A new penguin-like bird (Pelecaniformes:Plotopteridae) from the Late Oligocene Tokoro Formation, northeastern Hokkaido, Japan

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ABSTRACT - The skeleton of a large bird from Late Oligocene marine strata of the Tokoro Formation, exposed near Abashiri City in northeastern Hokkaido, Japan, represents a new genus and species of the extinct pelecaniform family Plotopteridae. This new specimen, *Hokkaidornis abashiriensis* new gen. et sp., was similar in size to *Copepteryx hexeris* Olson and Hasegawa, but differs from that species chiefly in characters of the anterior parts of the skeleton. The leg bones of *H. abashiriensis* and *C. hexeris* are nearly identical, and if found isolated, probably would be deemed congeneric/conspecific. The new animal from Hokkaido demonstrates that plotopterid generic diversity during Late Oligocene time was greater than previously suspected.

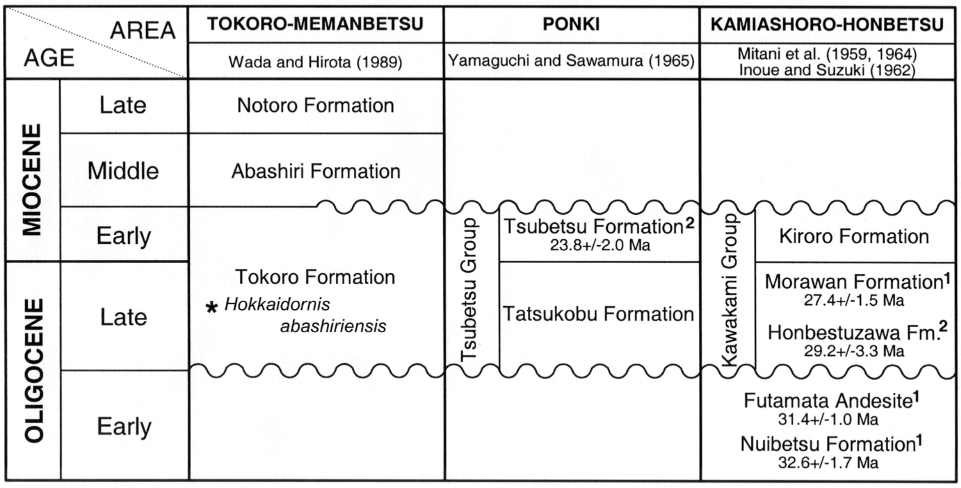
***Key words**: Plotopteridae, Late Oligocene, Japan*

Un nouvel oiseau plotopteridé (Pelecaniformes: Plotopteridae) de l'Oligocène supérieur (Formation Tokoro), Nord-Est d'Hokkaido, Japon - Le squelette d'un grand oiseau provenant des couches marines de la Formation Tokoro (Oligocène supérieur), près de la ville d'Abashiri dans le nord-est d'Hokkaido au Japon, représente un nouveau genre et une nouvelle espèce de Plotopteridae, famille éteinte de Pelecaniformes. Le nouveau specimen, *Hokkaidornis abashiriensis* n.g., n.sp., était comparable en taille au *Copepteryx hexeris* Olson & Hasegawa, mais diffère de cette espèce principalement par certains caractères de la partie antérieure du squelette. Les os des pattes postérieures de *H. abashiriensis* et de *C. hexeris* sont pratiquement identiques et seraient probablement considérés congénériques/conspécifiques s'ils étaient trouvés isolément. Le nouvel oiseau d'Hokkaido prouve que la diversité générique des Plotopteridae à l'Oligocène supérieur était plus grande que ce que l'on soupçonnait auparavant.

***Mots clés:** Plotopteridae, Oligocène supérieur, Japon*

INTRODUCTION

It is now well known that the extinct, penguin-like avian family Plotopteridae was erected by Howard (1969) and based only on the scapular end of a coracoid. A decade then passed before anything additional was published on this group (Olson and Hasegawa, 1979). Since that time, plotopterid fossils have been reported from Tertiary strata on both sides of the North Pacific (Olson, 1985; Olson and Hasegawa, 1996). Plotopterids have traditionally been classified as closely related to the anhingas (Anhingidae) and cormorants (Phalacrocoracidae) following Olson (1980) and Olson and Hasegawa (1979, 1996). The first attempt to perform a cladistic analysis of the Plotopteridae (Mayr, 2004) indicates that plotopterids and penguins (Spheniscidae) form a clade that is, in turn, the sister group to Suloidea (Sulidae + Phalacrocoracidae + Anhingidae). There are, however, several reasons why Mayr's (2004) provocative conclusions should be regarded as tentative. First of all, in the 68-character matrix used by Mayr (2004), 42 characters (or approximately 62 percent, nearly two-thirds of the data) for the Plotopteridae are missing, and for some the character state will never be determined (e.g., behavioral traits such as methods of feeding young and mating displays). Furthermore, there is much new plotopterid material still awaiting preparation and description (Barnes and Goedert, 1996; Olson and Hasegawa, 1996; Goedert and Cornish, 2002), especially the Late Eocene and Early Oligocene specimens. The same can be said for some important fossil penguin specimens, such as the incompletely prepared specimen from Argentina described by Clarke et al. (2003). When all of these specimens are studied along with the Paleocene penguins from New Zealand the outcome of future cladistic analyses (e.g. Slack et al., 2006) may be quite different from Mayr's



[1] K-Ar Age (Shibata and Tanai, 1982)

[2] Fission track age (Matsui and Ganzawa, 1987)

Figure 1 (left) - Correlation chart for Oligocene and lower Miocene formations in Eastern Hokkaido. Modified from Matsui and Ganzawa (1987).

Figure 2 (right) - Orientation and location of measurements for *Hokkaidornis abashiriensis* new genus and species. L = Left, R = Right.

(2004) results. Nothing is yet known regarding the origins of the family Plotopteridae. The oldest plotopterids are from deep-marine rocks of Late Eocene and Early Oligocene age in Washington and Oregon, along the northeastern margin of the Pacific Ocean (Goedert, 1988; Goedert and Cornish, 2002). The fossil record from Japan includes undescribed specimens possibly as old as Late Eocene and described specimens of Oligocene to Early Miocene in age, including the largest described species (Hasegawa et al., 1979; Olson and Hasegawa, 1996). Remarkably, an even larger species has recently been discovered (Kawano and Kawano, 2001) but has not yet been described.

Of the four genera and five species of plotopterids described so far, only two, *Tonsala hildegardae* Olson, 1980, and *Copepteryx hexeris* Olson and Hasegawa, 1996, are based on more than a single bone. The holotype specimen of *Copepteryx hexeris* is an incompletely prepared partial skeleton, lacking the skull and bones posterior of the sternum, from Late Oligocene strata exposed on Ainoshima Island, Japan. Olson and Hasegawa (1996) also designated a number of paratypes for *C. hexeris*, but only two of these were from the same formation as the holotype. Furthermore, several of the paratype specimens of *C. hexeris* represent only the posterior parts of the skeleton (femora, pelvis, tibiotarsi, tarsometatarsi) and thus, as noted by Olson and Hasegawa (1996), they are not directly comparable to the holotype and the paratype specimens from Ainoshima Island. However, referral of these specimens to *C. hexeris* seemed perfectly reasonable at the time of Olson and Hasegawa's (1996) study, based on the size of the bones and their geochronologic ages.

