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A NEW GENUS OF PENGUIN-LIKE PELECANIFORM BIRD FROM THE OLIGOCENE OF WASHINGTON (PELECANIFORMES: PLOTOPTERIDAE)

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ABSTRACT: New specimens from the state of Washington, USA, and from Japan show that the family Plotopteridae Howard, previously known only from a portion of a coracoid from the early Miocene of California, consists of flightless Pelecaniformes, with the wing modified as a paddle remarkably convergent towards that of penguins and flightless members of the Alcidae. The Plotopteridae is rediagnosed and a new genus and species, *Tonsala hildegardae*, is described from a partial associated skeleton from the late Oligocene of Washington. Postcranial morphology shows the Plotopteridae to be closest to the Anhingidae, although the specialized spearing apparatus of anhingas is lacking. Plotopterids are known only from the North Pacific and only from deposits of late Oligocene to early Miocene age. The apparently simultaneous disappearance of the Plotopteridae in the Northern Hemisphere and the giant penguins in the Southern Hemisphere may be correlated with the rise of seals and porpoises. Brief comments are appended on convergence in the evolution of diving birds.

A little more than ten years ago, Hildegard Howard (1969), in a brief and succinct note, introduced to science a new genus and species of bird, *Plotopterum joaquinensis*, based on the humeral end of a coracoid from an early Miocene deposit in Kern County, California. From this single specimen she concluded that *Plotopterum* should be made the type of a new family of Pelecaniformes, the Plotopteridae, related to anhingas and cormorants but with convergent similarities to penguins and alcids that suggested *Plotopterum* was a wing-propelled diver with a paddle-like forelimb. Although having no further information, Brodkorb (1971) assigned *Plotopterum* to a separate subfamily in the Phalacrocoracidae. However, subsequent discoveries of fossils from Japan and Washington have fully substantiated Dr. Howard's extraordinary perspicacity in recognizing the affinities and adaptations represented by the original fossil fragment.

Most of the new material of Plotopteridae, and also the best preserved, comes from several late Oligocene and early Miocene localities in Kyushu and Honshu, Japan, which I am studying in collaboration with Dr. Yoshikazu Hasegawa of the National Science Museum, Tokyo. We have summarized elsewhere some of our overall findings (Olson and Hasegawa 1979). The general nature of the Japanese specimens, with details of locality and stratigraphy, have been documented by Hasegawa et al. (1979). A more complete description of the Japanese material awaits preparation and study of recently discovered specimens. In the present paper I shall concentrate on the only specimen of Plotopteridae yet known from the eastern side of the Pacific, apart from the original fossil described by Howard.

The following diagnosis of the family Plotopteridae is based partially on characters ascertained from the as yet unnamed Japanese specimens, while that for the new genus is based on characters of the coracoid, the only element known for the sole taxon of the family hitherto named.

SYSTEMATICS

Order Pelecaniformes Sharpe 1891

In the following characters the Plotopteridae resemble the Pelecaniformes and differ from the Sphenisciformes and Charadriiformes: (1) absence of supraorbital furrows for salt glands; (2) deep transverse naso-frontal hinge; (3) sternum with large, pointed carina projecting far anterior to coracoidal sulci; (4) furcula articulating solidly by a large rounded facet with apex of carina (Fig. 1); (5) scapula with very large acromion projecting anteriorly well beyond coracoidal articulation; (6) coracoid with large flat furcular facet; (7) procoracoid process simple, without foramen (foramen lacking in certain alcids and incomplete in some penguins); (8) femur with proximal and distal ends proportionately broader, neck elongate; (9) internal condyle of tibiotarsus with marked medial deflection, and tendinal groove and openings wide; (10) tarsometatarsus with following combination of characters—metatarsals completely fused, hypotarsus with large medial crest, outer trochlea elevated well above others, inner trochlea elongate and at same level as middle trochlea.

Suborder Sulae Sharpe 1891

Family Plotopteridae Howard 1969

INCLUDED GENERA: *Plotopterum* Howard (1969); *Tonsala*, new genus; genus or genera unnamed (Japanese specimens).

