnipeds this

pit is very reduced or absent, and the ligament does not occur (King, 1983). In other arctoids, except *Enhydra* as noted by Taylor (1914), this pit is retained.

On the posterior side, the lesser trochanter is large, broad, and medially placed; it is small in otariids and odobenids and very reduced or absent in phocids (King, 1983).

A strong ridge extends from the lesser trochanter to the greater trochanter and defines a deep trochanteric fossa similar to that seen in *Potamotherium* (Savage, 1957); this fossa is present but small in otariids and phocines but absent or vestigial in monachines (King, 1983).

The medial condyle is situated more distad than the lateral condyle, as in all pinnipeds. Coupled with this is a slight angulation of the condylar surface of the tibia.

Patella—A poorly preserved patella is positioned slightly anterior to the medial condyle of the right femur. Little detail is discernible. The element is nearly circular, and the anterior surface is relatively deep and conical, although less so than in otariids and odobenids.

Tibia—The tibia is relatively elongate, slender, and slightly bowed medially, with expanded proximal and distal ends. The tibia is separate from the fibula, rather than being fused proximally as is characteristic of living otariids and most phocids (except *Monachus schauinslandi,* Repenning and Ray, 1977) (Fig. 5). In this feature, *Enaliarctos* resembles the fossil otariid *Thalassoleon mexicanus* and *Allodesmus* (Wyss, 1988b). The post-tibial fossa (=intercondyloid fossa) forms a prominent excavation in the shaft. This fossa is shallowly developed in most terrestrial arctoids, otariids, *Odobenus,* and *Allodesmus,* and deeply developed in phocine phocids (King, 1966).

At the distal end, the medial malleolus presents a strong distal projection. A shallow groove defined by a bony ridge arises from the posterolateral surface.

Fibula—The fibula is also long and slender. The proximal end is poorly preserved. On the distal end, the lateral malleolus displays a well-defined rounded keel, the processus lateralis fibulae (Fig. 5). This feature is lacking in otariids and odobenids but is present in *Potamotherium,* ursids, and phocines. In comparison with other arctoids, this element is unique in its distal extension beyond the processus lateralis fibulae.

Tarsus and Pes—The right pes is exposed dorsally and ventrally. The calcaneum and astragalus are articulated and exposed in lateral view (Fig. 1). The calcaneal tuber is long and slender, resembling that in terrestrial arctoids. Prominently displayed on the lateral surface of the calcaneum is the shelf-like peroneal tubercle. The sustentaculum is developed into a medially projecting shelf, which lacks the secondary shelf seen in extant otariids and most fossil otariids (Berta and Demere, 1986).

The cuboid is rectangular with large, broad proximal and distal facets. The proximal convex facet articulates with the calcaneum, and the slightly concave distal

facet articulates with metatarsals IV and V. There are conspicuous notches incised into the medial and lateral margins of this element, a feature that distinguishes *Enaliarctos* from related taxa.

The navicular is anteroposteriorly deep. The astragalar fossa is ovoid and shallowly concave. The plantar process is prominent on the posterolateral margin adjacent to the cuboid facet.

The three cuneiform bones are preserved. They are relatively large, blocky elements.

The digits of the pes are better preserved than those of the manus and are for the most part in natural position; they include metatarsals, proximal phalanges I–V, median phalanges II and III, and a single ungual phalanx. As was true for the manus, the pes is modified into a paddle with digit I and V elongated, as is characteristic of all pinnipeds. The metatarsals are long with rounded cross sections, and bear keeled heads and trochleated phalangeal articulations (Fig. 5).

A single ungual phalanx is preserved; it is very similar to those of the manus, with a large bony spur projecting from the dorsal surface and a flat distal surface for attachment of cartilaginous extensions, as in living otariids, odobenids, and *Allodesmus*.

FIGURE 6.   Hypothesis of relationships for pinnipeds, based on postcranial characters (see text). Derived characters marked prime (′) designate a multistate character (1–2 in Table 2). Postulated reversals to ancestral states are underlined.

PHYLOGENETIC RELATIONSHIPS

Cladistic analysis of skeletal features of Recent and fossil pinnipeds supports recognition of *Enaliarctos* as the sister group of all other pinnipeds. These features (Tables 1, 2) are part of an ongoing study of cranioskeletal features in pinnipeds and other carnivores (Berta, in prep.). Characters were analyzed using a computer algorithm, PAUP (Swofford, 1989). Using the branch and bound option, a single most parsimonious tree was obtained with a tree length of 35 and a consistency index (C.I.) of 0.864 (Fig. 6).