Initially, the Abashiri plotopterid described herein was assumed to be a new specimen of *C. hexeris* because of its similar geochronologic age, size, and other observed similarities to some of the paratype specimens figured by Olson and Hasegawa (1996). However, differences observed in some of the other parts of the skeleton, especially the coracoids preserved in the holotype of *C. hexeris*, made it apparent that the Abashiri specimen represented a new taxon, revealing an unexpected diversity within the larger Late Oligocene Plotopteridae. Fortunately, the Abashiri specimen includes bones that allow for some comparisons to be made with most of the specimens referred to *C. hexeris*. Olson and Hasegawa (1996) mentioned several factors (e.g. lack of associated skeletons, and other specimens that are noncomparable, isolated bones) making the study of the Japanese plotopterids difficult. Another factor that complicates these studies is the still incomplete preparation of the holotype specimen of *C. hexeris*.

Kimura et al. (1998) presented a preliminary description (in Japanese) of the Abashiri specimen. The purpose of this paper is to name this new plotopterid and offer more detailed illustrations and descriptions of the bones, as well as comparisons with some of the other named plotopterids. A new cladistic analysis for the Plotopteridae is not attempted herein, and is deferred until additional new specimens from Japan and Washington are fully prepared and described.

INSTITUTIONAL ABBREVIATIONS

AMP, Ashoro Museum of Paleontology, Ashoro-cho, Hokkaido, Japan

F, Institute of Earth Sciences, Faculty of Science, Kagoshima University, Japan

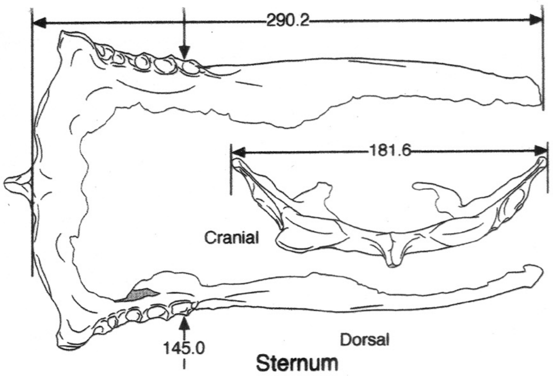
HUES, Hokkaido University of Education, Sapporo, Japan

KMNH, Kitakyushu Museum and Institute of Natural History, Kitakyushu, Japan

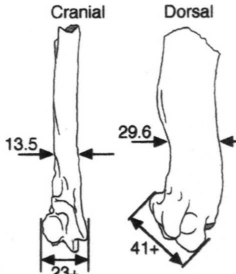
LACM, Natural History Museum of Los Angeles County, Los Angeles, California 90007, USA

NSMT, National Science Museum, Tokyo, Japan

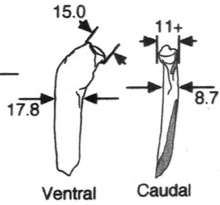
UWBM, Burke Museum of Natural History and Culture, University of Washington, Seattle 98195, USA



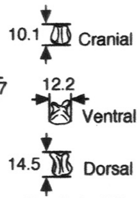
Sternum



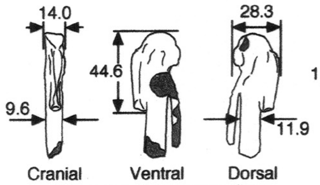
Humerus(L)



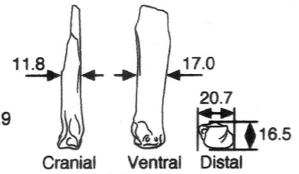
Radius(R)



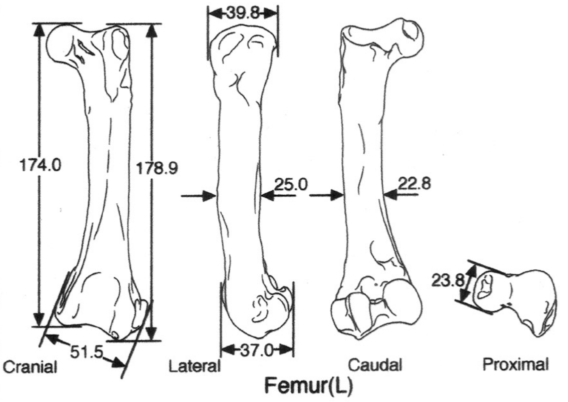
Radiale(R)



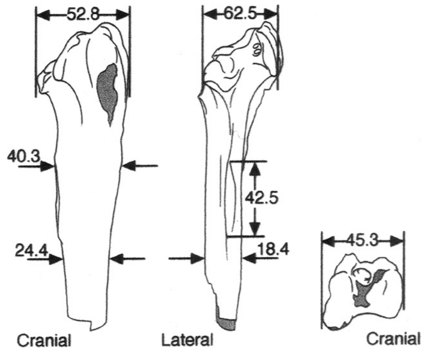
Carpometacarpus(R)



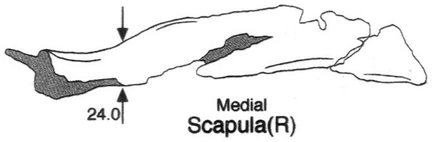
Ulna(R)



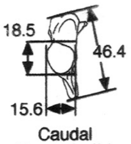
Femur(L)



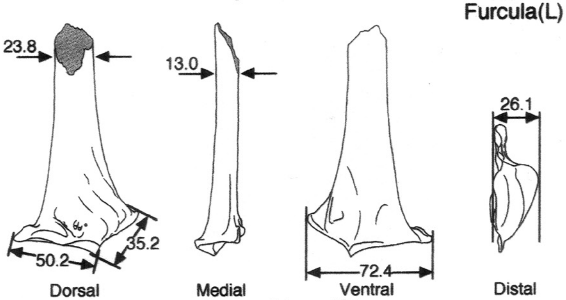
Tibiotarsus(R)



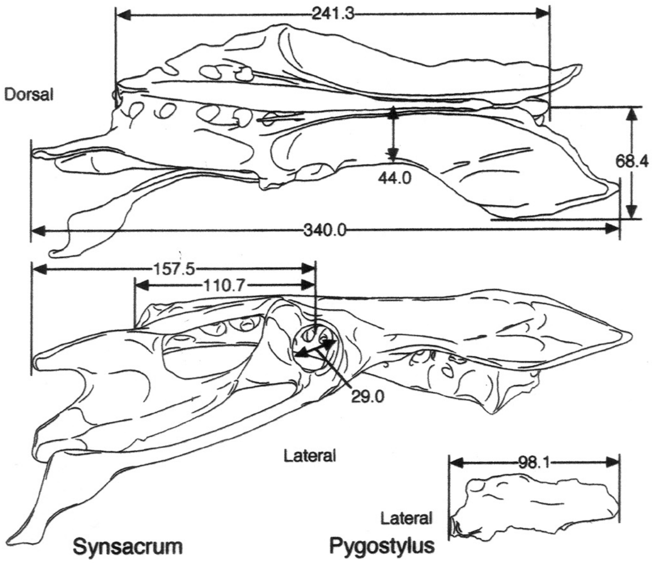
Scapula(R)