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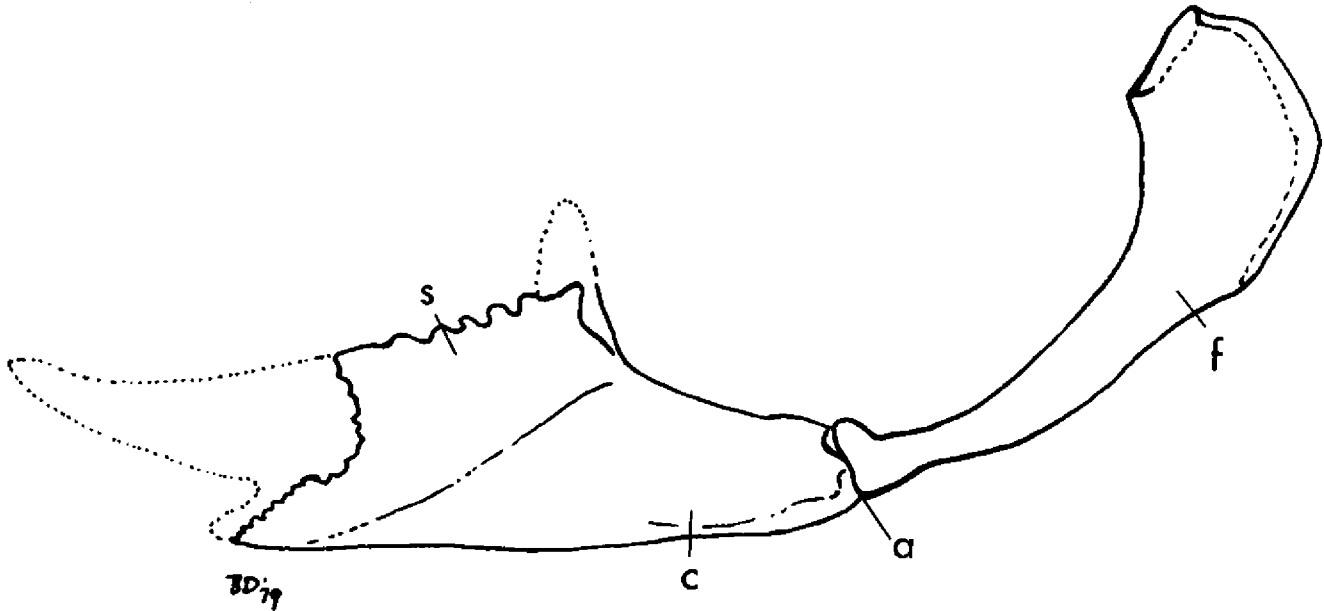


Figure 1. Right lateral view of the sternum (s) and furcula (f) in a plotopterid (specimen from Ainoshima Island, Japan), showing the far anterior projection of the carina (c) and its solid articulation (a) with the furcula, a characteristic of the Pelecaniformes.

DIAGNOSIS: Medium to extremely large, flightless, wing-propelled diving Pelecaniformes with forelimbs modified into penguin-like paddles. Humerus with shaft greatly flattened and curved, proximal end very heavy and rounded as in Spheniscidae, distal end appearing more similar to certain Alcidae. Ulna shortened, with row of distinct pits for attachment of secondaries. Radius flattened and expanded. Carpometacarpus short and flattened, with metacarpal I extending nearly half the length of the bone. Coracoid very straight and elongate; furcular facet projecting far ventrad; triosseal canal with lower part markedly convex, separated from glenoid facet by distinct longitudinal groove; procoracoid process long and acuminate. Scapula with blade thin and greatly expanded, somewhat as in Spheniscidae but acromion greatly elongated and narrow. Skull and cervical vertebrae not greatly narrowed and elongate as in Anhingidae; temporal fossae deep and post-orbital processes large as in Sulidae. Caudal vertebrae very large. Pelvis broad and shallow with anterior portions of ilia expanded as in Anhingidae and Phalacrocoracidae; acetabulum lying entirely anterior to obturator foramen, unlike other Pelecaniformes. Femur and tibiotarsus most similar to Anhingidae. Tarsometatarsus somewhat similar to Anhingidae, but much heavier, not as excavated anteriorly, and with distal foramen continuous with intertrochlear notch.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION: Known only from late Oligocene and early Miocene deposits of the North Pacific: Kyushu and Honshu in Japan; Washington and southern California, in the United States.

Tonsala new genus

TYPE SPECIES: *Tonsala hildegardae* new species.

