

A NEW GENUS AND TWO NEW SPECIES OF GIGANTIC PLOTOPTERIDAE FROM JAPAN (AVES: PELECANIFORMES)

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ABSTRACT—The Plotopteridae are wing-propelled, penguin-like diving birds of the order Pelecaniformes found in mid-Tertiary deposits of the North Pacific. Much new material representing a considerable radiation of genera and species has been discovered in Japan since the basic adaptations and characters of the family were revealed. A new genus and species, *Copepteryx hexeris*, is named here from previously known but undescribed material upon which much of our knowledge of the family had originally been based. A second new species, *C. titan*, is described from a single gigantic femur from a bird that was probably larger than any known diving bird, living or fossil.

INTRODUCTION

The discovery in mid-Tertiary rocks of the North Pacific of flightless, pelecaniform birds with specializations for wing-propelled diving similar to those of penguins (Howard, 1969; Olson and Hasegawa, 1979) provided one of the more striking examples of convergent evolution among vertebrates. This, coupled with the extremely large size of some of the species, has made the group of considerable popular as well as scientific interest.

The first of these birds to be described, *Plotopterum joaquinensis* Howard (1969), was based solely on the scapular end of a coracoid from the early Miocene of California. We have noted that Howard's (1969) correct diagnosis of this fragment as representing a new family, Plotopteridae, of wing-propelled Pelecaniformes convergent on penguins and auks, constitutes one of the most perceptive insights in the history of vertebrate paleontology (Olson and Hasegawa, 1979, 1980; Olson, 1980). Confirmation of the nature of the adaptations and relationships of the Plotopteridae was later obtained from fossils from the mid-Tertiary of Japan and the northwestern United States (Olson and Hasegawa, 1979; Olson, 1980). Of these, the only species to be described so far is *Tonsala hildegardae* Olson (1980), based on an incomplete associated skeleton from the Oligocene of the state of Washington.

Many more specimens have been accumulated from Japan, although the nature of the material often renders systematic interpretations extremely difficult. We can be fairly confident that there were at least six contemporaneous species in the deposits attributed to the upper Oligocene, and among these there are at least two very different genera. However, because of lack of association, lack of comparable elements, or poor preservation, it is still very difficult to determine which species belong to which genus, and which specimens belong to a given species. A number of the late Oligocene specimens have been mentioned in several preliminary scientific and popular papers, mainly in Japanese, although no names have been proposed for any of the taxa (Hasegawa, 1978, 1979; Hasegawa, Isotani, et al., 1979; Olson and Hasegawa, 1979, 1980).

The discovery of considerable new plotopterid material in older beds that are probably early Oligocene (but possibly late Eocene) in age has compounded the difficulty of determining species limits and attempting to discern ancestral-descendent versus sister-group relationships. There appear to be at least as many as six species of Plotopteridae in the collections from the older deposits, including one smaller than any of the species in

the late Oligocene sample. A femur of an additional small species from a medial Miocene deposit on Honshu that was at first assigned to the Phalacrocoracidae (Hasegawa et al., 1977), was later tentatively referred to *Plotopterum* itself (Olson and Hasegawa, 1985).

Because the largest of the late Oligocene Japanese plotopterids are represented by the most complete and diagnostic material, and because these present relatively few systematic problems, we have proceeded with the description and naming of two of these species, but much more remains to be done before the true diversity of the family will be reflected in its nomenclature.

As shown previously (Olson, 1980), the Plotopteridae belong in the traditional suborder Sulae, along with the Sulidae, Anhingidae, and Phalacrocoracidae. Within this suborder, the Plotopteridae definitely cluster with the Anhingidae and Phalacrocoracidae, with the Sulidae being the outlying sister group. In overall similarity, the morphology of the Plotopteridae is definitely most similar to that of the Anhingidae. It is not yet clear whether the similarities between plotopterids and anhingas are primitive, with the Plotopteridae being the primitive sister-group of the Anhingidae and Phalacrocoracidae, or if the Plotopteridae and Anhingidae constitute a clade that is the sister-group of the Phalacrocoracidae. Because the plotopterids are clearly most closely related to the anhingas and cormorants, the comparisons offered in the following descriptions are principally with those families.

Excellent casts of the Japanese specimens have been deposited in the collections of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (USNM), and their catalog numbers have been cited as well as those of the repository of the original specimens.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

PELECANIFORMES Sharpe, 1891

SULAE Sharpe, 1891

PLOTOPTERIDAE Howard, 1969

Type Genus—*Plotopterum* Howard, 1969, by monotypy.

Included Genera—*Plotopterum* Howard, 1969; *Tonsala* Olson, 1980; *Phocavis* Goedert, 1988; *Copepteryx* Olson and Hasegawa, new genus.

COPEPTERYX, new genus

Type species—*Copepteryx hexeris*, new species.

Included species—*Copepteryx hexeris*, new species; *C. titan*, new species.

