Skeleton of the Oldest Known Pinniped, *Enaliarctos mealsi*

ANNALISA BERTA, CLAYTON E. RAY, ANDRÉ R. WYSS

A nearly complete skeleton of the archaic pinniped *Enaliarctos*, found in late Oligocene or early Miocene rocks (approximately 23 million years old) of California, provides new evidence on the origin of pinnipeds. *Enaliarctos* retains many primitive features expected in the hypothesized common ancestor of pinnipeds. Skeletal modifications seen in *Enaliarctos* document swimming adaptations and indicate that pinnipeds primitively used the axial skeleton and both fore and hindflippers as sources of propulsion. Elongate hindlimbs with prominent bony processes (reflecting powerful musculature) suggest that *Enaliarctos* was more active on land than modern pinnipeds.

DISCOVERY OF A SKELETON OF THE oldest pinniped, *Enaliarctos mealsi*, from late Oligocene or early Miocene rocks of central California records an intermediate stage in the evolution of modern pinnipeds. Initial study suggested this taxon as transitional between bear-like forms, ursoids and otarioids [including otariids (sea lions), odobenids (walruses), and extinct desmatophocids] (*1*). This interpretation was couched within the diphyletic view of pinniped origins, which held that otarioids are derived from ursids, whereas phocids (true seals) originated from mustelids (*2*). Recently, compelling osteological evidence was used to support a single, monophyletic origin of pinnipeds (*3*), a view consistent with certain cytogenetic and biomolecular evidence (*4*). *Enaliarctos*, in this latter arrangement, is hypothesized as the sister taxon of all other pinnipeds, a key position in the higher level phylogeny of the group.

Knowledge of *Enaliarctos* has previously been limited to a few partial skulls and isolated teeth (*1, 5*). The skeleton of *Enaliarctos mealsi* (*6*) collected from the Pyramid Hill sandstone member of the Jewett Sand at Pyramid Hill, near Bakersfield, California, is nearly complete (Fig. 1). *Enaliarctos* was about the size of a small male harbor seal, approximately 1.4 to 1.5 m in length and weighing 73 to 88 kg (*7, 8*).

Skeletal anatomy of *Enaliarctos* documents a stage in the transition from land to water of pinnipeds from a terrestrial carnivoran ancestry and provides evidence of swimming adaptations among the earliest pinnipeds (*1*). Modifications for a pelagic existence are apparent in the axial skeleton and limbs of *Enaliarctos*. The lumbar vertebrae show considerable range of vertical and lateral movement, as evidenced by their long transverse processes and large metapophyses for attachment of epaxial and hypaxial muscles. *Enaliarctos* is characterized, as are extant pinnipeds, by limbs modified as flippers with powerful musculature (*9–12*). The large supraspinous fossa provides an expanded area of origin for the supraspinatus muscle, important in anterior rotation of the scapula. The humerus bears enlarged tuberosities, increasing the moment arm of the rotator cuff muscles, and a strong deltopectoral crest, enabling powerful flexion and adduction of the humerus. The olecranon process of *Enaliarctos* is broad and massive but lacks the posteriorly expanded hook-shape typical of later pinnipeds. This suggests that the forearm flexors and extensors in this animal had more extensive humeral origins than later members of this group; in this feature *Enaliarctos* resembles terrestrial arctoids (*11*). The distal half of the radius of *Enaliarctos* is slightly expanded along the radial border. In the manus the digits of the radial side are longest and those of the ulnar side are shortest. The terminal phalanges are marked distally by a flat articular surface for attachment of cartilaginous extensions, a feature seen in other nonphocid pinnipeds (*7*).