DIAGNOSIS: Distinguished from *Plotopterum* by having coracoid with (1) glenoid facet more elongate, with margins not as distinctly raised above shaft, and (2) sternal margin not sinuate; (3) furcular facet projecting farther ventrad; (4) coracohumeral surface relatively longer and narrower.

ETYMOLOGY: Latin, *tonsa*, oar, and *ala*, wing, feminine; so named for the paddle-like development of the forelimb.

Tonsala hildegardae new species

Figures 2a-f, 3a-h, 4a-c, 5b

HOLOTYPE: Partial associated skeleton, vertebrate paleontological collections, USNM 256518. The specimen consists of the distal two-thirds of a right humerus, right ulna, proximal and distal ends of right radius, right ulnare and radiale, right carpometacarpus lacking most of the proximal end, proximal and distal (pathological) portions of left humerus and shaft of left ulna (pathological), humeral ends of right and left coracoids (both worn), right scapula, anterior portion of synsacrum, and right patella; also, several vertebrae, ribs, and unidentified bone fragments still in matrix. Collected 1 January 1977 by Douglas Emlong (field number E-77-1). The condition of the holotype suggests considerable predepositional breakage and wear of the bones, although some of the elements remained nearly in articulation. The left humerus is in two pieces, possibly due to a premortem break as the distal end is grossly pathological and so grown over with spongy bone as to be almost unrecognizable. Likewise, the left ulna appears to be atrophied. The specimen was preserved in an excessively refractory sandstone, necessitating laborious preparation by grinding.

DIAGNOSIS: As for the genus. Much larger than *Plotopterum joaquinensis*.

TYPE LOCALITY: Washington, Clallam County, Olympic Peninsula, south side of Strait of Juan de Fuca. On Disque Quadrangle, U.S. Geological Survey 7.5-minute series topographic map, 1950 edition, the locality is about 0.4 km E of first point of land extending into strait, slightly more than 3.2 km W of mouth of Lyre River, and immediately W of the mouth of Murdock Creek.

HORIZON: Late Oligocene, Pysht Formation of Twin River Group (see correlation chart in Snavely et al. 1978). Spec-