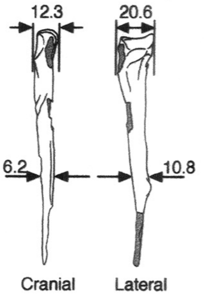
Furcula(L)



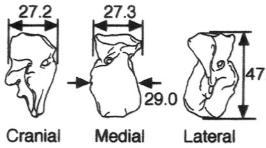
Coracoideum(R)



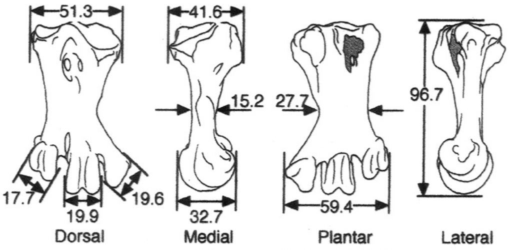
Synsacrum **Pygostylus**



Fibula(R)



Patella(R)



Tarsometatarsus(R)

100mm

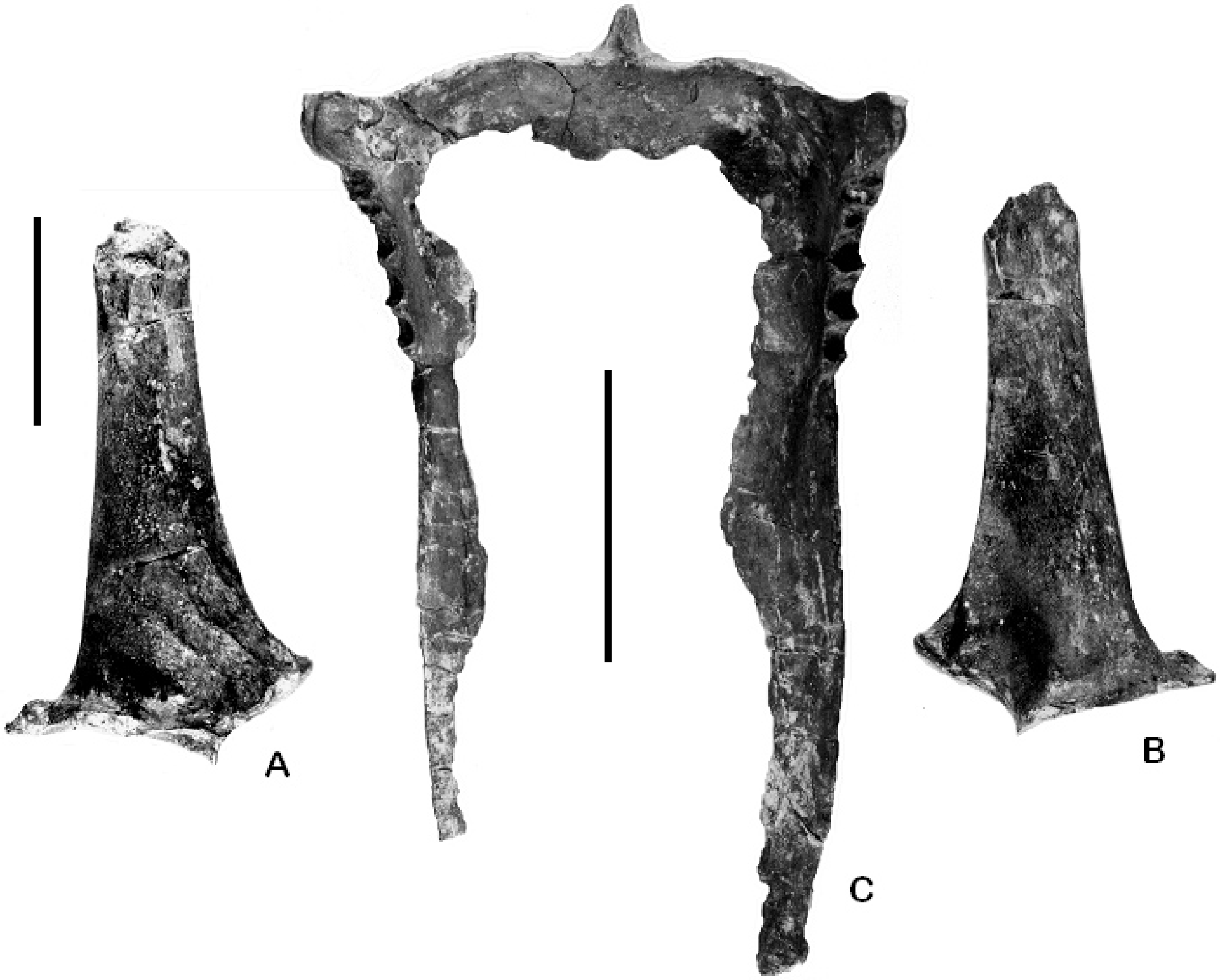


Figure 3 - *Hokkaidornis abashiriensis* new genus and species. *A*-*B*, distal portion of right coracoid; *A*, dorsal view; *B*, ventral view, scale bar is 50 mm long. *C*, sternum, dorsal view, scale bar is 100 mm long.

GEOLOGY, STRATIGRAPHY, AND AGE

The Abashiri specimen was found lying with its ventral side up, in a slightly muddy facies of a gray to grayish-white, structureless, fine-grained sandstone that was exposed in the banks of the Ubaranai River near the town of Abashiri, northeastern Hokkaido (Kimura et al., 1998). The skeleton was slightly disarticulated, but all of the bones were recovered from a very small area (Kimura et al., 1998). The sandstone is within the Tokoro Formation of Late Oligocene to Early Miocene age (Kato et al., 1990) and the facies corresponds to that described by Sasa and Inoue (1939).

The locality is in the center of the north-south trending Tokoro Unicline, and the area is underlain by the lower part of the Tokoro Formation (Wada and Hirota, 1989). There is no radiometric data for the age of the Tokoro Formation. The Tokoro Formation of the Tokoro-Memanbetsu area is correlative with the Tsubetsu Group of the Ponki area and the Kawakami Group of Kamiashoro-Honbetsu area (Fig. 1). The upper part of the Tsubetsu Formation is 23.8 +/-2.0 Ma (fission track, Matsui and Ganzawa, 1987) old. The Morawan Formation, correlative with the lower part of the Tokoro Formation, is 27.4+/-1.5 Ma (K-Ar) in age, and the Honbetsuzawa Formation is 29.2 +/- Ma (fission-track) in age. These data indicate that the age of the strata that yielded the Abashiri specimen is between 24 and 29 Ma, or Late Oligocene.

The fine-grained sandstone included thin beds of mudstone and medium to coarse-grained sandstone, in addition to limy sandstone nodules. Ripple marks occur on some sandstone bedding planes, and mollusks found with the skeleton included the bivalves *Periploma yokoyamai* and *Yoldia* sp., the gastropod *Turritella* sp., and the scaphopod *Dentalium* sp. These taxa together indicate a shallow marine environment (Shimada and Yazaki, 1958).