Osteological and soft anatomical evidence was marshalled recently by Wyss (1987, 1988a) in support of pinniped monophyly. In the present study 14 skeletal features support monophyly of pinnipeds and serve to distinguish pinnipeds from all terrestrial arctoids. Arctoid relationships were reviewed most recently by Flynn et al. (1988). They presented two phylogenetic alternatives. In the first alternative, the pinniped clade was considered an ursid sister group whereas, in the second alternative, pinnipeds were part of an unresolved multichotomy with other arctoid families. Based on a consideration of fossil evidence, Flynn et al. (1988) suggested ursids as the most likely sister group of pinnipeds. Ursid–pinniped cranial synapomorphies they presented include: lack of muscular process on malleus, shelf-like anteromedially placed P⁴ protocone, and excavated basioccipital sulcus for inferior petrosal sinus. To this list may be added the following postcranial features: knob-like acromion process and indistinct metacromion process on the scapula, and ulna with a robust olecranon process. Employing other arctoids
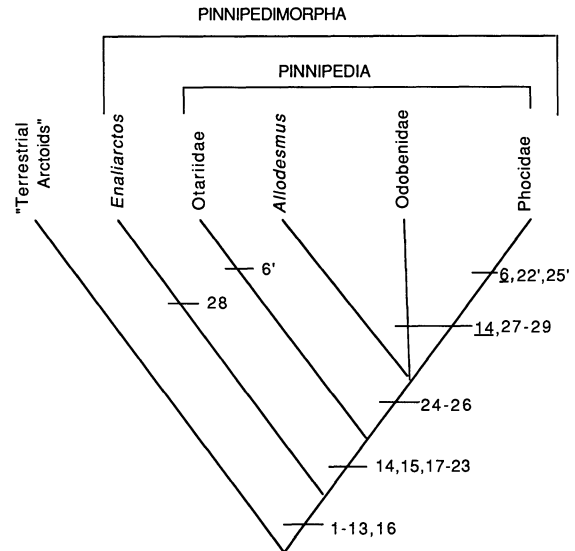
(mustelids or procyonids) as the pinniped sister group is not supported by the distribution of these characters. In the following discussion, the numbers refer to characters listed in Tables 1 and 2, where polarity assessments are summarized and a distribution of characters is provided.

1. *Scapula with expanded supraspinous fossa.* Typically in pinnipeds (except phocine phocids), the supraspinous fossa is considerably larger than the infraspinous fossa. The supraspinous fossae in ursids, procyonids, and *Potamotherium* are only slightly larger than the infraspinous fossae (Davis, 1949:fig. 70; Savage, 1957). Wyss (1988b) noted that the supraspinous fossa in phocines is reduced, thus approaching the primitive condition.

2. *Short, robust humerus.* The pinniped condition is approached but not matched by the condition in lutrines and *Potamotherium*. In terrestrial carnivores, the humerus is long and slender (see Table 4 for a comparison of limb ratios).

3. *Loss of the entepicondylar (=supracondylar) foramen.* This foramen, which transmits the median nerve and artery, is absent in all living pinnipeds except phocines (King, 1983). As noted by Wyss (1988b:18), the foramen is present in some fossil "monachines" (some species of *Monotherium* and *Homiphoca capensis*). Among ursids, an entepicondylar foramen is present in *Ailuropoda* and *Tremarctos* but otherwise absent in the living Ursidae (Davis, 1964). It is present in most Mustelidae and Procyonidae (Davis, 1964) and large in *Potamotherium* (Savage, 1957). It follows that the presence of an entepicondylar foramen represents an advanced condition at a level inside Phocidae, even

TABLE 1. Pinniped postcranial characters and polarity determinations discussed in text.

Character	Primitive	Derived
1. Scapula	supraspinous fossa slightly larger than infraspinous fossa	supraspinous fossa considerably larger
2. Humerus	long and slender	short and robust
3. Entepicondylar foramen	present	absent
4. Olecranon fossa	deep	shallow
5. Digits, length	digit III manus and pes elongated	digit I manus and digits I and V pes elongated
6. Digits, cartilaginous extensions	absent	present long, present short
7. Manus, digits I–V	not reduced	progressive decrease in size
8. Ilium	long	short
9. Femur	long and slender	extremely short, anteroposteriorly flattened
10. Femur, angle of inclination of condyles	perpendicular to shaft	medially inclined
11. Humerus, greater and lesser tuberosities	not enlarged	enlarged
12. Deltoid crest	not strongly developed	strongly developed
13. Patella	flat	conical
14. Lumbar vertebrae	6	5
15. Radius	convexly arched and not expanded	anteroposteriorly flattened and expanded distal half
16. Manus, fifth intermediate phalanx	not reduced	strongly reduced
17. Greater trochanter	knob-like	flattened
18. Olecranon process	knob-like	flattened and posteriorly expanded
19. Metapodials and phalanges	keeled heads	flattened heads
20. Pubic symphysis	fused	not fused
21. Fovea for teres femoris ligament	present, well developed	strongly reduced; absent
22. Trochanteric fossa	deep	shallow; absent
23. Fibula, processus lateralis	knob-like	reduced
24. Calcaneal tuber	long	short
25. Astragalus, calcaneal process	absent	present, slight posterior extension; large, well developed
26. Baculum	not enlarged	enlarged
27. Cervical vertebrae	larger than thoracics and lumbars; spinal canal less than one-half diameter centrum	smaller than thoracics and lumbars; spinal canal as large as centrum
28. Lumbar vertebrae, transverse processes	short	long
29. Manubrium	bony extension	cartilaginous extension
30. Tibia and fibula	not fused	fused proximally

though this character is undoubtedly primitive at a more general level, i.e., Arctoidea.