Swimming adaptations are equally apparent in the pelvic girdle and hindlimb. As in all pinnipeds, the ilium of *Enaliarctos* is short and heavy; the resulting increased puboischiatic length provided a large surface area for origin of the leg adductors. Presence of a well-defined pit on the femoral head for the teres femoris ligament provided increased fixation of the head of the femur to the pelvis, which suggests that *Enaliarctos* was presumably more highly terrestrial than later pinnipeds. The tibia and fibula of *Enaliarctos* are long, which resulted in the hindlimb being longer than the forelimb; in this feature *Enaliarctos* resembles terrestrial carnivorans and phocids (*8*). The increased length of these elements provided a large surface area for insertion of muscles that extend and flex the foot as well as those holding the leg close to the body (gracilis, biceps femoris, and semitendinosus). The hind foot of *Enaliarctos*, like the fore foot, is flattened and modified into a flipper. The tarsal joints retain a primitive arrangement restricting movement in the horizontal plane and limiting lateral rotation. As on the foreflipper, flat distal terminations of the ungual phalanges indicate probable development of cartilaginous extensions.

Enaliarctos documents an early, yet complete, stage in the acquisition of features associated with aquatic locomotion in pinnipeds (*1*). The major groups of extant pinnipeds have achieved distinctive methods of both aquatic and terrestrial locomotion (*9–16*). Otariids swim principally by use of the forelimbs, the hindlimbs and axial skeleton playing no role in the production of thrust. In phocids and odobenids on the other hand, hindlimbs are the major source of propulsion in the water, forelimbs being used for maneuvering. On land, the forelimbs in otariids fully support the body and propel the animal forward; movement of the axial skeleton (especially the head and neck), also contributes to production of forward

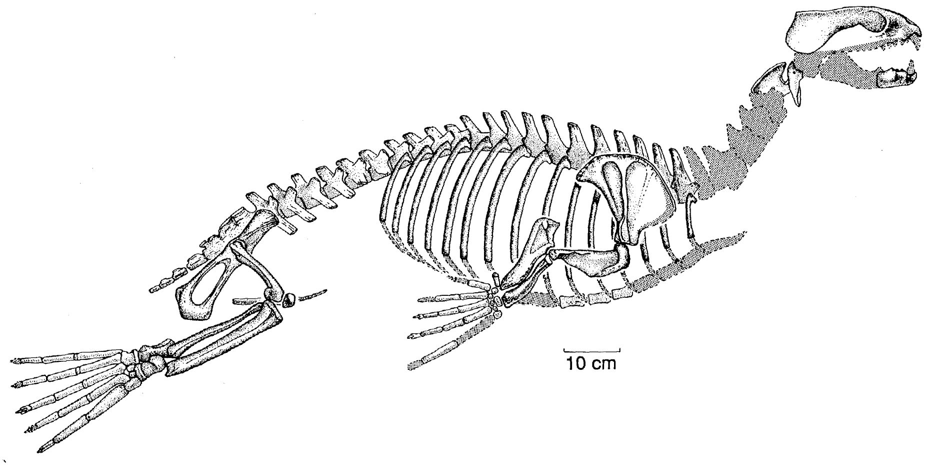

Fig. 1. Skeletal reconstruction of *Enaliarctos mealsi*, oldest known pinniped based on USNM 374272.

A. Berta, Department of Biology, San Diego State University, San Diego, CA 92182.
C. E. Ray, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.
A. R. Wyss, Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY 10024.

thrust. Phocids are incapable of turning the hindlimbs forward, and consequently their hindlimbs are not used in terrestrial locomotion but are rather passively carried forward. Movement on land by phocids is accomplished generally by undulations of the trunk. Odobenids support the body by the venter, and the limbs serve to propel the animal forward during the forward lunge phase. Movement of limbs at other times is only to position them for this lunge.

