Oldest Pinniped

In their report "Skeleton of the oldest known pinniped, *Enaliarctos mealsi*" (*1*), Berta, Ray, and Wyss hypothesize that *Enaliarctos* is the "sister taxon of all other pinnipeds." The describers of this species (*2*), as well as later authorities (*3, 4*), considered the Enaliarctids to be a family of the otarioid seals, whose evolution took place only in the North Pacific.

To consider the enaliarctid pinnipeds as a family of the otarioid pinnipeds required the evaluation of certain anatomical features common to all pinnipeds as being marine adaptations (for swimming, diving, underwater hearing, and maintaining body heat in a cold environment) mechanically advantageous for marine life—convergent in all marine mammals but different in methods and patterns between monophyletic lineages (*3*). In such previous evaluations, the enaliarctid seals differed from the phocoid seals in pattern, but were different from the otarioid seals only in degree. To contradict these previous interpretations Berta, Ray, and Wyss have interpreted these features as being characters exclusive to the pinnipeds and indicative of common ancestry (they have also recognized most of them as marine adaptations, but have considered only the adaptation for swimming).

Berta *et al.* state, "A large number of pinniped skeletal specializations . . . do not resemble those seen in other aquatic mammals and can only be reasonably interpreted as evidence of common ancestry." They then list these specializations: short, robust humerus with enlarged tuberosities and strong deltopectoral crest; anteroposterior flattening and distal expansion of radius; manus with elongation of digit I; short ilium; short femur; and elongate digits on the pes. These features are repeated, with a few additions such as "loss of entepicondylar foramen," as shared derived characters in the explanation of their cladogram.

The statement that these characters do not resemble those seen in other marine mammals is not correct. Even though there are only a few major lineages of marine mammals, the characters named have the following parallels: (i) the short, robust humerus of the pinnipeds is present and greatly exaggerated in the cetaceans and, in fact, is present in many aquatic vertebrates, such as the reptilian icthyosaurs (it provides greater leverage to the flipper); (ii) the enlargement of the tuberosities and the strong pectoral crest on the pinniped humerus are present and exaggerated in the Sirenia (they provide stronger insertions for the major muscles manipulating the flippers); (iii) although most marine mammals, including the otarioid seals, lack an entepicondylar foramen, the slightly adapted sea otter and all species of the phocine seals retain one, and the monachine seals have only recently lost them, as they are present on early Pliocene monachines; (iv) flattening and distal broadening of the radius is present and exaggerated in the cetaceans, as is "reduction" of the carpals; and (v) all living marine mammals have elongate digits in their flippers, although the pattern of elongation varies, as it does within the pinnipeds (contrary to the assertion of Berta and others). An elongate first digit of the manus is characteristic of the otarioid seals that evolved in the North Pacific and of some monachine phocoids, but not of the phocine phocoid seals that evolved in the North Atlantic. In many phocoid seals the first digit is shorter than the second, as in the cetaceans. In the sirenians, the fifth digit is usually the longest.

All of these skeletal modifications convert a terrestrial leg into an aquatic flipper; they are not evidence of common ancestry and in fact are developed to some degree in unrelated terrestrial mammals that use a "breaststroke motion" in digging (the mole or the badger) or in flying (the bat).

Evaluation of the characters of the hind limb is more difficult because, in marine mammals, only the pinnipeds and the sea otter have hind limbs. Nevertheless, even in the relatively primitive sea otter the femur is shorter than the tibia (intermediate in relative length between pinnipeds and terrestrial carnivores), the teres ligament is virtually lost, and the digits are elongate; these features are distinctly dissimilar to those of land carnivores and certainly would seem to be marine adaptations.

The contentions of Berta *et al.* appear to be an attempt to discredit a straw man set up 100 years ago—the statement "Pinnipeds are diphyletic." Of course they are monophyletic with respect to arctoid ("bear-like") land carnivores, but saying this does not automatically indicate that *Enaliarctos* and the Enaliarctidae have morphologic characters that are intermediate between terrestrial arctoids and all later pinnipeds. All shared derived characters of *Enaliarctos* indicate affinity with the otarioid seals of the North Pacific (*3, 4*); none indicates affinity with the phocine seals of the North Atlantic, and few indicate affinity with the monachine seals, whose fossil record indicates a late convergence on the otarioids. The common ancestor, sister taxon of all other pinnipeds, is still unrecognized, and we have no way of knowing whether it was a marine or terrestrial carnivore.

