

9 November 1979 • Vol. 206 • No. 4419

\$1.50

# SCIENCE

AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE



**COVER**

Reconstruction of the largest species in the fossil family Plotopteridae, shown to scale with the outline of the largest living penguin. These giant seabirds inhabited the North Pacific about 30 million years ago. They were flightless and had paddle-like wings similar to penguins, but belong to the unrelated order Pelecaniformes. See page 688. [B. Dalzell, Rockville, Maryland]

## Fossil Counterparts of Giant Penguins from the North Pacific

**Abstract.** *New fossils of giant, flightless penguinlike birds have been found in late Oligocene and early Miocene rocks in Japan and in the state of Washington. These birds belong to the order Pelecaniformes, in the extinct family Plotopteridae, previously known by a single fragment of bone from California. Hindlimb and pelvic morphology is most similar to that of Recent aningas, but the wing is paddlelike and remarkably convergent toward penguins and flightless auks. Both the Plotopteridae and the giant penguins became extinct by the middle Miocene, possibly because of competition from seals and porpoises.*

Fossils have recently revealed an unknown avian family which includes some of the largest swimming birds yet discovered. These marine birds were flightless, wing-propelled divers resembling penguins (Sphenisciformes) in their locomotory adaptations but belonging to the unrelated order Pelecaniformes (pelicans,

cormorants, aningas, and allies). They are known only from mid-Tertiary rocks bordering the North Pacific.

Knowledge of these birds began with a single humeral end of a coracoid described from an early Miocene deposit in southern California as a new genus and species, *Plotopterum joaquinensis* (1). With exceptional insight, Howard (1) diagnosed this as a new family of Pelecaniformes, the Plotopteridae, having affinities with aningas and cormorants (Anhingidae, Phalacrocoracidae) but showing adaptations for wing-propelled diving similar to those of auks (Charadriiformes, Alcidae) and penguins. However, because of its very fragmentary nature, *Plotopterum* drew little attention.

Newly discovered fossils fully confirm Howard's original conclusions. All are late Oligocene or early Miocene (2, 3) and consist of single elements or associated partial skeletons from six localities in Japan and one partial skeleton from the state of Washington. Of the major skeletal elements, only the end of the bill remains unknown.

Coracoids associated with the specimen from Washington and with two from Japan clearly show that the new fossils are referable to the Plotopteridae. Counting *Plotopterum*, at least three genera can be recognized (3). Differences in size indicate a minimum of four species from Japan, and the Washington specimen could represent a fifth. Considerable taxonomic diversity within the family is indicated.

*Plotopterum*, by far the smallest known member of the family, was the

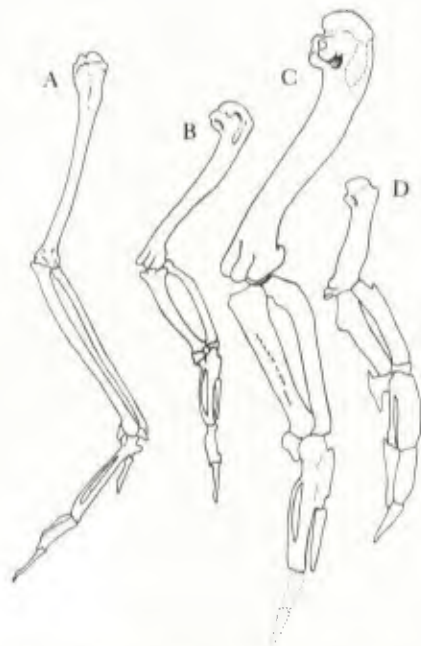
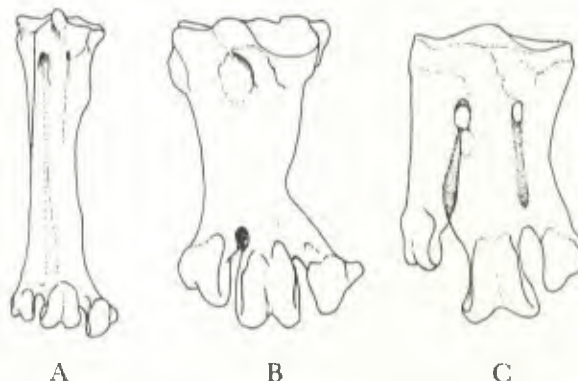


Fig. 1. Dorsal view of right wing skeleton. (A) Anhinga (Pelecaniformes); (B) great auk (Charadriiformes); (C) plotopterid (Pelecaniformes; largest Japanese species); and (D) penguin (Sphenisciformes). The similarities between the three wings on the right are due to convergence. The plotopterid (C) evolved from an ancestor with a wing like that of the anhinga (A). Drawn to scale.