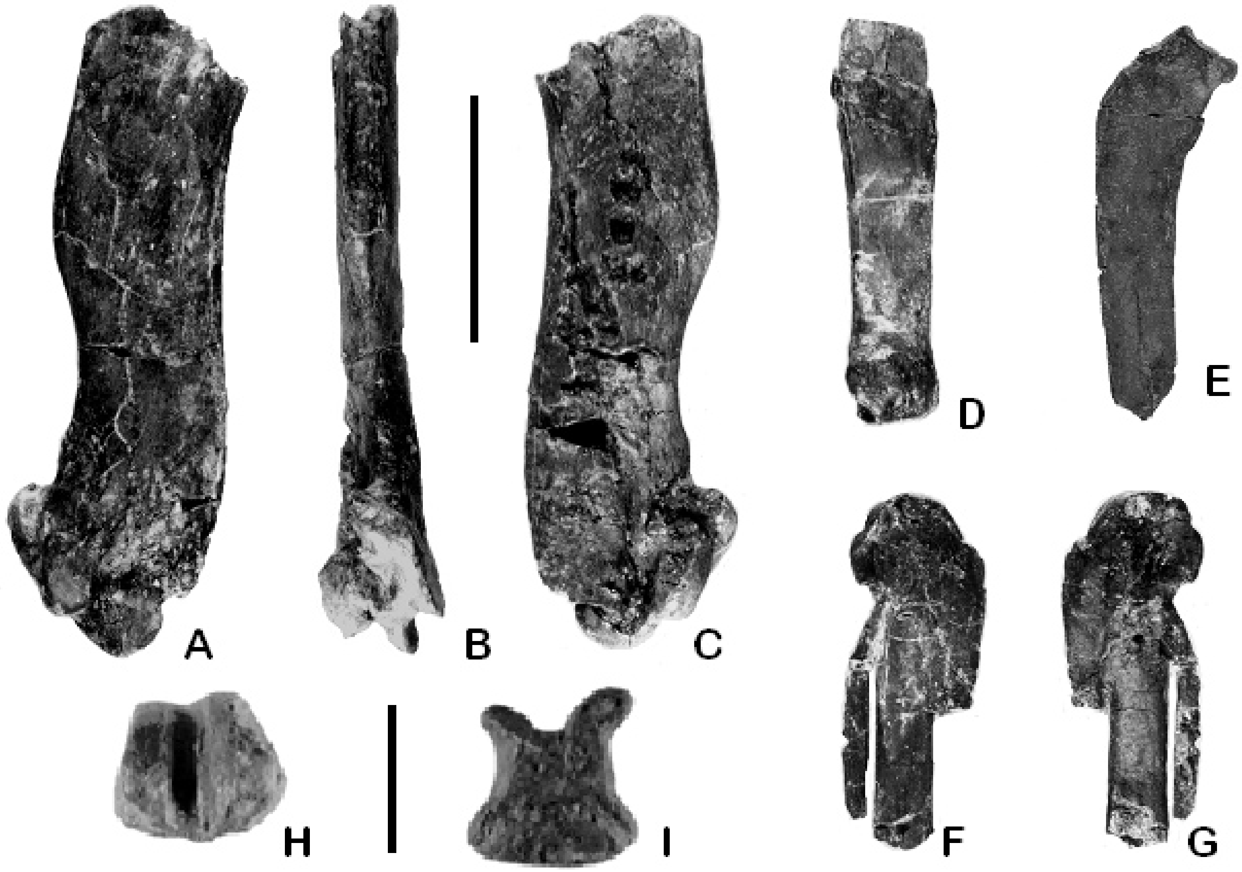


Figure 4 - Wing bones of *Hokkaidornis abashiriensis* new genus and species. *A-C*, distal portion of the left humerus; *A*, dorsal view; *B*, cranial view; *C*, ventral view. *D*, distal portion of the right ulna, ventral view. *E*, proximal portion of the right radius, ventral view. *F-G*, proximal portion of the right carpometacarpus; *F*, dorsal view; *G*, ventral view. Scale bar for *A-G* is 50 mm long. *H-I*, right radiale; *H*, cranial view; *I*, ventral view; scale bar is 10 mm long.

SYSTEMATIC PALEONTOLOGY

Suborder **SULAE** Sharpe, 1891

Remarks: Olson (1980) was able to confirm Howard's (1969) original diagnosis of the Plotopteridae as being a pelecaniform family, and listed characters to support inclusion of the Plotopteridae in the suborder Sulae, together with the families Sulidae, Anhingidae, and Phalacrocoracidae. According to Mayr (2004) the Plotopteridae and Spheniscidae are sister taxa that together form a clade that is the sister taxon to the Suloidea (a clade comprised of the families Sulidae, Phalacrocoracidae, and Anhingidae).

Family **PLOTOPTERIDAE** Howard, 1969

Type species: *Plotopterum joaquinensis* Howard, 1969.

Included genera: *Plotopterum* Howard, 1969; *Tonsala* Olson, 1980; *Phocavis* Goedert, 1988; *Copepteryx* Olson and Hasegawa, 1996; *Hokkaidornis* new genus.

Remarks: The Abashiri specimen is referred to the Plotopteridae on the basis of the following characters (see Olson, 1980, for a detailed diagnosis of the Plotopteridae): humerus with a flattened shaft, with distal end similar to that of Alcidae; ulna shortened, with a row of pits for attachment of secondaries; carpometacarpus short, flattened, with metacarpal I greatly elongated; coracoid shaft straight and elongate; scapula with a very thin and greatly expanded blade and very elongate acromion; femur similar to that of Anhingidae; tarsometatarsus shortened, with distal foramen continuous with intertrochlear notch.

We continue to provisionally recognize *Phocavis maritimus*, based on a tarsometatarsus from the Late Eocene or Earliest Oligocene Keasey Formation in Oregon, as a plotopterid. Mayr (2004) regarded the taxonomic position of *Phocavis* as uncertain, noting that it resembles the tarsometatarsus of the Early Eocene frigatebird, *Limnofregata azygosternon* Olson, 1977. The tarsometatarsus of *P. maritimus*