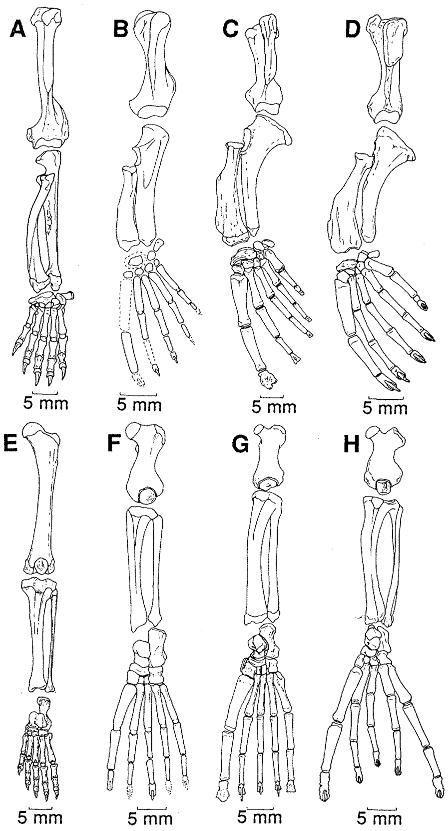

Fig. 2. Forelimb and hindlimb of representative pinnipeds and a generalized terrestrial carnivoran (**A** and **E**) *Ursus americanus*, (**B** and **F**) *Enaliarctos mealsi*, (**C** and **G**) *Zalophus californianus*, and (**D** and **H**) *Monachus tropicalis*.

The skeletal morphology of *Enaliarctos* suggests that pinnipeds primitively swam using the axial skeleton as well as both fore and hind flippers. Features suggestive of this locomotor behavior include large supraspinous fossa, well-developed deltopectoral crest, enlarged humeral tuberosites, and overall shortening of the limbs. The hindlimb of *Enaliarctos*, as in odobenids and otariids, was undoubtedly actively used in terrestrial locomotion. Presence of a large lesser trochanter and deep trochanteric fossa suggest that *Enaliarctos* was able to rotate laterally and adduct the hindlimb. Capabilities for extension and flexion of the foot are indicated by the elongated lower leg and keeled lateral process of the fibula for passage of peroneal muscles.

It may be argued that many of these skeletal features are "aquatically related" and therefore of dubious phylogenetic significance (*17*). A large number of pinniped skeletal specializations, however, do not resemble those seen in other aquatic mammals and can only be reasonably interpreted as evidence of common ancestry (*12, 18*). These specializations are particularly marked in the morphology of the limbs. Unique modifications of the pinniped forelimb include (i) development of a short, robust, humerus with enlarged tuberosities and a strong deltopectoral crest, (ii) radius with marked anteroposterior flattening and distal expansion, and (iii) manus with elongation of digit I and decrease in length of successive digits (Fig. 2). Hindlimb modifications of pinnipeds include a short ilium, an extremely short, anteroposteriorly flattened femur, and elongated digits I and V in the pes (Fig. 2). It is highly implausible to attribute these resemblances to convergence, given the differences in locomotor behavior described above.

In other respects *Enaliarctos* retains attributes that are primitive relative to those of other pinnipeds. This is depicted in a phylogenetic context in Fig. 3. Among terrestrial arctoid carnivorans it is the ursids that have received strongest support as the nearest relatives of pinnipeds. Osteological features uniquely shared by ursids and pinnipeds (including *Enaliarctos*) are a knob-like acromion process on the scapula, a lack of a muscular process on the malleus, and a shelf-like anteromedially placed P4 protocone (*8, 19*).

The following characters distinguish *Enaliarctos* from other pinnipeds. There are six lumbar vertebrae in contrast to five in most other pinnipeds. The ulna lacks the posteriorly expanded olecranon process and the radius lacks the strongly flattened and expanded distal end, features characteristic of more derived pinnipeds. The fifth intermediate phalanx of the manus is unreduced, whereas this element is markedly reduced in other pinnipeds. The femur bears a distinct pit on the head for the teres femoris ligament, a feature common also to terrestrial carnivorans. In other pinnipeds this pit is scarcely visible and the ligament is lost. The metapodial shafts are rounded in cross section, their heads are keeled, and the phalanges bear strongly trochleated articulations. Later pinnipeds (except phocine phocids) have unkeeled metapodial heads, flattened phalanges, and hinge-like phalangeal articulations (*12*). *Enaliarctos* thus presents morphologies intermediate between terrestrial arctoids and later pinnipeds, consistent with its phyletic position as the sister taxon of all other pinnipeds.