Diagnosis—The scapular end of the coracoid differs from that of *Plotopteryx* in the same manner as does that of *Tonsala* (Olson, 1980:52). In the distal end of the humerus, the tricripital grooves are much deeper than in *Tonsala*, especially in distal view, in which also the distal end is seen to be less flattened; the dorsal condyle is better developed and curves more toward the midline of the shaft. The tarsometatarsus differs greatly from that of *Phocavis* (Goedert, 1988) in being much stouter, lacking a closed canal in the hypotarsus, and having the trochleae in distal view in about the same antero-posterior plane rather than in a semi-circle.

Remarks—For several reasons, at this stage of our knowledge it is difficult to provide as many characters as probably exist to distinguish *Copepteryx* from *Tonsala*. The holotype of *Tonsala hildegardae* is quite fragmentary and worn, as well as exhibiting considerable pathology. In addition to the pathological condition already noted for the left humerus (Olson, 1980), we now believe the shaft of the right humerus to have been affected by exostosis and that what was identified as the distal end of the right radius may be the pathological proximal end of the left radius.

A nearly complete coracoid (Kitakyushu Museum and Institute of Natural History KMNH VP 200,003; cast USNM 243775) from the upper Oligocene Ashiya Group at Hikoshima Island, Shimonoseki City, southern Honshu (Hasegawa and Ota, 1979), exhibits the familial characters described for *Plotopteryx* by Howard (1969). In fact, it was this specimen that first permitted us to associate the Japanese fossils with Howard's family Plotopteridae (Olson and Hasegawa, 1980). This coracoid comes from a species larger than *T. hildegardae* but smaller than either species of *Copepteryx* and differs dramatically from the coracoid of *C. hexeris*. Although nearly as long (165 mm) as the coracoid in that species, it is of a very different shape, being more gracile, with the sternal end much narrower and having the lateral process much broader and more proximally situated (Fig. 1). This specimen, more than any other, proves the existence of two distinct genera among the Japanese Plotopteridae, and if referable to *Tonsala*, as we believe at present, based on a preliminary assessment of the smaller Japanese plotopterids (Olson and Hasegawa, unpubl. data), it provides the best means yet available for distinguishing *Copepteryx* from *Tonsala*.

Etymology—"Oar-wing" from Greek *kope*, f. oar, and *pteryx*, f. wing. The name is feminine and refers to the paddle-like wing that is characteristic of the family.

COPEPTERYX HEXERIS, new species

Holotype—Partial articulated skeleton (Figs. 1A, 2, 3, 4–6), Kitakyushu Museum and Institute of Natural History KMNH VP 200,006; casts National Science Museum Tokyo NSMT-PV 17757; USNM 486682. Collected in summer 1977 by Yoshikazu Hasegawa. The specimen consists of 17 presacral vertebrae, 3 ribs, complete furcula, left coracoid, partial left scapula, sternum with nearly complete carina but lacking most of the right side and some of the posterior portions, both wings, lacking the phalanges, except the right alular phalanx and the proximal end of right phalanx I of the major digit.

Type Locality—Southern end of Ainosima Island, Kitakyushu City, Fukuoka Prefecture, Kyushu, Japan (Hasegawa, Ono, et al., 1979).