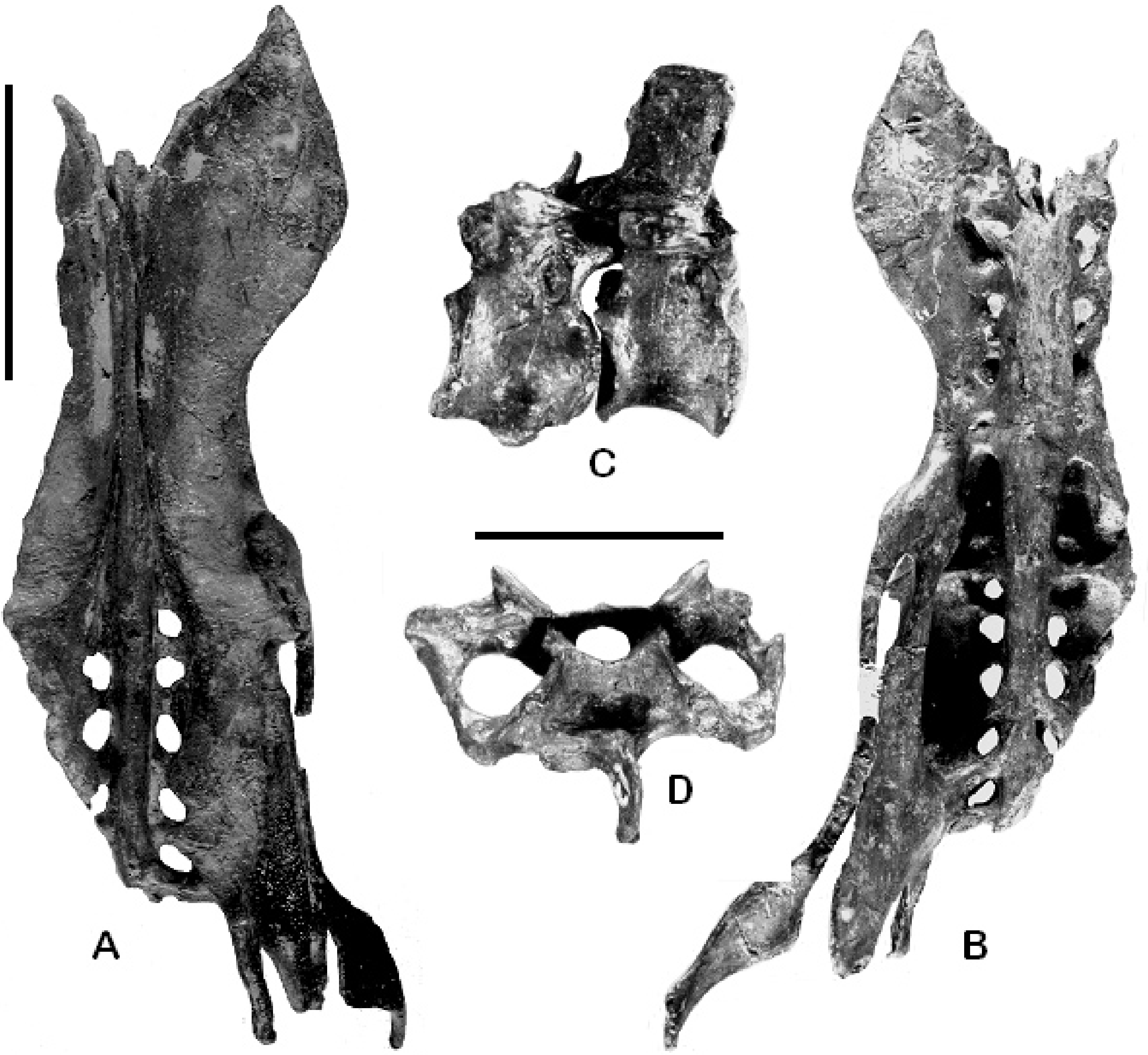


Figure 5 - Vertebrae and pelvis of *Hokkaidornis abashiriensis* new genus and species. *A-B*, pelvis; *A*, dorsal view; *B*, ventral view; scale bar is 100 mm long. *C*, thoracic vertebrae 36 and 37, right lateral view. *D*, cervical vertebra 13, anterior view. Scale for *C-D* is 50 mm long.

is more than twice the size of that of *L. azygosternon*, and much more robust. Development of the cotylae on the proximal end of the bone, as well as the expansion of the trochleae at its distal end is much more like that seen in plotopterids than in *L. azygosternon*. The closed distal foramen, which is continuous or open distally in other plotopterids for which that bone is known (although see figs. 2 and 6H herein), is the major reason that Mayr (2004) questions the affinities of *P. maritimus*.

In the following diagnosis and comparisons, we recognize only the holotype specimen (KMNH VP 200,006) and referred specimens from the Ainoshima Formation (KMNH VP 200,002; KMNH VP 200,005) as representing *Copepteryx hexeris*. The fragmentary tarsometatarsus and associated coracoid (F-5007) from the Shioda Bed, of the Nishisonogi Group also appear, tentatively, to be correctly referred (Olson and Hasegawa, 1996) to *C. hexeris*.

We tentatively accept other paratype specimens (KMNH VP 200,001; NSMT 15035) as representing *C. hexeris* as designated by Olson and Hasegawa (1996), but only because they are not referable to the new taxon from Hokkaido. They were not recovered from the same formation as the holotype of *C. hexeris* and are not directly comparable to the holotype or any of the other specimens from Ainoshima Island. The tarsometatarsus (F-5007) associated with a coracoid from the Nishisonogi Group is too fragmentary to al-

