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Source: Paleontological Research, 25(2) : 145-159

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/2020PR018

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Paleontological Research, vol. 25, no. 2, pp. 145–159, April 1, 2021
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doi:10.2517/2020PR018

Early Plotopteridae specimens (Aves) from the Itanoura and Kakinoura Formations (latest Eocene to early Oligocene), Saikai, Nagasaki Prefecture, western Japan

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Received September 23, 2019; Revised manuscript accepted April 29, 2020

Abstract. Plotopterids, commonly known as "penguin-like birds", are wing-propelled diving birds known from the latest Eocene to middle Miocene in the eastern and western Pacific Rim. Here, we describe two new specimens of the family Plotopteridae, a right femur from the Itanoura Formation (latest Eocene to earliest Oligocene), and a distal half of a right tibiotarsus from the Kakinoura Formation (early Oligocene), both at the lower part of the Nishisonogi Group, Saikai City, Nagasaki Prefecture, Kyushu, southwestern Japan. The femur is slightly younger than or potentially as old as the earliest plotopterid known from Japan and the U.S.A. CT scanning revealed that it has a dense cortical bone, justifying its taxonomic assignment to the family Plotopteridae. It resembles the femur of *Olympidytes*, which was previously considered endemic to North America, in its femoral neck, well developed trochanter femoris, and straight facies articularis antitrochanterica, but is not assignable to any known genus. The tibiotarsus resembles that of *Olympidytes* in the presence of a well-developed trochlea catilaginis tibialis, a large embossment lateral to the pons supratendineus, and a deep incisura intercondylaris, and therefore referable to *Olympidytes*. The possibility of hindlimb-propelled diving in the family Plotopteidae was also discussed. These new specimens suggest the early diversity of the family in Japan was higher than previously thought.

Key words: Eocene-Oligocene boundary, femur, Kyushu, Nishisonogi Group, Plotopteridae, tibiotarsus

Introduction

The family Plotopteridae Howard, 1969 consists of wing-propelled diving seabirds that flourished from the late Eocene to middle Miocene in the northern Pacific (e.g. Howard, 1966; Hasegawa *et al*., 1979; Olson and Hasegawa, 1979, 1985, 1996; Olson, 1980; Goedert, 1988; Sakurai *et al*., 2008; Dyke *et al*., 2011; Kaiser *et al*., 2015; Mayr and Goedert, 2016). In their review of the family, Ando and Fordyce (2014) noted that Plotopteridae reached its diversity peak in the late Oligocene. Since then, three new plotopterid genera were additionally recognized, and now eleven species in eight genera are known from North America and Japan (*Plotopterum* Howard, 1969; *Tonsala* Olson, 1980 *sensu* Mayr and Goedert, 2016; *Phocavis* Goedert, 1988; *Copepteryx* Olson and Hasegawa, 1996; *Hokkaidornis* Sakurai, Kimura and Katoh, 2008; *Stemec* Kaiser, Watanabe and Johns, 2015; *Olympidytes* Mayr and Goedert, 2016; and *Klallamornis* Mayr and Goedert, 2016). *Copepteryx* and *Hokkaidornis* are recognized as endemic to Japan (Olson and Hasegawa, 1996; Sakurai *et al*., 2008), while *Stemec*, *Olympidytes*, *Klallamornis*, and *Phocavis* are so far only known from North America.

This family, known as a group of "penguin-like birds", is generally regarded as closely related to the seabird or water bird families Anhingidae Reichenbach, 1852 and Phalacrocoracidae Reichenbach, 1852 (Howard, 1969; Olson and Hasegawa, 1979, 1996; Sakurai *et al*., 2008; Smith, 2010; Ando and Fordyce, 2013; Mayr, 2017; Ando and Fukata, 2018), although its phylogenetic position remains open to discussion. Mayr (2005) and Kawabe *et al.* (2014) suggested a close relationship between Plotopteridae and penguins (Order Sphenischiformes Sharpe, 1891), based on the similarities of their forelimbs (Mayr, 2005) and brains (Kawabe *et al*., 2014). Mayr and Goedert (2018) recently erected the subfamily Tonsalinae, which includes *Tonsala*, *Olympidytes*, *Klallamornis*, *Copepteryx*, and *Hokkaidornis* based on the synapomorphic characters of the coracoid and tarsometatarsus. However,