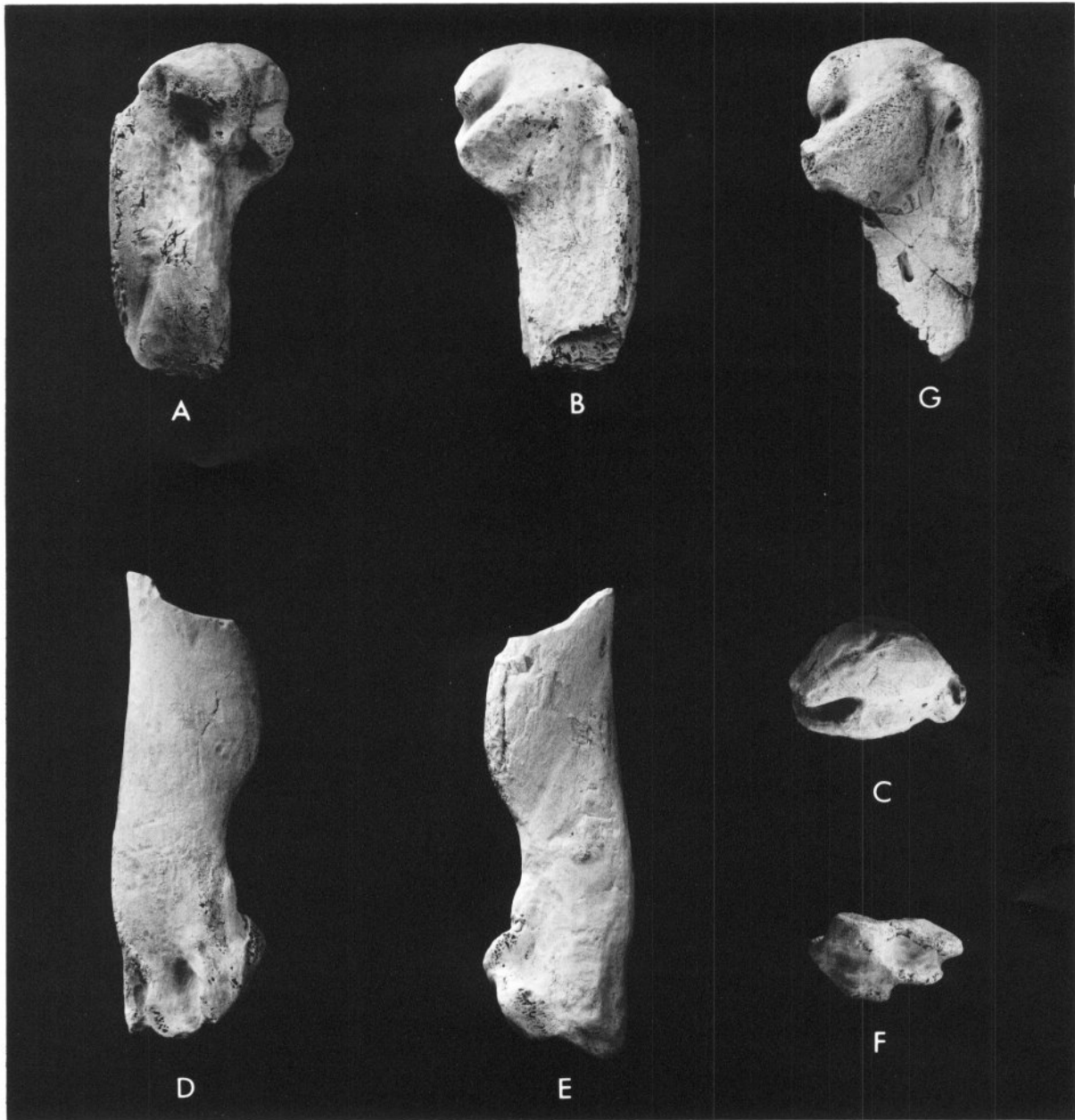


Figure 2. Humerus of *Tonsala hildegardae*, holotype (USNM 256518), and a late Eocene penguin. a, proximal end of left humerus of *Tonsala hildegardae*, external view; b, same, internal view; c, same, proximal view; d, distal portion of right humerus of *Tonsala hildegardae*, external view; e, same, internal view; f, same, distal view; g, internal view of proximal end of left humerus of a late Eocene penguin (gen. and sp. indet., USNM 244144) from Seymour Island, Antarctica, to show overall similarity in morphology to *Tonsala*. All figures $\times 1$ except g, which is about $\times \frac{1}{2}$. The specimens are actually dark, but in this and the following two figures they have been coated with ammonium chloride to enhance detail.

imen found in float about 10 m from bank. Matrix barren of microfossils (C.A. Repenning pers. comm.). The locality is in the reference section of the "upper member" of the Twin River "Formation" in the terminology of Brown and Gower (1958). It is close to or at "locality A3690" of Durham (1944) and is in his *Echinophoria rex* zone. It is also very near or at "locality f 11810" of Rau (1964), regarded as upper Zemorrian in the California benthic foraminiferal stages. The most recent data would make the age of this deposit greater than 30 million years (Addicott 1977).

ETYMOLOGY: In honor of Dr. Hildegarde Howard, in recognition of her many contributions to the study of fossil

birds, but more particularly of her correct diagnosis of an entirely new family from a single fragment of bone.

MEASUREMENTS OF HOLOTYPE (in mm): Humerus: proximal width 27.9, proximal depth 19.0, distal width (through external condyle) 22.7, distal depth (through internal condyle) 13.3, shaft width just distal to palmar crest 16.8, shaft depth at same point 7.9. Coracoid: distance from head to distal extent of glenoid facet 41.8, length of glenoid facet 24.6, breadth below head across triosseal canal 12.7. Scapula: total length (as preserved) 141.1, width at narrowest point 10.7. Ulna: length 72.5, proximal depth 18.7, proximal width 12.5. Carpometacarpus: distance from distal end of metacarpal