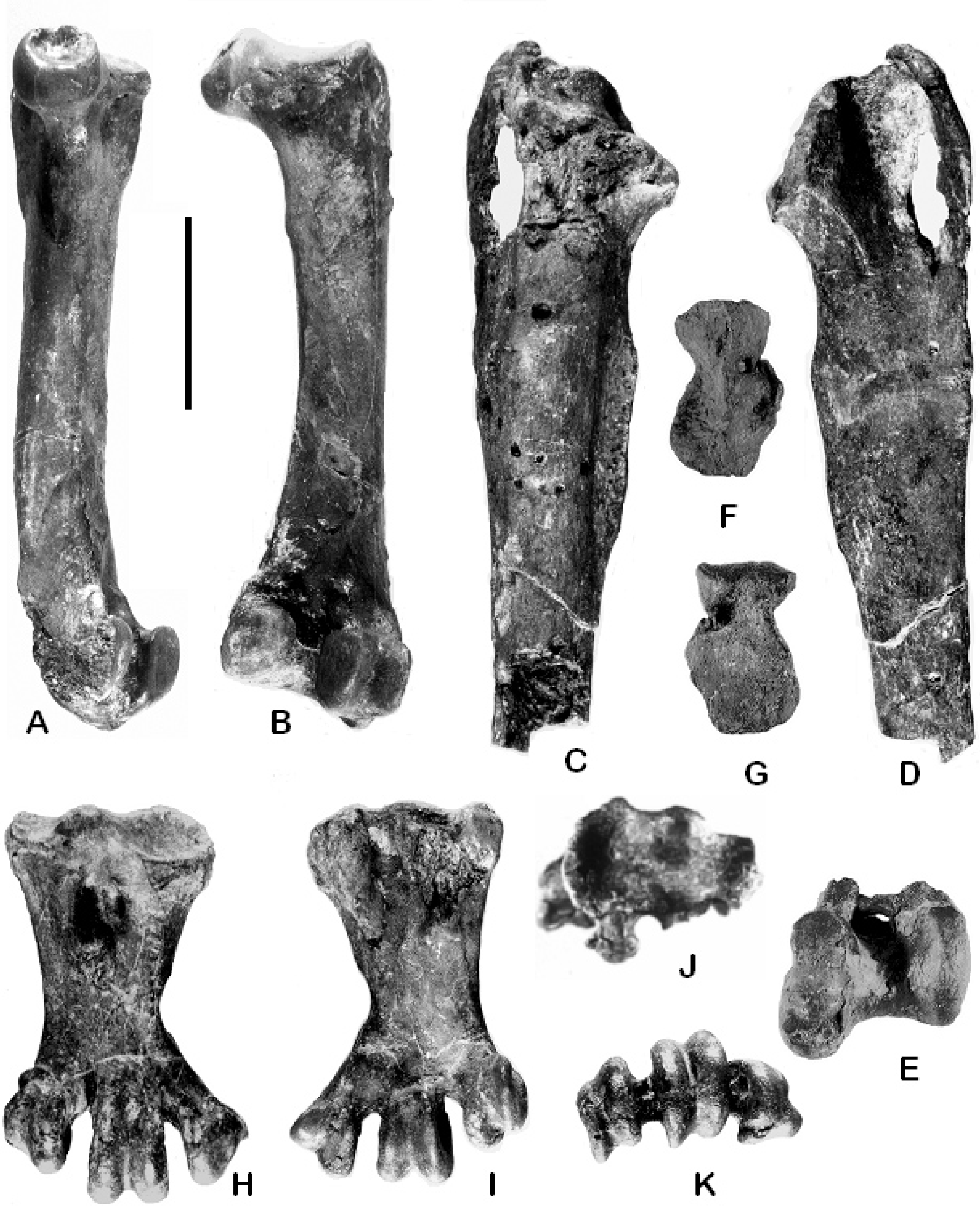


Figure 6 - Leg bones of *Hokkaidornis abashiriensis* new genus and species. *A-B*, right femur; *A*, medial view; *B*, caudal view. *C-D*, proximal portion of right tibiotarsus; *C*, caudal view; *D*, cranial view. *E*, distal end of left tibiotarsus, cranial view. *H-K*, right tarsometatarsus; *H*, dorsal view; *I*, plantar view; *J*, proximal view; *K*, distal view. Scale bar is 50 mm long.

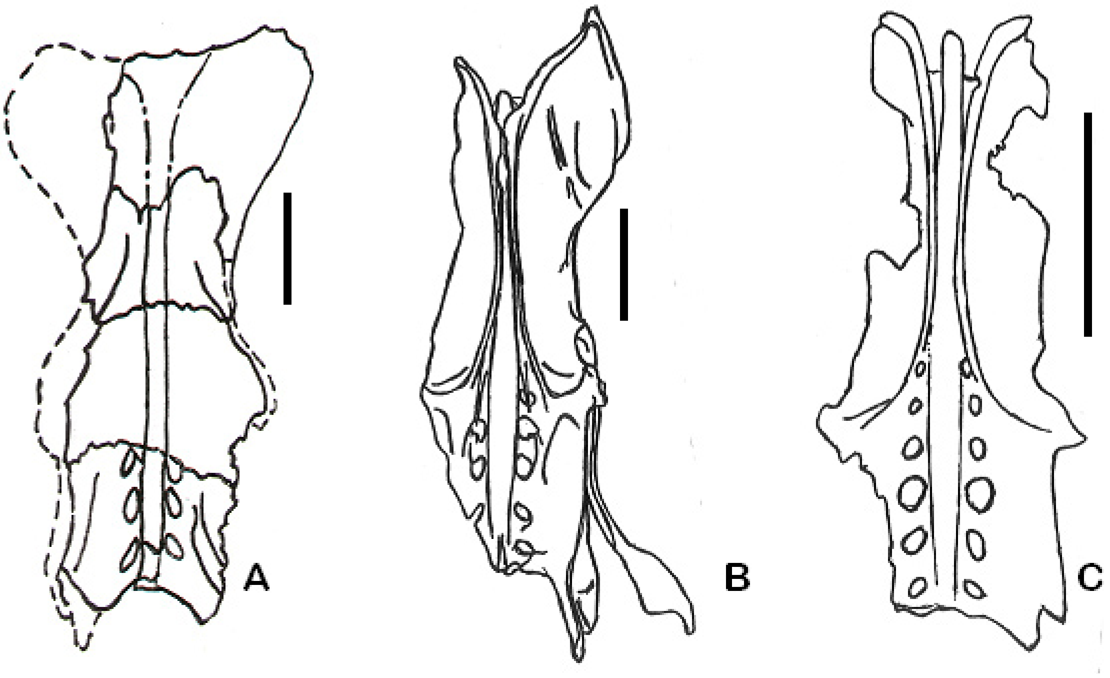


Figure 7 - Outline drawings comparing plotopterid pelves in dorsal view. *A*, *Copepteryx hexeris* Olson & Hasagawa, 1996; *B*, *Hokkaidornis abashiriensis* new genus and species; *C*, *Tonsala hildegardae* (from Goedert & Cornish, 2002). Scale bars equal 100 mm.

low accurate comparisons with either KMNH VP 200,001 or the new taxon from Hokkaido. The new specimen from Hokkaido demonstrates that there is more diversity within the Late Oligocene Plotopteridae than would have been otherwise suspected. It is possible that KMNH VP 200,001 and NSMT 15035 actually represent some other as yet unrecognized genus or species.

Genus ***HOKKAIDORNIS*** new genus

Type species: *Hokkaidornis abashiriensis*, new genus and species.

Differential diagnosis: Sternal end of coracoid differs greatly from that of *Copepteryx hexeris,* and also from that tentatively referred to *Tonsala* sp. (Olson and Hasegawa, 1996:fig. 1b) in having more angular sterno-coracoidal process; humerus with distal end differing from that of all other plotopterids in shape and arrangement of condyles (see Goedert and Cornish, 2002:fig. 4), with shaft more sinuous than that of *C. hexeris* and appearing more elongate than that of *Tonsala hildegardae* in palmar-anconal view; allular metacarpal of carpometacarpus not as long proportionately as in *C. hexeris*; femur much more robust than that of *T. hildegardae*, shaft more bowed with head more bulbous than that of either *C. titan* or those referred (Olson and Hasegawa, 1996:fig. 8b-c) to *C. hexeris*; tarsometatarsus much more robust and less elongate than that of *Phocavis maritimus*.

Etymology: Named for the island of Hokkaido, and *ornis*, Greek for bird.

Hokkaidornis abashiriensis new species

Figures 2-6, 7b

Plotopteridae gen. et sp. indet. (Kimura et al., 1998).

"Unidentified plotopterid" (Goedert and Cornish, 2002:67, fig. 3d).

Holotype: AMP 44 (originally cataloged at Hokkaido University of Education as HUES-10), partial skeleton, lacking the skull and some parts of the left side, but includes 10 ribs and 10 rib fragments, 5 partial cervical vertebrae, 1 complete and 5 partial thoracic vertebrae, 1 complete and 2 partial caudal vertebrae, partial sternum, proximal parts of the furcula, distal ends of both coracoids, partial right scapula, parts of both humeri, right radiale, proximal right radius, distal end of right ulna, proximal end of right carpometacarpus, pelvis, pygostyle, both femora, both patellae, parts of both tibiotarsi, parts of both fibulae, nearly complete right tarsometatarsus, 2 phalanx fragments.

Diagnosis: As for the genus, until additional species are found.

Measurements: See Figure 2 for location and orientation of measurements.

Locality: N43°58′, E144°04′. Banks of Ubaranai River, near Abashiri, Hokkaido, Japan.