Horizon—Medium-grained glauconite sandstone layer of Ai-

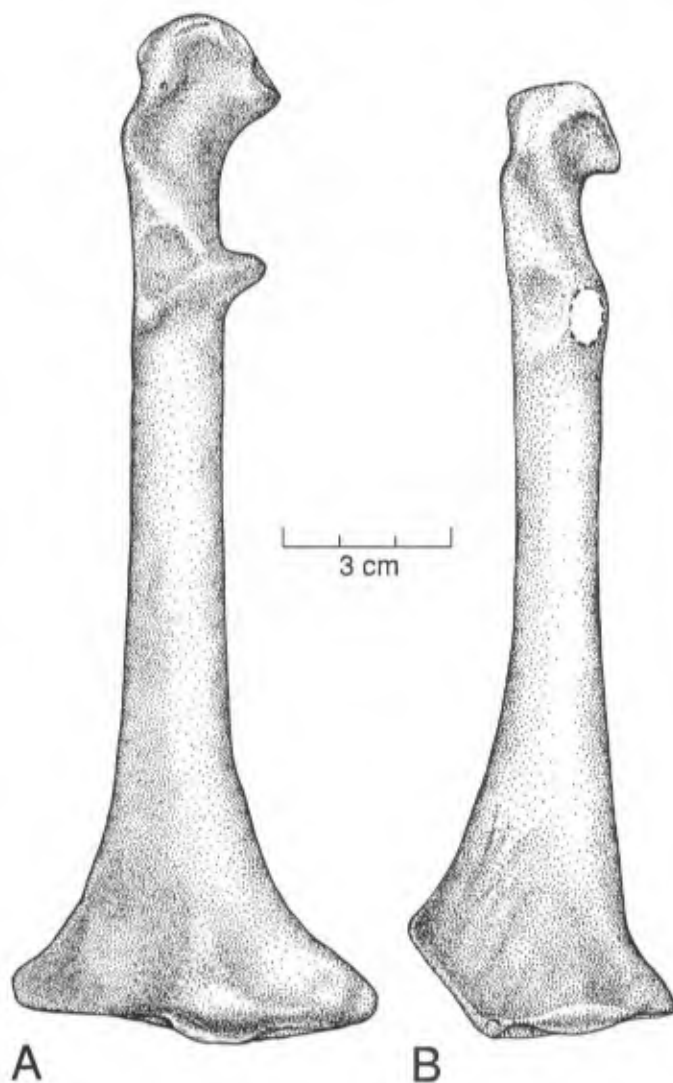


FIGURE 1. Left coracoids in dorsal view: A, *Copepteryx hexeris*, (drawn from the holotype, where still partly obscured by vertebrae and the sternum); B, *Tonsala? sp.*, specimen from the upper Oligocene Ashiya Group at Hikoshima Island, Shimonoseki, southern Honshu, Japan (KMNH VP 200,003, cast USNM 243775). The marked differences in these two coracoids indicate the presence of at least two genera of Plotopteridae in Japan. Scale = 5 cm.

noshima Formation, Ashiya Group, upper Oligocene (Hasegawa, Ono, et al., 1979).

Measurements of Holotype (in mm)—Sternum: depth of carina from apex to manubrium, 85; length of carina as preserved, 175; depth of apex of carina (clavicular articulation), 28; anterior width measured diagonally from midline, 77. Coracoid: total length from head to internal angle, 180; distal width, 66; distance from head to sternal extent of glenoid facet, 52; length of glenoid facet, 35; breadth below head across triosseal canal, ca. 17. Furcula: length, 166; depth of sternal articulation, 29; least anteroposterior width of shaft, 10; greatest anteroposterior diameter of dorsal expansion, 53. Humerus: length, 166; proximal width, ca. 38; proximal depth, 28; distal width through external condyle, 36; distal depth through internal condyle, 21; shaft width just distal to palmar crest, 23; shaft depth at same point, 9.5. Ulna: length, 99; proximal depth, 25; proximal width, 18; width and depth of

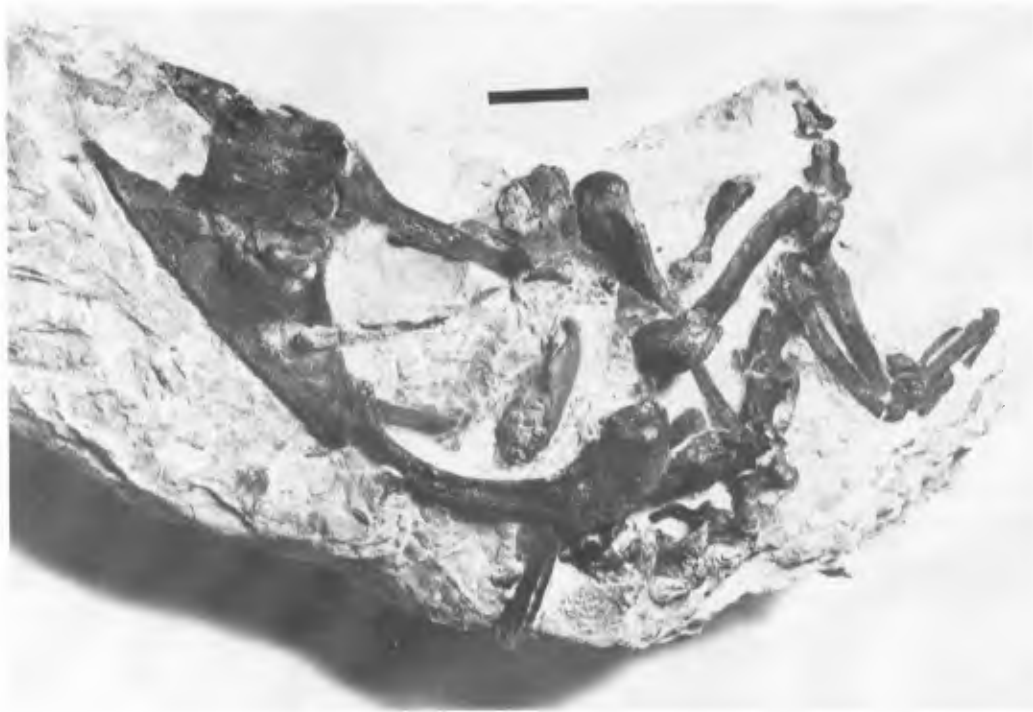


FIGURE 2. Holotype of *Copepteryx hexeris*, new species (KMNH VP 200,006), partial associated skeleton in the initial stages of preparation, with all elements still in place. Scale = 5 cm.

shaft at midpoint, 9×14 . Radius: length, 103; greatest diameter of proximal articulation, 12.5; greatest depth of shaft (at proximal bend), 16; depth of shaft at midpoint, 12. Carpometacarpus: length, 74; distance from distal end of alular metacarpal to distal end of major metacarpal, 38; length of alular metacarpal, 30; greatest proximal depth, 21; proximal width, 10; width and depth of shaft of major metacarpal just distal to the alular metacarpal, 7×9 . Alular digit: length, 33; proximal width and depth, 7.5×8 .