CHARLES A. REPENNING
Mail Stop 919,
U.S. Geological Survey, Box 25046,
Denver Federal Center, Denver, CO 80225

REFERENCES

1. A. Berta, C. E. Ray, A. R. Wyss, *Science* **244**, 60 (1989).
2. E. D. Mitchell, Jr., and R. H. Tedford, *Bull. Am. Mus. Nat. Hist.* **151**, 201 (1973).
3. C. A. Repenning, *Syst. Zool.* **25**, 374 (1976).
4. L. G. Barnes, *Nat. Hist. Mus. Los Angeles Co. Contrib. Sci. No. 403* (1989).

27 April 1989; accepted 2 November 1989

Response: Repenning's rejection of our interpretation of *Enaliarctos* as the sister taxon of all other pinnipeds (*1*) appears to stem from two misconceptions concerning current systematic methodology. First, his statement that "enaliarctid seals differed from the phocoid seals in pattern but from the otarioid seals only in degree" is highly subjective and ignores sweeping changes in systematic theory during the past 30 years—from an approach emphasizing a nearly literal reading of the fossil record and poorly constrained notions of character evolution to one emphasizing congruent distributions of shared derived characters.

Repenning's second objection to our placement of *Enaliarctos* stems from what he terms a problem of adaptive convergence. He argues that because a short, robust humerus, flattened broad radius, and elongate digits (among other features) are "modifications that convert a terrestrial leg into an aquatic flipper . . . they . . . are not evidence of a common [pinniped] ancestry." That it is possible for features to be functionally important yet remain phylogenetically informative is undeniable. The presence of flippers is clearly the structural consequence of an aquatic existence. This, however, in no way diminishes the phylogenetic relevance of the anatomical details of the structures in question (*2*). The presence of wings in birds, for example, is a modification that "converts" a terrestrial leg into an organ of flight. Yet the details of bird wing structure [despite their obvious relationship to life-style (and despite the fact that other vertebrates, such as bats, have developed wings)] are universally regarded as indicative of avian monophyly. "Flippers" have developed in-

dependently in a number of aquatic amniote lineages, including chelonians, squamates, crocodilians, sirenians, and cetaceans. Considered in isolation and in terms of only general descriptors, many characteristic features of the pinniped flipper occur in other dependent aquatic lineages. While it is true that a "short, robust humerus" occurs also in cetaceans and icthyosaurs, as Repenning points out, this characterization disregards the fact that pinniped humeri are otherwise highly distinctive and are not easily confused with those of the other two groups. Considered in concert, however, the constellation of derived features of the pinniped flipper as well as a larger number of cranial synapomorphies (*3*) occur nowhere else among vertebrates and indicate common heritage.

Behavioral considerations further corroborate a single, exclusive origin of pinnipeds. Otariids and phocids swim differently. Propulsion is generated almost exclusively by the forelimbs in otariids, but almost exclusively by the hindlimbs in phocids. In view of how differently these two types of limbs are employed, the striking similarity between them is curious. A hypothesis invoking common ancestry with subsequent divergence in swimming behavior is less cumbersome than any alternative that would be required by the multiple origin view supported by Repenning.