Fig. 2. Anterior view of right tarsometatarsus. (A) Anhinga (Pelecaniformes); (B) plotopterid (Pelecaniformes; largest Japanese species); and (C) penguin (Sphenisciformes). Not to scale.



size of the modern cormorant *Phalacrocorax penicillatus* (1). Other species were only slightly smaller than the largest living penguins, and two species far exceeded existing penguins in size. In life, the largest Japanese plotopterid (see cover) probably measured more than 2 m from bill tip to tail tip and may have been larger (4) than any of the giant fossil penguins from the Tertiary of the Southern Hemisphere (5).

The most striking feature of the Plotopteridae is the wing, which had lost all resemblance to that in other Pelecaniformes and was modified as a rigid paddle, unsuitable for flight. The wing bones show numerous parallels with those of penguins and the flightless Alcididae (Fig. 1). The head of the humerus is heavy, nearly spherical, and penguinlike, whereas the distal end of the humerus and the elongated first metacarpal more closely resemble those of flightless auks. A row of distinct pits on the dorsal surface of the ulna is unique; in most birds the secondaries attach to raised papillae. The articulating surfaces of the wrist bones indicate that the hand was capable of very little flexion (3).

As in penguins, the scapula was greatly expanded to provide increased attachment for the muscles used to raise the wing against water, a much denser medium than air. Also as in penguins, the limb bones were extremely dense and heavy, serving to reduce buoyancy.

Despite the great modification of the wing and scapula, the remainder of the skeleton in the Plotopteridae shows close affinity with the Pelecaniformes. The carina of the sternum articulates solidly with the furcula, there is a very large acromion process of the scapula, and the skull has a deep, transverse nasofrontal hinge and lacks supraorbital impressions for salt glands. These characteristic features of the Pelecaniformes are not found in penguins or auks. The tarsometatarsus, although quite robust, is most like that of aningas and has little resemblance to that of penguins, in which, for example, the metatarsals are incompletely fused (Fig. 2).

In much of the skeleton of the Plotopteridae, the greatest similarity is to aningas, which otherwise differ considerably in being freshwater, foot-propelled diving birds with the head and neck highly modified as a spearing device. Such specializations of the head and neck are absent in the Plotopteridae, however, and the skull is more like that in the Sulidae (gannets and boobies).

Adaptations for the use of the wings rather than the feet in underwater propulsion have evolved in several groups

of birds. The penguins are so modified to this end that their ancestry is no longer readily discernible. Nevertheless, despite earlier opinions to the contrary, they are now generally regarded as having descended from volant ancestors (6). The convergent adaptations of the Plotopteridae offer significant proof that almost any group of water birds could evolve an essentially penguinlike morphology in becoming specialized for wing-propelled diving.

Storer (6) remarked on the absence in the Northern Hemisphere of wing-propelled diving birds of the size of the larger Recent penguins or their giant fossil relatives. We now know, however, that the Plotopteridae occupied such niches in the North Pacific for an undetermined period prior to the end of the early Miocene. Plotopterids are not known from the more intensively studied younger deposits around the North Pacific, and it seems likely that they became extinct at the same time as the giant penguins in the Southern Hemisphere. Simpson (5) has suggested that niches for pelagic endotherms the size of giant penguins may have been pre-empted by seals and porpoises, which underwent their greatest diversification during the Miocene. Because plotopterids occupied niches similar to those of giant penguins but are unrelated and occurred in a different hemisphere, their si-

multaneous disappearance adds considerable support to Simpson's hypothesis. In addition, the Plotopteridae provide one of the more impressive instances of convergent evolution in the fossil record.

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#### References and Notes

1. H. Howard, *Condor* 71, 68 (1969).
2. The Washington specimen is from the Pysht Formation, Twin River Group, Japanese specimens are from the Asagai, Ashiya, Hatazu, and Nishisonogi formations [see Y. Hasegawa, *Proc. 1st Int. Congr. Pac. Neogene Stratigr.* (1977), p. 340; *Kagaku Asahi* 3, 71 (1978); *Bull. Kita Kyushu Mus. Nat. Hist.* 1, 41 (1979)].
3. S. Olson, *Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci.*, in press.
4. The length of a recently collected synsacrum of *Anthropornis nordenskjöldii*, the largest or next to largest of the giant fossil penguins, is 240 mm, whereas that in the largest Japanese plotopterid is approximately 330 mm.
5. G. Simpson, in *The Biology of Penguins*, B. Stonehouse, Ed. (Macmillan, London, 1974), pp. 30-32.
6. R. Storer, *Proc. 12th Int. Ornithol. Congr.* (1960), p. 694.
7. For collecting, preparing, or providing information on specimens we thank U. Akagi, H. Endo, D. Emlong, S. Isotani, K. Isozaki, Kita Kyusyu Natural History Museum, H. Kodama, K. Matsuo, J. Mori, S. Ota, H. Otsuka, C. Ray, K. Seki, G. Sullivan, Y. Suyana, T. Suzuki, and W. Zinsmeister. Illustrations are by B. Dalzell, J. Farrand, C. Ray, and D. Steadman commented on the manuscript.

13 April 1979; revised 14 May 1979