Paratypes—Partial associated skeleton (see Hasegawa and Seki, 1979) Kitakyushu Museum and Institute of Natural History KMNH VP 200,001; casts USNM 243773. The specimen consists of two sections of sacral vertebrae and impressions of the outline of much of the pelvis (Fig. 7A), 3 caudal vertebrae, fragments of one vertebral and two sternal ribs, left femur (Fig. 8C) lacking the posterior face and a section of shaft (reconstructed from impressions), proximal end of right femur, fragments of left fibula, left tibiotarsus lacking proximal end (Fig. 7B), right tarsometatarsus. Collected by Kunio Yozawa and Kenji Matsuo of Goto Sangyo Industries, from the sandstone quarry at Yoshida, Mizumaki-machi, Onga-gun, Fukuoka Prefecture, northern Kyushu, Japan, the site being 1.5 km south of the Orio Station of the National Railway, Yahatamishi, Kitakyushu City. The rocks from which it was recovered belong to the Orio member of the Yamaga Formation, this being the lowermost unit of the Ashiya Group, which is thought to be late Oligocene in age (Hasegawa and Seki, 1979).

Proximal end of left tibiotarsus (Fig. 9) on deposit in Kitakyushu Museum and Institute of Natural History KMNH VP 200,002; cast USNM 486684; collected in 1980 by Mr. Yoshihiko Okazaki on the southwestern end of Ainoshima Island, Kitakyushu City, Fukuoka Prefecture, Kyushu, Japan, in rocks of the Ainoshima Formation, Ashiya Group, upper Oligocene.

Left femur (Fig. 8B), complete but rather cracked and abraded (Hasegawa and Suzuki, 1979), National Science Museum, Tokyo NSMT VP 15035; cast USNM 243774. Collected 13 February 1972 by Tadashi Suzuki from a nodule embedded in a stone quarry south of the Yasaka Shrine in Tsuzuru-machi, Uchigo City, Fukushima Prefecture, Honshu, Japan. It is from beds referred to as the Asagai Sandstone, which is believed to be contemporaneous with the upper Oligocene Orio Sandstone (Hasegawa and Suzuki, 1979).

Right tarsometatarsus lacking posterior face, and associated sternal end of coracoid (Hasegawa and Otsuka, 1979), Institute of Earth Sciences, Faculty of Science, Kagoshima University F-5007; cast USNM 243772. Collected in 1976 by Hiroshi Endo from an outcrop at Otao village, southern part of Yuridake Mountain, Ōshima town, Nishisonogi District, Nagasaki Prefecture, Kyushu, Japan. The specimens are from the Shioda bed, in the upper part of the Nishisonogi Group, Upper Oligocene (Hasegawa and Otsuka, 1979). This is from a higher level than the Orio Sandstone, although there is no great difference in age.

Mandible, Kitakyushu Museum and Institute of Natural History KMNH VP 200,005; cast USNM 486683. Collected in 1983 by Mr. Ikeuchi at Umashima Island, Kitakyushu City, Fukuoka Prefecture, Kyushu, Japan, from rocks of the Ainoshima Formation, Ashiya Group, Upper Oligocene (Hasegawa, Ono, et al., 1979). The specimen is still largely in matrix and is assigned to this species on size. The only pterosaur skull yet known (Hasegawa and Isotani, 1979), we believe to be from a smaller bird than either of the species of *Copepteryx* described here. Descriptions of pterosaur cranial morphology are therefore reserved for future studies of the smaller species.

Measurements of Paratypes (in mm)—Orio specimen. Femur: length 192+; proximal width, 56; depth through trochanter, 32+; anteroposterior diameter of head, 27; dorsoventral di-