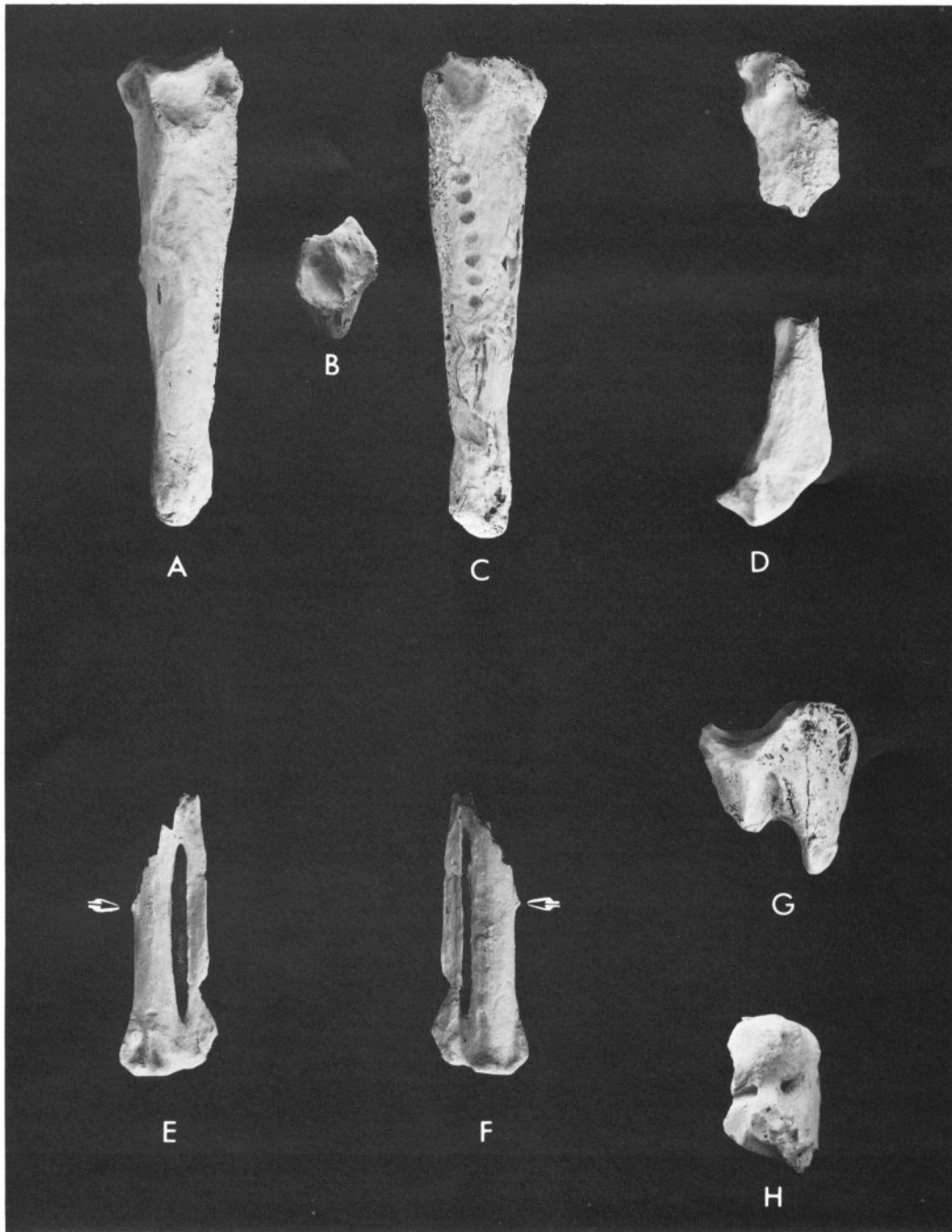


Figure 3. Distal wing elements and patella of *Tonsala hildegardae*, holotype (USNM 256518). a, right ulna, internal view (the lunate incision in the middle of the shaft is an artifact of preparation); b, same, proximal view; c, same, external view (note the pits for the attachment of the secondaries—these are obscured distally by breakage); d, right radius, external view (part of shaft missing); e, right carpometacarpus, lacking proximal end, internal view (arrow indicates distalmost portion of metacarpal I; retouched to eliminate matrix in intermetacarpal space); f, same, external view; g, right ulna, ventral view; h, right patella, anterior view. All figures $\times 1$ except g, which is $\times 2$.

I to distal end of metacarpal II 24.8, distal depth 14.4, distal width 6.0, length of intermetacarpal space 25.9. Radius: greatest diameter of proximal articulation 8.6. Radiale: greatest diameter 13.2. Patella: greatest diameter 25.5.