4. *Shallow olecranon fossa.* The humerus of all pinnipeds is characterized by shallow development of the olecranon fossa. The olecranon fossa of terrestrial carnivorans (except *Potamotherium*) is deep.

5. *Digit I manus and digit I and V pes elongated.* As noted by Wyss (1987:18, fig. 6; 1988a; 1989) pinnipeds elongate digit I in the manus (especially metacarpal I and the proximal phalanx) and digits I and V in the pes (especially metatarsal I and the proximal phalanx), whereas in all other carnivorans the

median digits tend to be the longest digits in the manus and pes.

6. *Development of cartilaginous extensions on the digits.* Cartilaginous extensions are cartilaginous rods distal to each digit that support an extension of the flipper border; as described by King (1983), long cartilaginous extensions occur on both the fore and hind flipper of otariids. Short cartilaginous extensions are present in walruses and *Allodesmus* (not preserved, but articulations indicate presence) (Mitchell, 1966), and still shorter extensions occur in phocids (King, 1969; Fay, pers. comm.). As Wyss (1987) suggests, it is pos-

TABLE 2. Distribution of pinniped postcranial features discussed in text. Features correspond to those listed in Table 4. Symbols: 0, primitive state; 1–2, derived states; ? not known.

	"Terrestrial Arctoids"	*Enaliarctos*	Otariidae	Odobenidae	*Allodesmus*	Phocidae
1. Scapula	0	1	1	1	1	1
2. Humerus	0	1	1	1	1	1
3. Entepicondylar foramen	0	1	1	1	1	1*
4. Olecranon fossa	0	1	1	1	1	1
5. Digits	0	1	1	1	1	1
6. Cartilaginous extensions	0	1	2	1	1	0
7. Manus, decrease in size	0	1	1	1	1	1
8. Ilium	0	1	1	1	1	1
9. Femur	0	1	1	1	1	1
10. Femur, condyles	0	1	1	1	1	1
11. Humerus, greater and lesser tuberosities	0	1	1	1	1	1
12. Deltoid crest	0	1	1	1	1	1
13. Patella	0	1	1	1	1	0
14. Lumbar vertebrae	0	0	1	0	1	1
15. Radius	0	0	1	1	1	1
16. Manus, fifth intermediate phalanx	0	?	1	1	?	1
17. Greater trochanter	0	0	1	1	1	1
18. Olecranon process	0	0	1	1	1	1
19. Metapodials and phalanges	0	0	1	1	1	1
20. Pubic symphysis	0	0	1	1	?	1
21. Fovea for teres femoris ligament	0	0	1	1	1	1
22. Trochanteric fossa	0	0	1	1	1	2*
23. Fibula, processus lateralis	0	0	1	1	1	1†
24. Calcaneal tuber	0	0	0	1	1	1
25. Astragalus, calcaneal process	0	0	0	1	1	2
26. Baculum	0	0	0	1	1	1
27. Cervical vertebrae	0	?	0	1	0	1
28. Lumbar vertebrae, transverse processes	0	1	0	1	0	1
29. Sternum, manubrium	0	?	0	1	0	1

*, "primitive" condition secondarily developed in phocines (Wyss, 1988b, 1989).
†, distribution of character uncertain.

sible that the short cartilaginous extensions of the walrus may represent the primitive pinniped condition. In otariids, with their emphasis on forelimb propulsion, these extensions have become greatly elongate, whereas in phocids, with their emphasis on hind limb propulsion, the forelimb extensions may have become secondarily reduced. Of importance in choosing between these alternatives was the discovery of ungual phalanges on both the fore and hind flipper of the *Enaliarctos* skeleton described in this study. The terminal phalanges in this specimen are marked distally by a flat articular surface presumably for a cartilaginous rod. Thus, the presence of short cartilaginous extensions, as hypothesized by Wyss, is the primitive condition based on their probable development in *Enaliarctos*. The presence of long cartilaginous extensions in otariids is here regarded as an autapomorphy, and the reduction of extensions in phocids is considered a secondary derivation.

7. *Progressive decrease in size of digits I–V in the manus.* The pinniped condition was discussed by Wyss (1988a, b). The manus of pinnipeds can be described as ectaxonic (Brown and Yalden, 1973), the digits of the pollical side being longest, and those of the ulnar side being smallest (English, 1975:110). Terrestrial carnivorans show a more symmetrically arranged mesaxonic manus, with digit III the longest, second and fifth next longest, and pollex shortest (English, 1976: 3, table 1).

8. *Short ilium.* Compared with terrestrial mammals, the pinniped pelvis has a shortened ilium and an elongated ischium and pubis (King, 1983). Tarasoff (1972:340, table 4) provided a comparison of measurements among *Canis, Lutra, Pagophilus* and *Zalophus*.