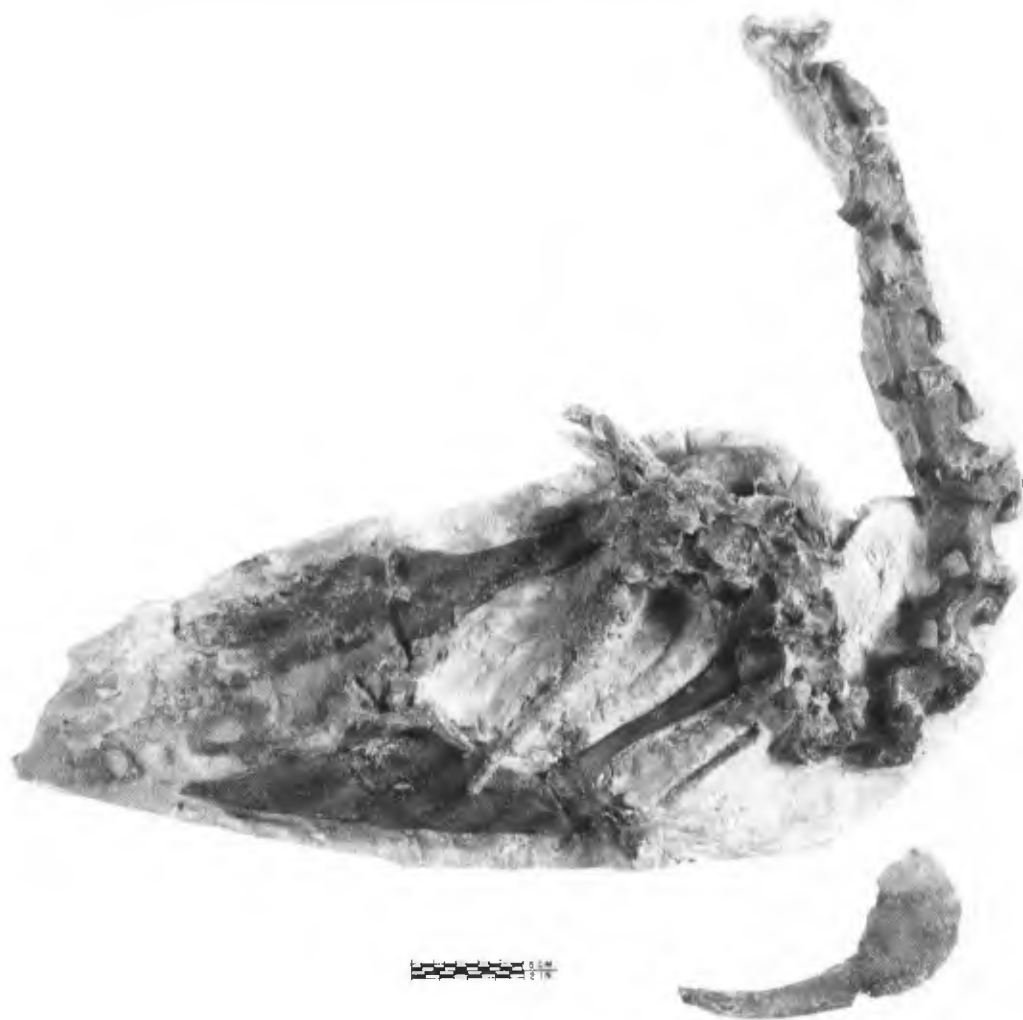


FIGURE 3. Holotype of *Copepteryx hexeris*, new species (KMNH VP 200,006), at a later stage of preparation, with the wings and right clavicle removed, the latter being shown displaced below. Scale = 5 cm.

ameter of head, 24. Tibiotarsus: estimated total length including cnemial crests as determined by comparison with the proximal end of tibiotarsus from Ainoshima, 300; length from distal end of fibular crest to midline of distal end, 158; width and depth of shaft at midpoint, 23.6×17.7 ; minimum circumference of shaft, 64; estimated distal width, 51. Tarsometatarsus: length from intercotylar knob to middle trochlea, 104; proximal width, 52; proximal depth through medial ridge of hypotarsus, 43; least width and depth of shaft, 26.5×14 ; distal width 60.3; width and depth of outer trochlea, 17.0×28.7 ; width and depth of middle trochlea, 19.2×28.4 ; width and depth of inner trochlea, 17.2×23.2 . Pelvis: estimated length of fused sacral vertebrae, 275+; estimated greatest width across anterior iliac shields, 170; estimated width across antitrochanters, 130. Caudal vertebra (4th?): height through neural crest 47.4; width through transverse processes (by doubling one side), 54; width and depth of centrum, 19.8×14.3 .

Umashima mandible: estimated length, 230.

Asagai femur: length, 198; proximal width, 60; depth through trochanter, 36+; anteroposterior diameter of head, 27; dorsoventral diameter of head, 25; width and depth of shaft at midpoint, 26.5×27.5 ; distal width, 56; depth of external condyle,

42.5; depth of internal condyle, 36; least circumference of shaft, ca. 87.

Ainoshima tibiotarsus: length from proximal extent of cnemial crest to distal end of fibular crest, 120; width of proximal articular surface, 38; anteroposterior depth through outer cnemial crest, 62.

Nagasaki tarsometatarsus: length 96; proximal width 46.5; distal width, 53.

Etymology—Latin, f. *hexeris*, a vessel propelled by six banks of oars, in allusion to the large size of the species and to its means of propulsion; the name is a noun in apposition.

Diagnosis—As for the genus; smaller than *Copepteryx titan*, new species, but larger than any other previously described species of Plotopteridae.

Description—This species, and particularly the holotypic specimen, provided much of the basis for the diagnosis and characters of the family Plotopteridae in Olson and Hasegawa (1979) and Olson (1980).

The sternum, as previously shown (Olson, 1980:fig. 1) has the apex of the carina directed far anteriorly and articulates strongly with the furcula in typical peleciform fashion. At least five ribs articulate with the sternum, posterior to which



FIGURE 4. Left humerus of the holotype of *Copepteryx hexeris*, new species: A, anconal view; B, palmar view; C, distal view. Scale = 5 cm.

the only available specimen has been eroded away. Five is the likely number, as in the Pelecanidae, Sulidae, and Phalacrocoracidae, and unlike the Phaethontidae and Fregatidae (six) or AnHINGIDAE (four—this reduced number appears to be uniquely derived within the order).

The furcula (Figs. 2, 3) is very large and robust, with a strong ovoid articulation with the coracoid, as in *Balaeniceps*

and all modern Pelecaniformes except Phaethontidae and Fregatidae, although the postarticular spine (extremitas omalis claviculae) characteristic of those families appears to be altogether lacking in *Copepteryx*. The anterior (or dorsal) portion of the clavicles is greatly expanded and lateromedially flattened, being most similar to the condition in the AnHINGIDAE.