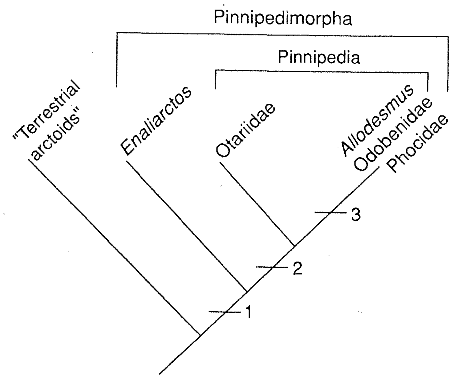

Fig. 3. A cladogram showing the relationship of *Enaliarctos* to other pinnipeds on the basis of postcranial characters (*8, 12*). The shared derived characters for each of the numbered groups. (**1**) Pinnipedimorpha (*20*): short, robust humerus with enlarged tuberosities; strongly developed deltopectoral crest; loss of entepicondylar foramen (*21*); reduction of carpals; digit I manus and digits I and V pes elongated; development of cartilaginous extensions on digits (*22*); progressive decrease in size of digits I to V on manus; short ilium; and extremely short, anteroposteriorly flattened femur and laterally inclined condyles. (**2**) Pinnipedia: five lumbar vertebrae (*7, 23*); radius with marked anteroposterior flattening and expanded distal half; fifth intermediate phalanx on manus strongly reduced (*21*); large, broadly developed greater trochanter; capitulum inclined posteriorly and laterally on humeral shaft; olecranon process laterally flattened and posteriorly expanded; unkeeled metapodial heads; nontrochleated, hinge-like phalangeal articulations; flattened phalanges; strong reduction or loss of trochanteric fossa; conical patella; and reduced processus lateralis on fibula. (**3**) *Allodesmus*, Odobenidae, and Phocidae (*24*): short calcaneal tuber; presence of caudally directed process on the astragalus (intermediately derived in odobenids and *Allodesmus*); and enlarged baculum. This arrangement is corroborated by numerous cranial features discussed in (*3*) and (*8*).

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20. The Pinnipedimorpha is a new term for the monophyletic group consisting of all pinnipeds including *Enaliarctos*.
21. These features are not present in some phocids although they are almost certainly secondary modifications; A. R. Wyss, *Am. Mus. Novit.*, no. 2924 (1988).
22. This interpretation requires acceptance of the loss of this feature in phocids.
23. This interpretation requires acceptance of a reversal of this feature among walruses.
24. The extinct Desmatophocidae include *Allodesmus* and *Desmatophoca*. Skeletal elements for *Desmatophoca* are known but undescribed; however, on the basis of cranial characters this taxon is recognized as a member of this clade.
25. We thank the late D. R. Emlong for collection of the specimen, A. D. Lewis for preparation, M. Parrish for illustrations, and R. H. Tedford for criticism and helpful comments. Support from NSF grant BSR 8607061 to A.B. is gratefully acknowledged.

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Anomalous Scattering Study of the Bi Distribution in the 2212 Superconductor: Implications for Cu Valency

P. Lee, Y. Gao, H. S. Sheu, V. Petricek,* R. Restori,
P. Coppens,† A. Darovskikh, J. C. Phillips, A. W. Sleight,
M. A. Subramanian

The distribution of the bismuth atoms over the cation sites in the 2212 Bi-Sr-Ca-Cu-O superconductor has been determined by anomalous scattering synchrotron crystallography. The analysis of reflection pairs measured at wavelengths of 0.9243 and 0.9600 angstrom shows a delocalization of the bismuth atoms over the calcium and strontium sites. The "mixed" plane between the CuO_2 layers contains 6.0(1.4) percent bismuth (where the number in brackets represents the statistical standard deviation derived from the least-squares refinement of the data), and a much smaller amount of strontium than often assumed. The strontium deficiency is charge-compensated by the creation of electron holes in the CuO_2 layer. The result supports the view that neither extra oxygen nor overlap of the bismuth 6*p* and copper 3*d* bands is needed to account for the holes, which are an essential feature of the superconductivity mechanism.