9. *Extremely short, anteroposteriorly flattened femur.* As noted by Wyss (1988a, 1989), this character is a common feature among all pinnipeds. In terrestrial carnivorans the femur is long and slender (see Table 4 for a comparison of limb ratios among pinnipeds and fissipeds).

10. *Medially inclined femoral condyles.* The angle

of inclination of the femoral condyles is the angle formed between the condyles and a line perpendicular to the shaft (see Tarasoff, 1972:table 4 for comparisons). The pinniped condition is approached but not matched by *Potamotherium*.

11. *Humerus with enlarged tuberosities.* Although the greater tuberosity is more enlarged in otariids and the lesser tuberosity more enlarged in phocids, both are very prominent in pinnipeds relative to the primitive carnivoran condition (Wyss, 1988a, 1989).

12. *Strongly developed deltopectoral crest.* The deltopectoral crest in most pinnipeds extends approximately three-fourths the length of the shaft. The strong but shorter, more abruptly ending crest in phocines is regarded by Wyss (1988b) as not representing the generalized phocid condition but is more likely a secondary derivation. The deltopectoral crest of terrestrial carnivorans has a distinct but low deltoid crest that extends over the proximal one-third to one-half of the bone (English, 1975).

13. *Conical patella.* As noted by King (1983), the patella of phocids is flatter, while that of otariids and walruses is conical. Terrestrial carnivorans display the primitive condition, a flat patella. Our observation differs from that provided by Repenning and Tedford (1977), who describe the patella of the modern walrus and the fossil odobenid *Imagotaria* as being flat.

All other pinnipeds except *Enaliarctos* form a clade here designated the Pinnipedia recognized by the following 10 skeletal synapomorphies:

14. *Five lumbar vertebrae.* In all pinnipeds except walruses, the number of lumbar vertebrae is five (King, 1983). As noted by Fay (1981), six lumbars is the usual number in walruses. Six lumbars are typically present in arctoids (Davis, 1964:table 9). As we have coded this character, it serves to diagnose the pinnipeds exclusive of walruses with an apparent reversal in walruses to the primitive condition of six lumbars. It is equally possible, however, that five lumbars developed twice, once among otariids and once among phocids plus their close fossil allies.

15. *Radius with marked anteroposterior flattening and expanded distal half.* As noted by Wyss (1989), the pinniped condition is approached slightly in *Potamotherium* (Savage, 1957). In terrestrial carnivores, the radius is convexly arched, bent in a sigmoid curve in the lateral plane, and the distal portion is unexpanded (English, 1975).

16. *Fifth intermediate phalanx of manus reduced.* All extant pinnipeds, with the exception of phocines, show the derived condition (Wyss, 1988b, 1989). As discussed by Wyss, the condition of this character in *Allodesmus* is uncertain. In *Enaliarctos* this element is not preserved.

17. *Large, broadly developed greater femoral trochanter.* As noted by Wyss (1989), this character represents a pinniped synapomorphy. Ursids and *Enaliarctos* with a knob-like greater trochanter represent the primitive condition.

18. *Olecranon process laterally flattened and posteriorly expanded.* As noted by Wyss (1988a, 1989), the pinniped condition is not seen elsewhere in the Carnivora or in other aquatic mammals.

19. *Unkeeled metapodial heads and non-trochleated, hinge-like phalangeal articulations.* The derived condition was described by Wyss (1988b, 1989) as a feature common to all pinnipeds except phocines. In contrast to the pinniped condition is the condition seen in terrestrial carnivorans and *Enaliarctos,* in which the metapodial heads are keeled and associated with trochleated phalangeal articulations.

20. *Pubic symphysis unfused.* In terrestrial carnivorans the pubic symphysis forms a fully ossified union, whereas in pinnipeds only a ligament binds adjoining bones (Savage, 1957). As judged from the rugose articular surfaces of the pubic bones in *Enaliarctos,* a fused pubic symphysis represents the primitive pinniped condition.

21. *Strong reduction or loss of fovea for teres femoris ligament.* As noted by King (1983), the position of the fovea is barely visible on the head, and the ligament does not occur in pinnipeds.

22. *Strong reduction or loss of trochanteric fossa.* According to King (1983), the trochanteric fossa is small but present in phocines and otariids, absent in monachines. But, as de Muizon (pers. comm.) has pointed out, a trochanteric fossa is present in some fossil "monachines" (i.e., *Homiphoca* and *Piscophoca*). The primitive condition, a deep trochanteric fossa, is present among ursids (Davis, 1964) and *Potamotherium* (Savage, 1957).

23. *Reduced processus lateralis of fibula.* As defined by Davis (1964:118), the lateral surface of the lateral malleolus in ursids bears a prominent elevation, processus lateralis fibulae, that separates the peroneal tendon into two groups: the long peroneal tendon lies immediately anterior to the process, while tendons of the brevis and tertius lie immediately behind it. In the primitive condition seen in ursids, this process is a sharply projecting knob-like structure. In otariids and odobenids, this process is very reduced. According to de Muizon (pers. comm.) the processus lateralis is well developed in fossil monachines and phocines; hence its presence in phocines is regarded as plesiomorphous.