The coracoid (Fig. 1) has not been fully prepared in the holotype but is seen to have the greatly elongated shaft and distinctive modifications of the scapular end characteristic of the Plotopteridae. The scapula is very poorly preserved but has the acromion greatly elongated and slender, as described for *Tonsala hildegardae*.

The pelvis of *Copepteryx hexeris* is known only from the imperfect Orio specimen, in which little actual bone remains. The general outlines, however, can be relatively accurately reconstructed from impressions in the adjacent rock (Fig. 7A), which show the expanded "butterfly" shape of the anterior iliac shields as in the Sulidae, AnHINGIDAE, and Phalacrocoracidae. The postacetabular portion of the pelvis is about the same length as the preacetabular part, unlike the elongate postacetabular pelvis in the Sulidae and Phalacrocoracidae. The overall configuration of the pelvis in *Copepteryx* is thus much more like that in the AnHINGIDAE.

The wing elements of *Copepteryx* are highly specialized for underwater propulsion and consequently bear not the slightest resemblance to those of any living pelecaniform bird (Figs. 4–6). As described for *Tonsala*, the proximal end of the humerus is very round and bulbous, being most similar to that in penguins, whereas the shaft and distal end are flattened and modified to a lesser degree than in modern penguins and more closely resemble the condition in flightless forms of Alcidae such as *Pinguinus* Bonnaterre and especially *Mancalla* Lucas. The radius and ulna are short and stout, with the radius being flattened and the shaft expanded proximally. The ulna bears pits for the attachment of the secondary quills, as in *Tonsala*. The carpo-metacarpus in the Plotopteridae has the very long, low alular metacarpal typical of wing-propelled divers, and is most similar to the stage of development seen in *Mancalla*.

The femur of *Copepteryx* (Figs. 8, 11) has the shaft relatively straight, as in the AnHINGIDAE and unlike the Phalacrocoracidae, in which the shaft is more robust and strongly curved in lateral or medial view.

The tibiotarsus (Figs. 7B, 9), despite its much greater size, is quite like that in the AnHINGIDAE and differs markedly from that of the Phalacrocoracidae in the larger, more anteriorly expanded medial cnemial crest and in lacking the strong medial and distal displacement of the medial condyle.

The tarsometatarsus (Figs. 10) is very short and stout, more so than in the AnHINGIDAE but more similar to that family than to either the Sulidae or Phalacrocoracidae, in which the tarsometatarsus is more elongated. The inner trochlea extends distally to the level of the middle trochlea, not slightly beyond as in the AnHINGIDAE, and the outer trochlea is elevated relative to the middle one, as in the AnHINGIDAE and very different from the Phalacrocoracidae. The medial calcaneal ridge in *Copepteryx* is situated more medially than in either the AnHINGIDAE or Phalacrocoracidae and does not extend far posteriorly as in the latter. There are no closed canals in the hypotarsus, unlike either the AnHINGIDAE or Phalacrocoracidae. The scar for the hallux appears to be situated almost entirely on the medial face of the shaft, rather than mostly on the posterior face as in the AnHINGIDAE and Phalacrocoracidae. The distal foramen is not closed and is continuous with the intertrochlear space.

Goedert (1988) described a new genus and species of Plotopteridae, *Phocavis maritimus*, from late Eocene marine deposits of Oregon, based on a single large (60 mm) tarsometatarsus. Because of its large size, robustness, and obvious pele-



FIGURE 5. Distal elements of the right wing of the holotype of *Copepteryx hexeris*, new species, in dorsal view, in articulation as originally preserved. Scale = 5 cm.