DESCRIPTION: Through modification for underwater locomotion, the wing elements of *Tonsala hildegardae* have lost all resemblance to those of any other peleciform birds and have become remarkably similar to those of other wing-propelled divers, i.e., penguins and auks (Sphenisciformes: Spheniscidae and Charadriiformes: Alcidae). This is most ap-

parent in the proximal end of the humerus (Fig. 2a-c), which is very heavy, with a deep, rounded head having a resemblance among known birds only to penguins. The ligamental furrow is very deep and diagonally oriented and the bicipital surface is well demarcated—in contrast to Recent penguins but quite similar to the condition seen in certain late Eocene penguins (Fig. 2g). The capital groove is better developed than in living or fossil penguins, but the tricipital fossa is considerably smaller and shallower.

The shaft of the humerus is sigmoid and very compressed

dorsoventrally, having a large anterior crest most similar to that seen in the humerus of the flightless alcids of the fossil genus *Mancalla*, but better developed (Fig. 2d, e; see Miller and Howard 1949, for illustrations of *Mancalla*). At the distal end, the tricripital grooves are very deep, as in penguins and alcids. The entepicondyle extends slightly more distad than the ridge between the tricripital grooves, *Tonsala* being intermediate in this respect between the flightless alcid *Pinguinus* and the more specialized flightless alcid *Mancalla*. The brachial depression is still fairly well developed, as in *Pinguinus* and unlike either *Mancalla* or penguins.

Overall, the humerus is more specialized for wing-propelled diving than in any birds except penguins, although the distal end is slightly less modified in this direction than in *Mancalla*.

The ulna is quite distinctive (Fig. 3a–c). The shaft is not curved, and it tapers evenly from a broad proximal end to a relatively small distal articulation. Along the dorsal surface is a row of approximately 13 deep circular pits for the attachment of secondaries. This is a unique condition in birds, and quite unlike that in penguins, in which the remiges can no longer be differentiated morphologically from other feathers of the wing. The olecranon is reduced. The internal cotyla is quite large and deep, but the external cotyla is so modified as to be convex in proximal view.

The radius of the holotype (Fig. 3d) lacks a section of shaft, so that it is not possible to determine its exact shape. It is highly distinctive in being flattened and in having both a proximal and a distal expansion on the anterior edge. This is much more modified than the radius in *Pinguinus*, but somewhat similar to, though still more specialized than, that of *Mancalla*. In the latter the radius is also expanded, but by a single crest located farther distally than the proximal crest in *Tonsala*.

The radius and ulna in *Tonsala* are not nearly as modified as in the flattened, almost unrecognizable structures of penguins, nor are they quite as foreshortened as in *Mancalla*, although in other respects they are perhaps more modified than in that genus.

The ulnare (Fig. 3g) is flattened, with a large posterior expansion, foreshadowing the even more specialized structure of penguins. The ulnar condyle is a distinct lunate incision that is on a line with the notch for the carpal trochlea, quite in contrast to typical birds in which these two articulating surfaces are nearly perpendicular to each other. This indicates that the distal portion of the wing in *Tonsala* was held parallel to the ulna and was probably capable of very little flexion.

The carpometacarpus of the holotype lacks most of the proximal end, but the distalmost part of metacarpal I is preserved (Fig. 3e, f). From this, and one Japanese specimen in which the carpometacarpus is complete, it is seen that metacarpal I was greatly elongated—to about the same extent as in *Mancalla*. The entire metacarpus is flattened and the distal end, particularly the tuberosity of metacarpal II, is much more expanded than in *Mancalla*.

The scapula of *Tonsala* has a very thin, sheetlike, greatly expanded blade (Figs. 4a, 5b), unlike that of any other birds except penguins. This is also an adaptation for wing-propelled diving; the dorsal elevators of the wing arise mainly from the scapula and are enlarged because the upstroke must be made against water and also provides propulsive force. The very long, narrow acromion in *Tonsala* is a peleciform feature, this process being small and poorly developed in both penguins and alcids. The acromion in *Tonsala* is longer and