Etymology: Named for the town of Abashiri. The town name is derived from the word "apashiri" meaning "to be discovered in rock" in the language of the aboriginal Ainu people of Hokkaido.

Comparisons: *Hokkaidornis abashiriensis* was one of the largest known plotopterids, comparable in size to *C. hexeris*. It was, therefore, much larger than any of the plotopterids from the eastern North Pacific Ocean. Bones discussed, but not photographed, are illustrated in fig. 2. as referenced.

***Sternum*:** The sterno-coracoidal margin of the sternum is not as anteriorly produced as in species of either the families Phalacrocoracidae or Anhingidae. The carina is missing, but the base of the anterior carinal margin is nearly in line with the anterior ends of the sterno-coracoidal processes. The anterior ends of the sterno-coracoidal processes are not directed dorsally as strongly as in the Phalacrocoracidae and Anhingidae. It is lacking the well-developed coracoidal grooves possessed by Phalacrocoracidae and Anhingidae; dorsally, the articular surface merges smoothly with the anterior part of the sternal plate, and ventrally they are well-defined only at the lateral margins. In ventral view, the lateral outline is most like that in *Phalacrocorax* spp., not extended laterally as in *Anhinga* spp. It is also much more flat in lateral view than the sternum of the Phalacrocoracidae and Anhingidae. Four well-defined costal facets are on each side.

***Furcula*:** Only the anterior ends (fig. 2) of the furcula are preserved. They are proportionately narrower and anteroposteriorly deeper than in the Phalacrocoracidae, more like the condition found in *Anhinga* spp. The coracoidal facets are proportionately smaller than those of the Phalacrocoracidae; however, they are a little chipped and would have been larger. The scapular tuberosities are relatively massive, with very short and pointed processes that reach only a few millimeters beyond the level of the coracoidal facet. These processes are not apparent in the furcula of *C. hexeris* and Olson and Hasegawa (1996:746, fig. 3) mention that they are 'altogether lacking'.

***Coracoid*:** Only the sternal ends of the coracoids are preserved for *Hokkaidornis abashiriensis*, however, these demonstrate more clearly than any of the other bones that the Hokkaido bird is generically distinct from both *Copepteryx hexeris* and *Tonsala*? sp. (Olson and Hasegawa, 1996:fig. 1b: KMNH VP 200,003). The distal end of the coracoid is proportionately less expanded mediolaterally than in *C. hexeris* (Olson and Hasegawa, 1996:figs. 1a, 2, 3). The sterno-coracoidal process is sharply angled anterolaterally, ending in a slight, but distinct hook, whereas it is blunt and nearly at the same level as the sternal facet in *C. hexeris*. Medially, the coracoid of *Hokkaidornis abashiriensis* ends in a distinct, delicate, flange-like spur.

The coracoid of *Hokkaidornis abashiriensis* differs from that of *Tonsala*? sp. (Olson and Hasegawa, 1996) in having a more evenly expanded distal end, a distinct flange-like spur medially, and a sterno-coracoidal process ending in a hook-like point.

***Scapula*:** Most of the right scapula (fig. 2) is preserved. It is much like that of *Tonsala hildegardae* in possessing a thin and greatly expanded blade with an elongated acromion.

***Humerus*:** A portion of the proximal end of the right humerus is preserved along with the distal part of the left. A brachial depression is present, distal width nearly the same as in *C. hexeris*, but the shaft is much broader, and more sinusoidal, somewhat like *T. hildegardae*. The external tricipital groove is much more broad than in *C. hexeris*. The shaft is more angular just proximal to the external condyle than in *C. hexeris*, again resembling *T. hildegardae* in this respect.

Only a small piece of the head of the right humerus was preserved. In palmar view, it appears as though the ligamental furrow widens anteriorly more abruptly than in *C. hexeris* (Olson and Hasegawa, 1996:fig. 4b). The internal tuberosity is more expanded than in *T. hildegardae* (Olson, 1980:fig. 2b). A very shallow groove, three-mm wide crosses the bicipital surface.

***Radiale*:** The right radiale is complete. On its dorsal surface is a deep, well-defined groove.

***Radius*:** The proximal half of the right radius is preserved and is flattened similar to that of *C. hexeris* (Olson and Hasegawa, 1996:figs. 5, 6b) and *T. hildegardae* (Olson, 1980:fig. 3d). It differs from that of *C. hexeris* in being slightly larger. The proximal part of the radius of *T. hildegardae* was originally interpreted (Olson, 1980) as being the distal end, but later (Olson and Hasegawa, 1996) discovered to be the proximal portion. It differs from the proximal radius of *T. hildegardae* in being much larger, more robust, with the cranial edge of the proximal bend more rounded.

***Ulna*:** The distal part of the right ulna is preserved and is similar to that of *C. hexeris*, but differs chiefly in being larger and slightly more robust. It is much larger and more robust than that of *T. hildegardae* (Olson, 1980:fig. 3a-c), but the ulna of *T. hildegardae* is not well enough preserved to allow more comparisons.

***Carpometacarpus*:** The proximal part of the right carpometacarpus is larger and more robust than that of *C. hexeris*. The intermetacarpal space is proportionately more narrow than in *C. hexeris* or *T. hildegardae* (Olson, 1980:fig. 3e-f). The allular metacarpal (I) is not as broad as in *C. hexeris* (Olson and Hasegawa, 1996:fig. 6c). The only other thing that can be said in comparison with *T. hildegardae* is that the carpometacarpus of *H. abashiriensis* is much larger and more robust. The carpometacarpus of an unnamed Late Eocene plotopterid from Washington State (Goedert and Cornish, 2002:fig 5c) differs from that of *H. abashiriensis* in having a longer allular metacarpal that is proportionately not as broad, and having an overall more elongate proximal end.

***Pelvis*:** The pelvis of *H. abashiriensis* is proportionately more narrow than that referred (Goedert and Cornish, 2002:fig. 7a-c) to *T. hildegardae*. Likewise, it appears to be more elongate than that referred to *C. hexeris* by Olson and Hasegawa (1996:fig. 7a), although that fragmentary specimen (KMNH VP 200,001) is heavily restored. In lateral view, the median ridge is concave anteriorly, whereas in the pelvis of *T. hildegardae* it is convex. The anterior iliac crest of *T. hildegardae* is more widely divergent anteriorly than that of *H. abashiriensis*. The pelvis of *H. abashiriensis* is very similar to that of *Anhinga* spp., especially the posterior half, but differs from that of both the Phalacrocoracidae and Anhingidae in the greater dorso-ventral expansion of the posterior portion of the pubis.

***Pygostylus*:** The left side of the pygostylus (fig. 2) is preserved and it is a long, tall platelike structure.

***Femur*:** The left femur is complete and the right femur is nearly so. The femora of *H. abashiriensis* differ from those referred to *T. hildegardae* by Goedert and Cornish (2002:figs. 6d-h) and *Plotopterum* sp. by Olson and Hasegawa (1985) in being much larger, more robust, and proportionately less elongate. The femora of *H. abashiriensis* are most similar to those referred to *C. hexeris* by Olson and Hasegawa (1996:figs. 8b-c), and of these, appears to bear closest similarity to the "Orio specimen" (KMNH VP 200,001). The femora of *H. abashiriensis* differ from that of *C. titan* Olson and Hasegawa (1996: figs 8a, 11a-b) in having a more inflated or bulbous head, with the head elevated more proximally (posteriorly), distal end not as deep, with a proportionately wider intercondylar fossa.