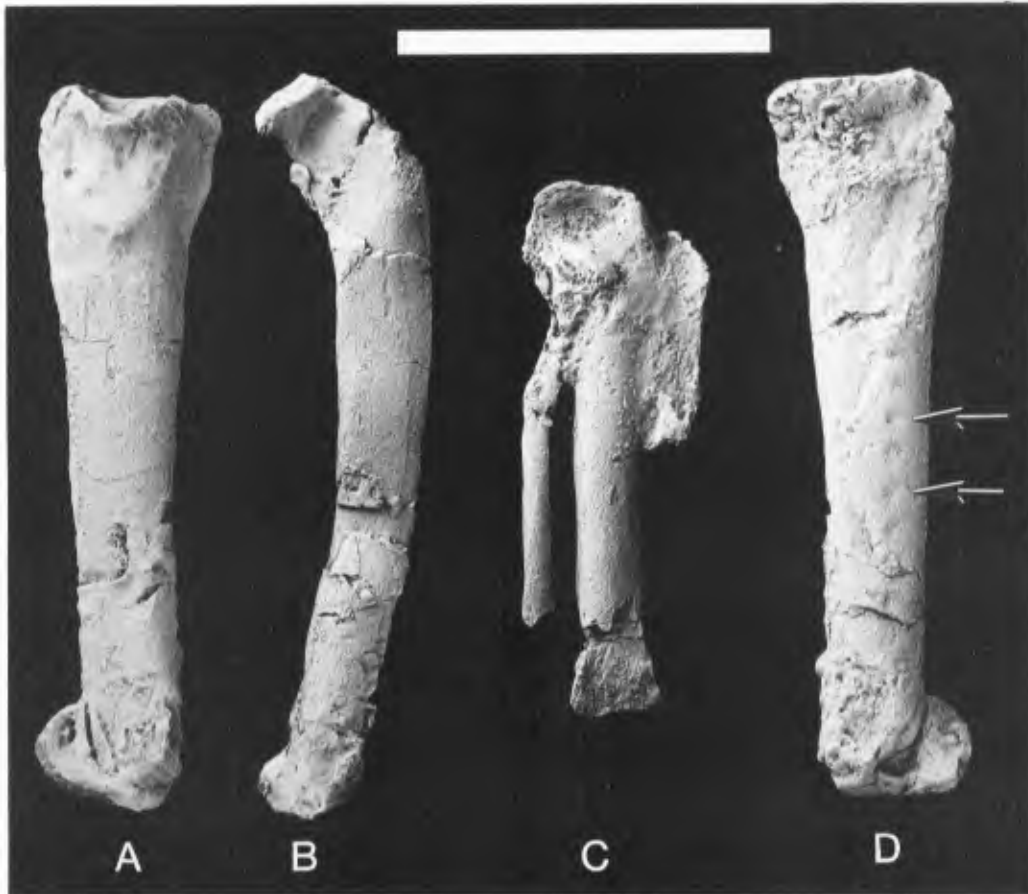


FIGURE 6. Distal elements of the left wing of the holotype of *Copepteryx hexeris*, new species, in ventral view: A, ulna; B, radius; C, carpometacarpus; D, ulna in dorsal view with arrows indicating the row of pits for attachment of secondary quills. Scale = 5 cm.



FIGURE 7. A, pelvis reconstructed largely from outline impressions (cast USNM 243773) of the Orio specimen of *Copepteryx hexeris*, new species, in dorsal view; B, tibiotalus, lacking proximal end, of the same specimen, anterior view. Scale = 5 cm.



FIGURE 8. Femora in anterior view: **A**, *Copepteryx titan*, new species, holotype (KMNH VP 200,004; cast USNM 486685); **B**, *Copepteryx hexeris*, new species, Asagai specimen (cast USNM 243774); **C**, *Copepteryx hexeris*, new species, Orio specimen (KMNH VP 200,001); **D**, Emperor Penguin, *Aptenodytes forsteri* Gray (USNM 347340). The Emperor Penguin is the largest living diving bird and is shown to provide some indication of the immensity of the pterosaurs described here. Scale = 5 cm.

caniform morphology, assignment to the Plotopteridae would seem reasonable, but the specimen differs so much from the tarsometatarsus of *Copepteryx hexeris* that it probably indicates a considerably more primitive form. Goedert's comparisons were made with the then-unnamed tarsometatarsus of *Copepteryx hexeris* described here and as illustrated and discussed by Hasegawa, Isotani, et al. (1979) and Olson and Hasegawa (1979). Thus his diagnosis of *Phocavis* serves as well to diagnose *Copepteryx*.

Remarks—The two most complete associated specimens of *C. hexeris* unfortunately preserve no elements in common, which at first made it difficult to be certain that the pelvis and leg elements from Orio could be properly associated with the holotypic wing and pectoral elements from Ainoshima Island. Comparisons with the largest of modern penguins were not helpful in this regard, as their proportions are very different. For example, the coracoid in *Aptenodytes* is much longer in proportion to the femur than is true of the Plotopteridae. We have based the above association on the Nagasaki specimen, under the assumption that the tarsometatarsus and partial coracoid found together in a nodule there came from a single individual.

COPEPTERYX TITAN, new species

Holotype—Left femur (Fig. 11), Kitakyushu Museum and Institute of Natural History KMNH VP 200,004; cast USNM 486685. Collected in 1983 by Mr. Ikeuchi.

Type Locality—North end of Ainoshima Island, Kitakyushu City, Fukuoka Prefecture, Japan.

Horizon—Ainoshima Formation, Ashiya Group, late Oligocene.

Etymology—Greek, Titan, son of Uranus and Gaea, symbolic of large size.

Diagnosis—Much larger than *Copepteryx hexeris*. Compared with the femur referred to *Plotopterum* (Olson and Hasegawa, 1985), the shaft in lateral or medial view is straighter, and in anterior or posterior view is more robust, so that the distal end does not appear as expanded as in *Plotopterum*; the head is nearly perpendicular to the long axis of the shaft and on a level with the trochanter, not angled strongly proximally and rising well above the level of the trochanter as in *Plotopterum*; in lateral view the proximal end is wider due to great posterior extension of the trochanter; in distal view the intercondylar fossa is wider, deeper, and much more distinct. To the extent that these features can be discerned in the available material of *C. hexeris*, that species is similar to *C. titan* and different from *Plotopterum*, so that their assignment to the same genus seems justifiable in the absence of knowledge of the morphology of the femur in *Tonsala*.

Measurements of Holotype (in mm)—Length, 223; proximal width, 65.5; depth through trochanter, 43.5; anteroposterior diameter of head, 30.8; dorsoventral diameter of head, 28.2; width and depth of shaft at midpoint, 32 × 31; distal width,



FIGURE 9. Proximal end of tibiotarsus of *Copepteryx hexeris*, new species (KMNH VP 200.002; cast USNM 486684). A, medial view; B, anterior view. Scale = 5 cm.