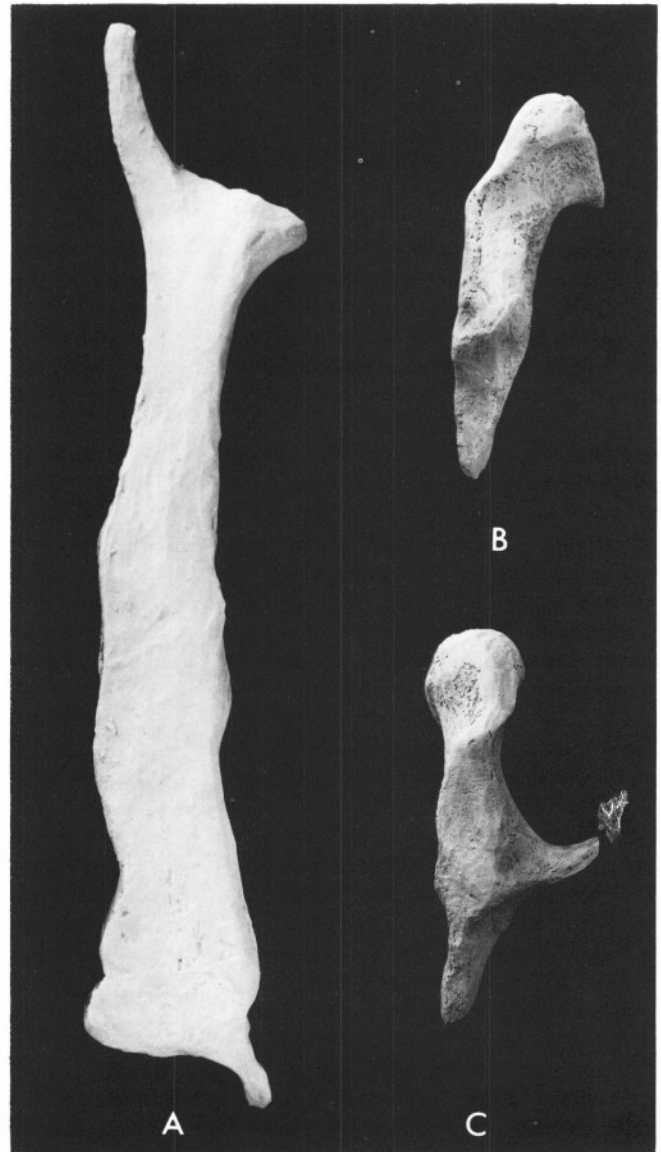


Figure 4. Pectoral girdle of *Tonsala hildegardae*, holotype (USNM 256518). a, right scapula, dorsal view (most irregularities in margins of blade are probably artifacts of preservation); b, humeral end of left coracoid, dorsal view; c, same, lateral view. All figures $\times 1$.

more slender than in any of the other members of the Pelecaniformes.

Both coracoids of the holotype of *Tonsala* are poorly preserved and lack the sternal two-thirds. The left coracoid, however, shows the distinctive features of the Plotopteridae as discussed by Howard (1969) and in the familial and generic diagnoses above. In this specimen (Fig. 4b–c), the procoracoid process is preserved. It is a large, anteriorly curved spine, much larger than in the Anhingidae or Phalacrocoracidae, but not too unlike that in the Sulidae.

The patella was the only element of the hindlimb preserved in the holotype of *Tonsala hildegardae*. It is a large and heavily ossified bone with a distinct small transverse perforation for the tendon of the ambiens muscle (Fig. 3h). An ossified patella occurs only in the Sulidae, Anhingidae, and Phalacrocoracidae, among the Pelecaniformes. The form of the patella of *Tonsala* is more similar to that in the Anhingidae, differing mainly in being a heavier bone and in having the dorsal por-