The Bi-Sr-Ca-Cu-O superconductors contain CuO_2 layers separated by a cation layer of mixed composition, as well as layers consisting of bismuth and oxygen and strontium and oxygen atoms. The mixed layer has been described as containing Sr and Ca in about equal amounts (*1–5*), though other authors have described the layer's composition as either Sr/Ca or Bi/Ca (*6*), and as containing 20% Bi (*7*). The highest Bi percentage is listed by Sastry *et al.* (*8*), who estimate that there is a substantial amount (>50%) of Bi/Sr at the Ca sites, in addition to 30% Bi at the Sr sites. The exact composition of a site in the complex crystals is hard to determine from single wavelength x-ray diffraction data because the occupancies correlate with the atomic temperature factors. But the chemical occupancy is of importance, as substitution of a bivalent atom (Ca or Sr) by a trivalent atom (Bi) changes the hole concentration in the CuO_2 planes, as does a deficiency in the occupancy of the cation layers (*9*). Cheetham *et al.* (*10*) propose that the oxidation of Cu is controlled by a depletion of the Sr content according to the general formula $Bi_2Sr_{2-x}CaCu_2O_8$.

We report here the application of x-ray anomalous scattering techniques to the study of the cation distribution in high transition temperature (T_c) superconductors. The method used is applicable to many elements and can provide crucial information not available with other techniques.

The strong variation of the Bi scattering factor in the immediate vicinity of the Bi L_{III} edge at 0.924 Å (13.42 keV) makes it possible to do Bi-specific diffraction experiments by means of tunable synchrotron radiation. The real part of the anomalous scattering factor f' varies from −21.15 at 0.924 Å (the edge) to −9.51 at 0.9600 Å (Fig. 1). The variation of the imaginary part f'' is of less importance in this almost centrosymmetric structure, which has commonly been described in the space group *Amaa*. The variation of f'' can be minimized by a judicious choice of wavelengths at the lower part of the edge and well below the edge.

With a (220) perfect Si double-crystal monochromator at the SUNY X3 beamline at the National Synchrotron Light Source an energy resolution of about 5.4 eV was obtained. Using new software (*11*) and a single crystal described previously (*2*), we have collected 154 pairs of reflections with $\sin\theta/\lambda < 0.54$ Å^{-1} and $I(\lambda_2) - I(\lambda_1) > 3\sigma(\Delta I)$, at wavelengths of 0.9243 and 0.9600 Å, where λ, θ, and *I* are the wavelength, the Bragg angle, and the intensity of the diffracted beam, respectively. The two reflections of a wavelength pair were measured sequentially to reduce the effect of instabilities in the synchrotron source. Intensities were scaled with an incident beam monitor count and the variation of two standard reflections measured at regular intervals every 30 reflections.

Data were corrected for absorption by means of an analytical integration procedure (*12*), and values of the absorption coefficient of 377.7 cm^{-1} and 369.4 cm^{-1} at the two wavelengths, respectively. These values were obtained by calculation (*13*) and subsequent interpolation for the on-edge-wavelength, using our experimental EXAFS curve (Fig. 1). X-ray scale factors at each wavelength were obtained by refining the scale factor for each of the data sets, keeping the other parameters fixed. Scattering factors for Bi at each of the wavelengths were averaged over the experimental band width. Values of f' of −18.56 and −9.51 for λ = 0.9243 and 0.9600 Å, respectively, were obtained, while f'' equals 3.96 and 4.21 at the two wavelengths.

After scaling $\Delta F = F(\lambda_2) - F(\lambda_1)$ values were calculated. As the scattering factors of the other atoms show very little variation (<0.15 electrons), the ΔF values are only dependent on the scattering of the Bi atoms.

P. Lee, Y. Gao, H. S. Sheu, V. Petricek, R. Restori, P. Coppens, Department of Chemistry and Institute on Superconductivity, State University of New York at Buffalo, Buffalo, NY 14214.
A. Darovskikh and J. C. Phillips, National Synchrotron Light Source, Brookhaven National Laboratory, Upton, NY 11973.
A. W. Sleight and M. A. Subramanian, Central Research and Development Department, E. I. du Pont de Nemours and Company, Experimental Station, Wilmington, DE 19898.

*On leave from the Institute of Physics, Czechoslovak Academy of Sciences, Na Slovance 2, 180 40 Praha 8, Czechoslovakia.
†To whom correspondence should be addressed.