***Patella*:** Both patellae are complete. This bone in *H. abashiriensis* is a rather complicated structure and is very heavy. It has the transverse perforation for the tendon of the ambiens muscle as described by Olson (1980:55, fig. 3h) for *T. hildegardae*. In *H. abashiriensis*, this perforation becomes a well-defined channel posterolaterally. The proximal end of the patella is broad, flattened, and has a roughened surface. There is a distinct ridge on the distal half of the anterior face.

***Tibiotarsus*:** The anterior part of the shaft and the distal end of the left tibiotarsus, and the proximal half of the right tibiotarsus are preserved. The tibiotarsus of *H. abashiriensis* has an anteroposteriorly flattened shaft that is well excavated below the head. It is similar in size and proportion to that referred to *Copepteryx hexeris* (KMNH VP 200,001; Olson and Hasegawa, 1996: figs. 9a-b). The surface of the proximal end is strongly directed posteriorly, the flexor attachment is large with a small crest on the external border. The fibular crest is thick anteroposteriorly but not as prominent as that of *Copepteryx hexeris*. The area between the distal ends of the cnemial crests appears to be proportionately less broad than the same in *C. hexeris*.

This bone appears to be more robust than the tibiotarsi referred to *Tonsala hildegardae* (Goedert and Cornish, 2002:fig. 6i, k). The proximal end of the tibiotarsus of *H. abashiriensis* differs from that of *T. hildegardae* in the following respects: in posterior view, the proximal (articular) surface of the head slopes more steeply mediolaterally; articular surface is proportionately wider; the area of the shaft between the fibular crest and articular surface is more inflated; fibular crest more prominent.

The distal end of the tibiotarsus of *H. abashiriensis* differs from that referred to *C. hexeris* (Olson and Hasegawa, 1996: fig. 7b) in that the supratendinal bridge is more distally located.

***Fibula*:** The proximal part of the right fibula (fig. 2) and the shaft of the left are preserved. The fibula of *H. abashiriensis* is much more robust than that referred (Goedert and Cornish, 2002:fig. 6j, 6l) to *T. hildegardae*. The proximal surface of the head has an anteroposterior ridge separating two long and shallow cotylae in *T. hildegardae*, whereas in *H. abashiriensis* the articular suface makes a smooth transition from the internal surface to the external edge.

***Tarsometatarsus*:** The right tarsometatarsus is nearly complete. The tarsometatarsus of *H. abashiriensis* differs significantly from that of the smaller and more elongate holotype specimen (LACM 123897) of *Phocavis maritimus* Goedert, 1988, from Oregon (Goedert and Cornish, 2002: fig. 3). In most respects, however, this bone is nearly indistinguishable from that of the paratype specimen (KMNH VP 200,001) of *C. hexeris* (Olson and Hasegawa, 1996:figs. 10a-d). If we did not know more about the skeleton of *H. abashiriensis*, this tarsometatarsus, if found isolated, would probably have been referred to *C. hexeris* as well. The internal calcaneal ridge (crista medialis hypotarsi) appears to be somewhat less bulbous, and the trochleae seem a little larger, proportionately, and more defined than in *C. hexeris*, but the differences are slight. The distal foramen is open by a gap of about one mm, but may have been originally bridged by thin bone.

CONCLUSIONS

As noted by Fordyce and Jones (1990), the structure of bones of the legs of penguins (analogues of plotopterids sensu Olson and Hasegawa, 1979; sister taxa to plotopterids sensu Mayr, 2004), and the tarsometatarsi especially, likely reflect evolutionary selection of features related to loadbearing and upright low-speed bipedalism in a relatively heavy bird. Therefore, the few differences discernable in the leg bones designated as paratypes of *C. hexeris* (Olson and Hasegawa, 1996) and those of *H. abashiriensis*, especially for the tarsometatarsus, would not be unexpected in these evolutionarily conservative elements. However, because the differences between some of the specimens referred to *C. hexeris* by Olson and Hasegawa (1996) and *H. abashiriensis* from Hokkaido appear to be so slight, the identity of some of the paratype specimens of *C. hexeris* must now be regarded as tentative until the discovery of material from the posterior part of the skeleton that can be unequivocally assigned to that species.

The largest plotopterid known has so far only been reported in an abstract (Kawano and Kawano, 2001), but if estimates of it size (up to twice the size of *C. hexeris*) hold true, it will be the largest seabird to ever have existed. The pattern in the northwestern Pacific Ocean, where the largest plotopterids evolved in Late Oligocene time (Olson and Hasegawa, 1979, 1996), is quite different from the situation in the northeastern Pacific Ocean, where the largest known plotopterids (all much smaller than the large Japanese species) are found in the oldest rocks (Goedert and Cornish, 2002).

There is still nothing known regarding the origins of the Plotopteridae. Plotopterid fossils have been reported from California, Oregon, and Washington along the northeastern Pacific Ocean, and all of the northwestern Pacific Ocean fossils are from Japan. Olson and Hasegawa (1996:742) mention undescribed plotopterid fossils, representing as many as six species, from Late Eocene to Early Oligocene rocks of Japan. Slightly fewer species appear to have been present in the northeastern Pacific Ocean during Late Eocene to Early Oligocene time (Barnes and Goedert, 1996; Goedert and Cornish, 2002). This Late Eocene-Early Oligocene diversity coupled with the observations that the earliest plotopterids were already highly derived for underwater flight obviously points to much earlier origins. Mayr (2004) has stressed similarities between some Late Oligocene plotopterid fossils and some of the oldest penguin fossils. Comparison of bones from the oldest (Late Eocene and Early Oligocene) plotopterid taxa, for example the femur of an undescribed species (Goedert and Cornish, 2002:fig. 5e) and femora referred to *Tonsala hildegardae* (Goedert and Cornish, 2002:fig 6d-h) from the late Early Oligocene part of the Pysht Formation, with that of the Eocene penguin described by Clarke et al. (2003:fig. 5) better illustrate the differences. The leg bones of geochronologically older plotopterid fossils (e.g., Goedert and Cornish, 2002: figs. 3a-c, 5e, 6d-l) are more gracile and elongate than those of Late Oligocene plotopterids and of even the oldest penguins, a function not only of smaller body size with consequently less weight to bear, but also reflecting ancestry. Likewise, regarding bones of the wing, there are as many differences between the older plotopterid fossils and the oldest penguin fossils as there are similarities. For example, compare the Late Eocene distal humerus and associated carpometacarpus illustrated by Goedert and Cornish (2002; figs.4c, 5c) with the fossil penguin bones illustrated by Simpson (1971; fig. 5) and Marples (1952; plate 5, figs. 6-8, 10). Further discussion regarding whether the similarities between bones of plotopterids and penguins reflect convergence or common ancestry is beyond the scope of this paper. The idea put forth by Mayr (2004) is stimulating, but Mayr noted and future researchers should bear in mind Olson's (1980: 56) comment regarding "blind adherence to cladistic methodology".

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