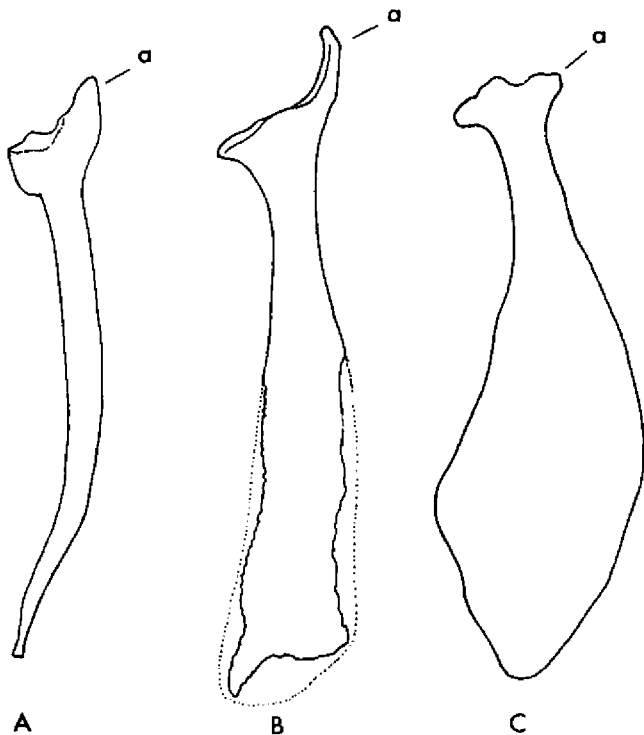


Figure 5. Ventral view of right scapula of (A) *Anhinga anhinga*, Anhingidae, Pelecaniformes; (B) *Tonsala hildegardae*, Plotopteridae, Pelecaniformes; (C) *Eudyptes chrysolophus*, Spheniscidae, Sphenisciformes. The acromion (a) is well developed in the two Pelecaniformes, in contrast to the penguin; however, the very broad but thin blade occurs only in penguins and the convergently similar Plotopteridae. Not to scale.

tion projecting anteriorly as a distinct knob. In the Sulidae the patella is a more flattened, simpler structure, lacking the enclosed canal for *M. ambiens*. The patella in the Phalacrocoracidae, while varying within the family, is quite different, taking the form of a pyramid with a tetragonal base and projecting much farther anteriorly than in *Tonsala*.

DISCUSSION

Tonsala hildegardae was a much larger bird than *Plotopterum joaquinensis* and also exceeded in size any of the living penguins except the two species of *Aptenodytes*. It is generically distinct not only from *Plotopterum*, but also from a much larger and as yet unnamed Japanese species for which comparable elements are known. The holotype of *Tonsala hildegardae* is the only specimen of bird yet known from the Oligocene marine deposits of the eastern Pacific. It is somewhat older than *Plotopterum joaquinensis*, but probably nearly contemporaneous with most of the plotopterids from Japan. In the deposits in which they occur, plotopterids are the only birds so far known. Yet they are absent from later deposits and thus evidently became extinct toward the end of the early Miocene. The giant penguins in the Southern Hemisphere died out at the same time. There is a strong possibility that the disappearance of these two unrelated groups in different hemispheres is linked with the contemporaneous ascendancy of seals and porpoises (Simpson 1974; Olson and Hasegawa 1979).

The Plotopteridae not only belong in the Pelecaniformes, but are clearly derived from members of the suborder Sulae, which includes the Sulidae, Anhingidae, and Phalacrocoracidae. The species in the latter two families are entirely foot-propelled divers, but at least some of the Sulidae, all of which are plunge divers, are known to use the wings occasionally underwater to extend the depth of their dives (Thomas R. Howell pers. comm.). Increased specialization for such locomotion in some early pelecaniform group led ultimately to the development of the Plotopteridae.

In the course of modifying the forelimb into a paddle-like propulsive organ, plotopterids, penguins, and alcids have evolved numerous "shared derived character states," but only by blind adherence to cladistic methodology could these three families be classified as a monophyletic group. The profound differences between plotopterids and penguins or alcids and the many characters, including presumably derived ones, that link the Plotopteridae and the Pelecaniformes have been outlined above. To ignore such differences in favor of emphasizing similarities in what are clearly locomotor adaptations is to disregard the very information that leads to a true understanding of the evolutionary history of these taxa. This is nevertheless what Cracraft (1972:387) has done in attempting to resurrect the hypothesis that foot-propelled diving birds of the orders Gaviiformes, Podicipediformes, and Hesperornithiformes "evolved from a common ancestor" that was also a foot-propelled diver.

The physical constraints of extreme specialization of one or the other set of limbs for underwater propulsion obviously impose a certain morphological uniformity on those organs in the bird that happens to adopt such a mode of locomotion, regardless of relationships. Storer's (1960) analysis of evolution in diving birds, which does not ignore differences and which requires independent development of similarities in locomotor adaptations, is logical and in full accordance with observed facts. To this the Plotopteridae add a striking new example of the significance of convergence.

ACKNOWLEDGMENTS

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