The clade containing the odobenids, *Allodesmus* and phocids is united by three skeletal synapomorphies:

24. *Short calcaneal tuber.* As reported by Wyss (1987:11), "in all fissipeds when the astragalus and calcaneum are in articulation the calcaneal tuber extends far proximal to the astragalar head. This also tends to be the case in otariids, but in phocids the calcaneal tuber is shortened and projects posteriorly only as far as the process of the astragalus. Similarly, in odobenids and *Allodesmus* the calcaneal tuber is short and extends only slightly beyond the head (from Mitchell, 1966, pls. 21 and 22)."

25. *Presence of caudally directed process on the astragalus.* The phocid astragalus is characterized by a

strongly caudally directed process (=calcaneal process), over which passes the tendon of the flexor hallucis longus. In the living walrus there is at least a slight posterior extension of this element; in otariids there is not (Howell, 1930). According to Repenning and Tedford (1977), this process is enlarged in the fossil odobenid *Imagotaria* (more so than in *Odobenus*), and *Allodesmus* appears to be characterized by a similar astragalar protuberance (see Mitchell, 1966:pls. 21 and 22).

26. *Enlarged baculum.* As noted by Wyss (1987), based on data from Scheffer and Kenyon (1963) odobenids and phocids have large bacula, whereas otariids retain the primitive condition, a small baculum.

Odobenids and phocids are united by their shared possession of the following three characters:

27. *Cervical vertebrae smaller than the thoracics and lumbars, with the spinal canal nearly as large as the centrum.* According to Fay (1981:10, as cited by Wyss, 1987:8), the derived condition is seen in phocids and *Odobenus.* Otariids display the primitive condition in which the cervicals are larger than the thoracics and lumbars, and the spinal canal is less than one-half the diameter of the centrum.

28. *Lumbar vertebrae with long transverse processes.* According to Fay (1981:10, as cited by Wyss, 1987:8), in *Odobenus* as in the Phocidae the transverse processes are two to three times as long as they are wide, whereas in otariids these processes are about as long as they are wide.

29. *Manubrium elongated by cartilaginous extension.* In the derived condition, the length of the manubrium is increased by cartilage. Thus, the attachment of the first pair of ribs is near the anterior end of the manubrium in phocids and *Odobenus.* In otariids the manubrium is elongated by a bony extension anterior to the attachment of the first pair of ribs, and the attachment of the first pair of ribs is more than halfway back along the length of the manubrium.

One character appears to have been independently derived in phocids and living otariids (Wyss, 1988b):

30. *Tibia and fibula fused proximally.* The tibia and fibula are fused together at their proximal ends in living otariids. The unfused condition in the fossil otariid *Thalassoleon mexicanus* (Repenning and Tedford, 1977) suggests that this represents the primitive condition in otariids. These elements are fused in phocids (except *Monachus schauinslandi* King, 1983), rarely fused in *Odobenus* (King, 1983), and separate in *Allodesmus* (Mitchell, 1966) and *Enaliarctos* (Berta and Demere, 1986). Based on this distribution, the ancestral pinniped condition is considered to be unfused.

The hypothesis of relationships among pinnipeds presented here is very similar to that proposed by Wyss (1987). Our data indicate that phocids and odobenids are closest allies, whereas Wyss hypothesized *Allodesmus* and phocids as sister taxa. It should be noted that Wyss' analysis included cranial, soft anatomical, and behavioral characters in addition to postcranial features, whereas the present study examined only the latter. On the basis of work currently in progress, we have collapsed this node and represented odobenids, *Allodesmus,* and phocids as a tritomy (Fig. 6). This study suggests that, although *Allodesmus* is derived in many respects, it apparently retained a relatively primitive skeleton. Evaluation of these characters in terms of method of locomotion suggests that *Allodesmus* relied on fore-flipper propulsion, as do otariids, rather than hind-flipper propulsion, as is characteristic of odobenids and phocids. Most importantly, this analysis points up the fact that relationships among members of the clade including *Allodesmus* + odobenids + phocids clearly warrant additional study.

LOCOMOTOR ADAPTATIONS

Limb proportions and other indices provide a measure of the locomotory capabilities of quadrupeds. Functional limb lengths were measured as described by Hildebrand (1952) and English (1977:338, fig. 12) (Table 3). These measurements were then expressed as a percentage of total vertebral column length (excluding sacral and caudal vertebrae) (Table 4). Since the cervical series is mostly missing in *Enaliarctos,* estimates were made of its length. Data provided by Bisaillon et al. (1976) listed the relative proportion of cervical to thoracolumbar vertebrae as 24.6% in odobenids, 27.8% in phocids, and 34.3% in otariids. Among terrestrial carnivorans, both ursids and mustelids fall within this pinniped range (Davis, 1964:75, table 10). A range between both extremes (24–34%) is listed in Table 3 for *Enaliarctos* and was used to estimate cervical length in the calculation of limb length proportions relative to total vertebral column length. These values were then compared with measurements obtained by English (1975) for modern pinnipeds and terrestrial carnivorans. Limb indices for *Enaliarctos* also were calculated and compared as described above (Table 5).