66.5; depth of external condyle, 48.8; depth of internal condyle, 44.3; least circumference of shaft, 97.

Remarks—Although the single known specimen is very well preserved, the same is not true of comparable specimens of *C. hexeris*, so that at this point the distinguishing characteristic of the species is size. *Copepteryx titan* was a species of immense size, being the largest diving bird of any sort ever known to have existed, as at least the femora of the two species of *Copepteryx* are considerably larger than the femur of any of the species of giant penguins from the early to mid-Tertiary of Antarctica and New Zealand in which that element is known.

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FIGURE 10. Tarsometatarsus of *Copepteryx hexeris*, new species, Orio specimen (KMNH VP 200.001). A, anterior view; B, posterior view; C, distal view; D, proximal view. Scale = 5 cm.

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The photographs (except Fig. 2) are by Victor E. Krantz, Smithsonian Institution; Figure 1 was kindly rendered by Mary Parrish, Smithsonian Institution.



FIGURE 11. Femur of *Copepteryx titan*, new species, holotype (KMNH VP 200,004; cast USNM 486685); A, posterior view; B, lateral view. Scale = 5 cm.

LITERATURE CITED

- Goedert, J. L. 1988. A new late Eocene species of Plotopteridae (Aves: Pelecaniformes) from northwestern Oregon. *Proceedings of the California Academy of Sciences* 45:97–102.
- Hasegawa, Y. 1978. [There were penguins in Japan also!]. *Kagaku Asahi*, [March 1978]:71–75. [In Japanese].
- . 1979. [A history of studies of Oligo-Miocene penguin-like birds]. Part I; pp. 41–43 in Hasegawa, Isotani, et al., *Bulletin of the Kitakyushu Museum of Natural History* 1.
- and S. Isotani, 1979. [Hatatsu specimens from Yukiaino Sandstone Bed, Imari-shi, Saga Prefecture]. Part IV; pp. 48–50 in Hasegawa, Isotani, et al., *Bulletin of the Kitakyushu Museum of Natural History* 1. [In Japanese].
- *———, S. Isotani, K. Nagai, K. Seki, T. Suzuki, H. Otsuka, M. Ota, and K. Ono. 1979. [Preliminary notes on the Oligo-Miocene penguin-like birds from Japan (Parts I–VII)]. *Bulletin of the Kitakyushu Museum of Natural History* 1:41–60. [In Japanese].
- , Y. Okumura, and Y. Okazaki. 1977. [A Miocene bird fossil from Mizunami, Central Japan]. [*Bulletin of the Mizunami Fossil Museum*] 4:169–171. [In Japanese].
- , K. Ono, H. Otsuka, K. Nagai, and M. Ota. 1979. [Avian wing bones from Ainoshima Island, Kita-Kyushu, Japan; Part VII; pp. 55–60 in Hasegawa, Isotani, et al., *Bulletin of the Kitakyushu Museum of Natural History* 1.
- and M. Ota. 1979. [Hikoshima specimens from the Orio Sandstone Bed, Shimonozeiki City, Yamaguchi Prefecture]; Part V, pp. 51–52 in Hasegawa, Isotani, et al., *Bulletin of the Kitakyushu Museum of Natural History* 1.
- and H. Otsuka. 1979. [Nishisonogi specimens from Nishisonogi Formation, Nagasaki Prefecture]; Part VI, pp. 53–54 in Hasegawa, Isotani, et al. *Bulletin of the Kitakyushu Museum of Natural History* 1.
- and K. Seki. 1979. [New fossil birds from the Orio Sandstone Bed, Northern Kyushu]; Part II, pp. 43–46 in Hasegawa, Isotani, et al. *Bulletin of the Kitakyushu Museum of Natural History* 1.
- and T. Suzuki. 1979. [Left femur from Asagi Sandstone, Fukushima Prefecture]; Part III, pp. 46–48 in Hasegawa, Isotani, et al. *Bulletin of the Kitakyushu Museum of Natural History* 1.
- Howard, H. 1969. A new avian fossil from Kern County, California. *Condor*, 71:68–69.
- Olson, S. L. 1980. A new genus of penguin-like peleciform bird from the Oligocene of Washington (Pelecaniformes: Plotopteridae); pp. 51–57 in K. E. Campbell, Jr. (ed.), *Papers in avian paleontology honoring Hildegard Howard*. *Contributions in Science Natural History Museum of Los Angeles County* 330.
- and Y. Hasegawa. 1979. Fossil counterparts of giant penguins from the North Pacific. *Science* 206:688–689.
- *——— and ———. 1980. [Fairy-tale-like penguins that lived in Northern Hemisphere: search for the mystery of fossil birds of 30,000,000 years ago]. *Anima* 92:59–66. [In Japanese].
- and ———. 1985. A femur of *Plotopterum* from the early middle Miocene of Japan (Pelecaniformes: Plotopteridae). *Bulletin of the National Science Museum, Tokyo*. Series C, 11:137–140.

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