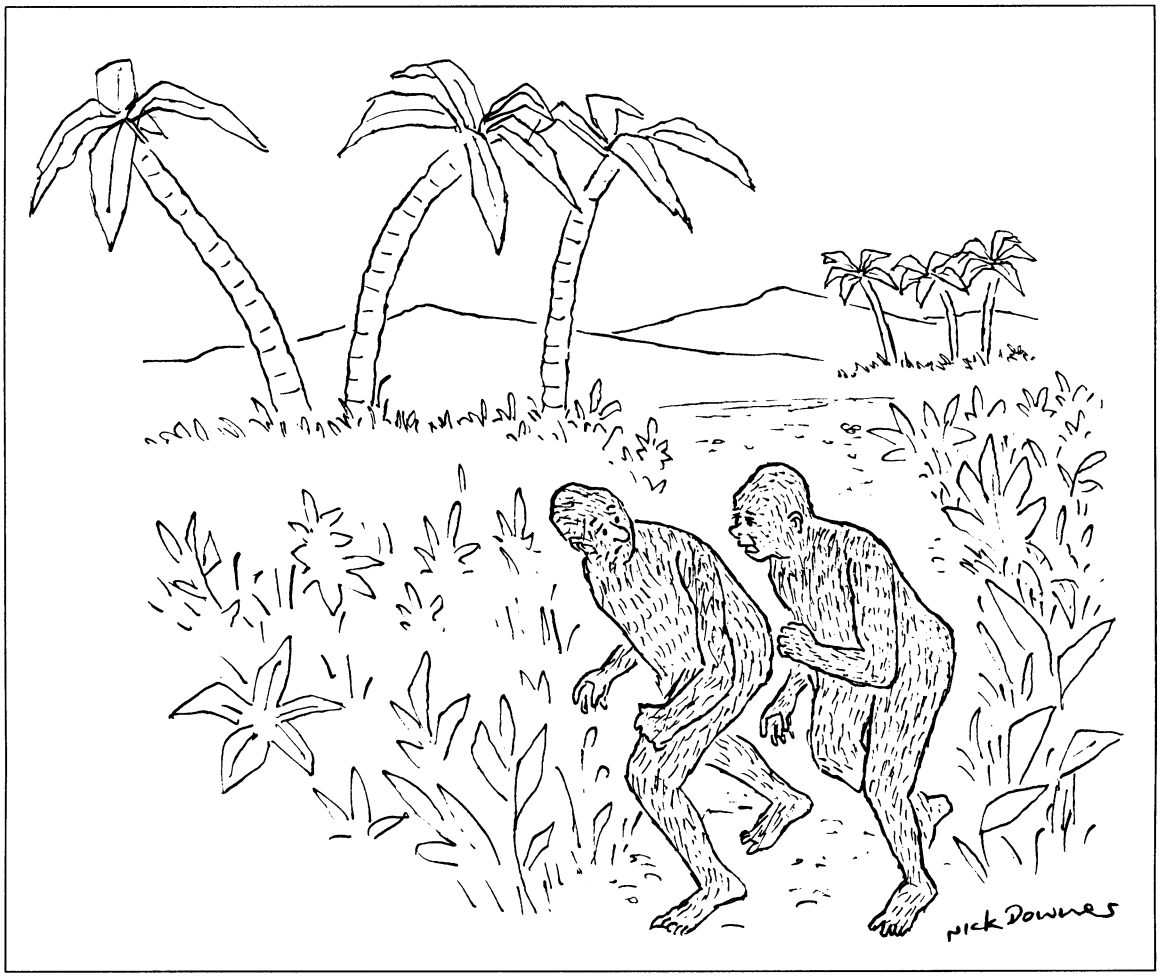
Finally, Repenning's suggestion that the double origin view of pinnipeds is a "straw man" appears to contradict his own latest publication on the subject (*4*). Contrary to his statement, few if any shared derived characters of *Enaliarctos* indicate an exclusive affinity with otarioids [a subset of pinnipeds including sea lions, fur seals (*Otariidae*), and walruses (*Odobenidae*), but not true seals (*Phocidae*)]. There is ample evidence (*1, 3*) that "otarioids" represent a taxonomic artifact that is based on the shared retention of primitive features, rather than a natural phylogenetic unit. We find it untenable that, while remaining steadfast in his espousal of the more restrictive hypothesis of *Enaliarctos* as the ancestor of otarioids, Repenning states that the identity of the sister taxon of pinnipeds is "still unrecognized."

ANNALISA BERTA
Department of Biology, San Diego State University, San Diego, CA 92182
ANDRÉ R. WYSS
Department of Geological Sciences, University of California, Santa Barbara, CA 93106

REFERENCES

1. A. Berta, C. E. Ray, A. R. Wyss, *Science* **244**, 60 (1989).
2. A. R. Wyss, *Mar. Mamm. Sci.* **5**, 4 (1989).
3. ———, *Am. Mus. Novit.* 2871 (1987); A. Berta, *Smithson. Contrib. Paleobiol.*, in press.
4. C. A. Repenning, C. E. Ray, D. Grigorescu, in *Historical Biogeography, Plate Tectonics, and the Changing Environment*, J. Gray and A. J. Boucot, Eds. (Oregon State Univ. Press, Corvallis, OR, 1979), pp. 357–369 (especially figure 1).
5. We thank J. David Archibald, C. Crumly, and R. Etheridge for comments. Supported by NSF grant BSR-8607061 to A.B.

16 January 1990; accepted 2 April 1990



" Is it me or has the Pleistocene Age dragged on forever?"

In Reply: Oldest Pinniped

Annalisa Berta and André R. Wyss

Science **248** (4954), 499-500.
DOI: 10.1126/science.248.4954.499-a