From the analysis of limb proportions, it can be seen that the limbs of *Enaliarctos* are shorter than those of terrestrial carnivorans (Table 4). *Enaliarctos* differs from otariids and odobenids in having hind limbs that are proportionally longer than forelimbs; in this feature *Enaliarctos* is most similar to phocines. The long hind limbs in *Enaliarctos* indicate that the tibia had not yet shortened to the degree seen in later pinnipeds. Scapular length in *Enaliarctos* is relatively shorter than in generalized fissipeds and comparable to that of lobodontine seals.

The low scapular index in *Enaliarctos* and all pinnipeds except walruses (Table 5) indicates a scapula that is longer and wider than in terrestrial carnivorans. The length to width ratio is comparable to that found in living otariids and lobodontine phocids. The high humeroradial index of *Enaliarctos* indicates that the radius is proportionally shorter than the humerus. In most other pinnipeds radial length is equal to or slightly greater than humeral length. The low index found in

TABLE 3. Measurements (in mm) of skeleton of *Enaliarctos mealsi*, USNM 374272. Abbreviations: R, right; L, left.

Scapula, length	154.01 R
width	179.56 R
Humerus, length	146.78
Ulna, length	159.55 L
Radius, length	117.19 R
Metacarpal I, length	?
II, length	56.31, 56.02
III, length	57.45
IV, length	45.67
V, length	43.85
Proximal phalanx II, length	41.32
III, length	40.45
IV, length	43.99
V, length	?
Median phalanx II, length	41.23
III, length	27.43
IV, length	?
Ungual phalanx, length	22.4
length	22.2
Pelvis, length	261.00
acetabulum–ilium length	65.01
ischial depth	97.19
Femur, length	136.80 L
Tibia, length	230.00 L
Fibula, length	210.00 R
Metatarsal I, length	91.54, 89.08
II, length	89.73
III, length	88.57
IV, length	87.04
V, length	85.09
Proximal phalanx I, length	70.80
II, length	54.72
III, length	52.02
IV, length	54.07
V, length	66.57
Median phalanx II, length	41.88
Baculum, length	217.00
Cervical vertebrae 1–7, estimated length	236–335
Thoracic vertebrae 1–15, length	572.50
Lumbar vertebrae 1–6, length	290.77
Sacrum, length	121.67
Caudal vertebrae 1–4, length	113.64
Tip of snout–end of sacrum, estimated length	144.4–154.3

the walrus reflects proportional shortening of both the radius and the humerus in walruses, rather than the marked humeral shortening found in other pinnipeds (English, 1977). As judged from the femorohumeral index, in *Enaliarctos* the femur, although shortened, is not as extremely shortened as in otariids and *Odobenus*. The tibioradial index of *Enaliarctos* is markedly

different from that of any other pinniped or terrestrial carnivoran. The high tibioradial index of *Enaliarctos* results from a tibia that is nearly twice as long as the radius. Only *Potamotherium* approaches this condition. The low intermembral index in *Enaliarctos* suggests that the hind limbs are better developed than the forelimbs. This same tendency is seen in lobodontine and phocine phocids. In otariids and *Odobenus* forelimb length is equal to or slightly greater than hind limb length.

Among modern pinnipeds, terrestrial and aquatic locomotion are achieved differently (Backhouse, 1961; Tarasoff, 1972; English, 1976; Gordon, 1981, 1983). Otariids swim principally by the use of the forelimbs, the hind limbs and axial skeleton playing no active role. Propulsive thrust is generated by medial rotation, adduction, and retraction of the forelimbs. Medial rotation orients the flattened surface of the forelimb such that it is turned obliquely or feathered, with the anterior border forming its leading edge. This is in contrast to terrestrial carnivorans, which generate thrust primarily by driving the water directly backward or by retraction (English, 1976).

Terrestrial locomotion in otariids differs from that of fissipeds in movements of the manus and the extensive use of the anterior axial skeleton (head and neck), rather than hind limb movements (English, 1976). Phocids use their hind limbs as the major source of propulsion in the water and their forelimbs for maneuvering. Odobenids also use the hind limbs for propulsion, but they have a slightly different way of generating thrust (Gordon, 1979, 1983). On land, locomotion in these two groups is very different. The hind limbs of phocids are not involved in terrestrial locomotion, but are rather passively dragged. Movement on land is accomplished by a peculiar hitching forward of the trunk (Backhouse, 1961). In contrast to phocids, odobenids bring the hind limbs under the body in a manner similar to that of otariids. In the walrus, however, the body is supported by the venter and forward progression occurs only during the lunge phase. In otariids, the limbs support the body and are used to propel it forward (Gordon, 1981).

What then are the implications of data derived from a functional analysis of skeletal morphology and limb mechanics on the locomotor capabilities of *Enaliarctos*? The suggestion here is that the primitive pinniped pattern, as illustrated by *Enaliarctos*, most likely was one that employed the fore and hind flippers and the axial skeleton.

Lateral and vertical movement of the vertebral column during locomotion is indicated by long transverse processes on the lumbar vertebrae and large, loose-fitting zygapophyses. In phocids, the elongate transverse processes provide larger attachment points for hypaxial musculature (Mm. quadratus lumborum, longissimus thoracis, and iliocaudalis), which is correlated with horizontal movements in the posterior end of the body (Tarasoff, 1972). A similarly developed lumbar musculature is suggested for *Enaliarctos*. In analogy

TABLE 4. Length of limb bones in pinnipeds expressed as a function of total vertebral column length (data from English, 1975, and this study; see text).

	Scapula	Humerus	Radius	Femur	Tibia
Enaliarctos mealsi	14.00–12.86	13.35–12.25	10.66–9.78	12.44–11.42	20.92–19.20
Otariidae (N = 21)	19.71	16.43	16.75	10.56	21.63
Odobenus rosmarus (N = 7)	24.96	20.12	15.52	12.92	21.91
Phocinae (N = 20)	16.82	13.48	13.67	11.06	26.67
Lobodontinae (N = 10)	12.95	10.91	11.34	7.69	18.44
Allodesmus kernensis	17.18	17.95	16.57	11.77	17.16
Generalized fissipeds (N = 21)	15.40	27.54	21.56	29.72	31.59

with extant pinnipeds, the small tail surely was not used in aquatic locomotion (Howell, 1930).

Principal skeletal features seen in *Enaliarctos,* such as a large supraspinous fossa, expanded caudal angle of the scapula, and extensive deltopectoral and supracondylar crests on the humerus, suggest that the forelimbs were important in propulsion. The large supraspinous fossa provided an expanded area of attachment for the M. supraspinatus. The large acromion process indicates that the attachment of the M. deltoideus had not yet expanded from the acromion to the lateral surface of the scapula, as in all pinnipeds except walruses (English, 1977). The expanded posterovertebral border of the scapula suggests in *Enaliarctos* (as in otariids) a large area for insertion of M. serratus magnus and origin of M. teres major and posterior portion of Mm. infraspinatus, subscapularis, and deltoideus (Gordon, 1983). An expanded scapular angle in otariids is correlated with the moment arm of the M. serratus magnus, which implies a greater contribution of scapular rotators to the production of forward thrust than in terrestrial carnivorans (English, 1977).

The extensive deltopectoral crest in *Enaliarctos* provides evidence of well-developed flexors and adductors of the humerus (Howell, 1929; Gordon, 1983). Since the humeral tuberosities serve as sites for the insertion of the rotator cuff muscles (Mm. supraspinatus, infraspinatus, and subscapularis) by lying at the same level as the head, the moment arm of these muscles as humeral protractors and retractors is decreased over that seen in otariids and odobenids. Nonetheless, the range of movement of these muscles is increased, since the humeral tuberosities offer little resistance to movement (English, 1975).

The wing-like supracondylar ridge and lateral epicondyle of *Enaliarctos* resemble those of other pinnipeds and provide an expanded area of origin for carpal and digital extensor muscles, as well as forelimb flexors (Mm. brachioradialis and anconeus externus) (English, 1977). A large supracondylar ridge also is found in fossorial fissipeds and bears, especially fossorial bears (English, 1975). According to Jenkins (1973), enlargement of musculature in this area (i.e., digital flexors) acts to stabilize the elbow joint. A similar function in pinnipeds was suggested by English (1975). The large medial epicondyle in *Enaliarctos* and presumed associated musculature (as in other pinnipeds) may have increased the moment arm for these muscles (Mm. pronator teres, anconeus internus, flexor carpi radialis), which are involved in flexion and pronation of the manus (Mitchell, 1961).

The expanded hook-like olecranon process of the ulna in pinnipeds houses on the medial side the origins of Mm. flexor carpi ulnaris and flexor digitorum communis, which are separated by a bony ridge; the lateral and caudal sides provide insertion for the triceps complex (English, 1977). The lack of a hook-like olecranon

TABLE 5. Limb indices in pinnipeds and other carnivores (based on measurements from: [1]English, 1975; [2]Mitchell, 1966; [3]Savage, 1957; [4]Davis, 1964, and this study).

	Scapular (length/width)	Humeroradial	Femoro-humeral	Tibioradial	Intermembral (forelimb/hind limb)
Enaliarctos mealsi	85.77	125.25	93.20	196.26	71.97
Otariidae[1] (N = 21)	82.18	102.58	159.44	77.03	105.49
Odobenus rosmarus[1] (N = 7)	133.89	77.64	155.73	71.83	100.20
Phocinae[1] (N = 21)	94.04	100.87	122.15	50.56	72.79
Lobodontinae[1] (N = 10)	87.26	110.47	135.89	67.92	88.21
Allodesmus kernensis[2]	—	92.31	152.51	96.5	—
Generalized fissipeds[1]	133.23	78.95	94.09	67.15	80.68
Potamotherium valletoni[3]	92.85	118.64	92.85	145.76	85.43
Ursus americanus[4] (N = 2)	—	81.1	86.4	96.9	90.8
Lutra canadensis[4] (N = 3)	—	71.5	98.9	63.5	80.2
Enhydra lutris[4] (N = 2)	—	75.7	95.9	64.6	79.7

FIGURE 7. Life restoration of *Enaliarctos mealsi*. Total estimated length, snout to tail, 144–154 cm.

process in *Enaliarctos* suggests that the forearm flexors and extensors had more extensive humeral origins than in other pinnipeds and were more like those in terrestrial carnivorans (Jenkins, 1973).

The ulna of pinnipeds including *Enaliarctos* is characterized by a well-developed coronoid process that reinforces the proximal radial articulation and acts to limit rotary movements. In use of the forelimb in aquatic locomotion, rigidity of the radioulnar joints is advantageous in permitting precise orientation of the limbs with respect to the direction of body movement, and for providing a smooth limb contour over which water can flow (English, 1977).

Principal skeletal features of the hind limb in *Enaliarctos* including flattening, shortening, and broadening of the shaft of the femur and increased length of the tibia and fibula provide evidence for its use in locomotion.

The increased pubo-ischiatic length of all pinnipeds, including *Enaliarctos,* permits greater surface area for the origin of muscles that adduct the hind limb (Howell, 1929; Tarasoff, 1972). The flared ilia provide an increased area of origin of the Mm. gluteus medius and minimus and pyriformis, which act to rotate the femur laterally (Tarasoff, 1972).

The deep pit on the head of the femur for the teres femoris ligament in *Enaliarctos* resembles that of terrestrial carnivores, where it is associated with rotational movements of the femur and provides increased fixation of the head of the femur to the pelvis when an animal is on land (Tarasoff, 1972). The presence of a large lesser trochanter and a deep trochanteric fossa suggests that *Enaliarctos* was able to bring the femur forward, as well as laterally rotate, abduct, and adduct the hind limb (Howell, 1929; Nakanishi et al., 1978; Gordon, 1983).

The short femoral shaft of all pinnipeds, including *Enaliarctos,* enables the entire limb to be brought closer to the body. It also serves to reduce the length of the Mm. vastus and rectus femoris, which insert on the patella and function in extension of the hind limb, resulting in an increase in power at the expense of speed (Tarasoff, 1972). Broadening of the shaft provides an increased surface area for insertion of the adductor muscles. According to Howell (1929), three possible additional functions include lack of a need for anteroposterior thickness, need for laterally placed greater trochanter with rotary muscles, and need for a broad distal extremity for the articular condyle of the tibia.

Capabilities for extension and flexion of the foot are indicated by the elongated lower leg and a keeled lateral process of the fibula for passage of peroneal muscles. These features also increase the area for insertion of adductor muscles (Mm. gracilis, biceps femoris, semitendinosus, and semimembranosus) that hold the limb close to the body (Tarasoff, 1972).

The tarsal joints of *Enaliarctos* resemble those of *Zalophus* and terrestrial carnivorans; they confine movement in the horizontal plane and prevent lateral rotation (Tarasoff, 1972).

The restoration of *Enaliarctos* in Figure 7 in swimming pose is based on information from the skeleton of *E. mealsi* described in this report. The oldest known pinniped was a small-bodied animal with well-developed flippers. Since this animal was well adapted for aquatic life, it is depicted with a coat of short, dense fur, similar to that of smaller pinnipeds and aquatic carnivores and rodents, presumably developed as a heat conservation measure during submergence. Large pinnipeds, cetaceans, and sirenians have sparse or no hair but a protective coat of blubber (Mitchell, 1966). We have depicted the fore and hind limbs of *Enaliarc-*

tos as only partially incorporated within a loose body skin. This differs from other pinnipeds, in which there is no external appearance of the elbow or knee, as a result of increased incorporation of the limbs within the body skin (Tarasoff, 1972). Several features, notably of the hind limb, including the presence of the teres femoris ligament on the femoral head and an elongate tibia and fibula with well-developed processes for rotational movements, suggest that *Enaliarctos* was highly capable of maneuvering on land and probably spent more time near the shore than extant pinnipeds. The heterodont dentition of *Enaliarctos* argues even more strongly for close ties to the land. According to Repenning (1976), prey probably were hauled ashore to eat, since eating in the water would require swallowing prey whole, which is not suggested by the blade-like carnassials and crushing molars of *Enaliarctos*.

The entire animal is estimated at 144–154 cm in length from snout to tail. The weight of this animal (calculated as the log of body weight) is estimated at 73–88 kg, roughly the weight of a small male harbor seal (King, 1983). This figure was derived from a regression of head–body length against body weight for 36 species of extant male otariids, odobenids, and phocids (data from King, 1983). This regression produced the following equation and correlation coefficient (r):
$y = 2.855x + 3.238$ ($r = 0.92$).

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