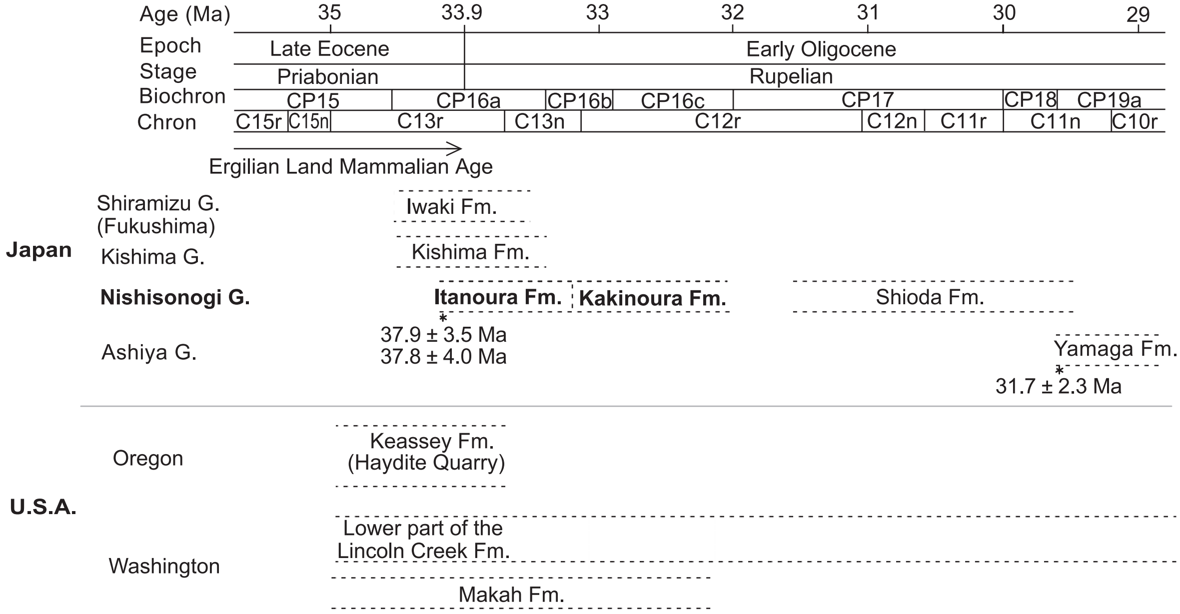

Figure 1. Chronostratigraphy of plotopterid-bearing formations from the latest Eocene to early Oligocene, in Japan and the U.S.A. The asterisks indicate the approximate horizons of the radiometric ages (FT) constrained the plotopterid ages in Japan. Although not figured here, the FT-age of the Sari Formation underlying the Yukiaino Formation (Kishima Group) was reported as 33.9 ± 3.3 Ma (Miyachi and Sakai, 1991).

a cladistic analysis has not been conducted due to the paucity and incompleteness of material.

The early plotopterids have been recorded from the U.S.A. and Japan (Figure 1), and the beginning of inter-Pacific plotopterid diversity slightly predates the Eocene–Oligocene boundary (*ca.* 33.9 Ma; Vandenberghe *et al.*, 2012). These earliest plotopterid materials show derived features in the humerus and coracoid as a wing-propelled diving seabird; thus, Goedert and Cornish (2002) assumed that plotopterids originated even earlier than the early Eocene. Currently, the Eocene–Oligocene boundary is placed within the paleomagnetic interval Chron C13r (*ca.* 35.0-33.7 Ma; Vandenberghe *et al.*, 2012). The oldest possible plotopterid in the U.S.A. is the latest Eocene *Phocavis maritimus*, discovered from the Haydite Quarry of the Keasey Formation, Oregon (Goedert, 1988), probably within Chron C13r (Prothero and Hankins, 2000). In Washington State, one of the earliest plotopterids, ‘*Tonsala*’ *buchanani* Dyke, Wang and Habib, 2011, was collected from the Whiskey Creek, late Eocene and lower Oligocene portion of the Makah Formation (Dyke *et al.*, 2011; Mayr, 2015; Mayr and Goedert, 2016), which spans from the Chron C12r to C13r (Prothero *et al.*, 2009). Also from Washington, *Olympidytes thieli* was reported from the lower part of the Lincoln Creek Formation, which is the late Eocene or early Oligocene in age (Mayr and Goedert, 2016). However, the ages of the early plotopterid horizons in Washington are poorly constrained. According to Mayr and Goedert (2016), the generic assignment of ‘*Tonsala*’ *buchanani* by Dyke *et al.* (2011) is questionable, because the species represents more than one taxon (Mayr and Goedert, 2016) and we follow their taxonomic treatment for the Washington species here. The Jansen Creek Member, an upper part of the Makah Formation, also yields ?*Klallamornis clarki*, *Tonsala* cf. *hildegardae*, and unidentified plotopterid materials (Mayr and Goedert, 2016, 2018). Although Prothero *et al.* (2009) concluded that the Jansen Creek Member is C12r (early Oligocene) from their magnetostratigraphy study, Mayr and Goedert (2016, 2018) consider the Jansen Creek Member can be as old as late Eocene.

In Japan, more than a hundred of plotopterid specimens were collected in the late 1980s from the upper part of the Iwaki Formation (Shiramizu Group), Fukushima, and were briefly reported (Koda *et al.*, 1991). The plotopterid assemblage was found with other avian taxa belonging to six families: Pelagornithidae Fürbringer, 1888, Alcidae Leach, 1820, Sulidae Reichenbach, 1849, Accipitridae Vieillot, 1816, Anatidae Leach, 1820, and Phalacrocoracidae (Koda *et al.*, 1991). These avian specimens, including plotopterids, are not formally described, but the plotopterid assemblage is potentially the oldest record in the western Pacific Rim (Tsubamoto *et al.*, 2015). The age of the Iwaki assemblage is ambiguous, although the Asagai Formation which overlies the Iwaki Formation is correlated within the nannofossil zone CP 16 (latest Eocene to earliest Oligocene) based on dinoflagellate and calcareous nannofossils (Kurita and Matsuoka, 1994;

Kato *et al.*, 1996; Kurita, 2004; Suto *et al.*, 2005). Suto *et al.* (2005) concluded the upper Iwaki Formation is the earliest Oligocene in age based on the terrestrial floral and molluscan faunal shifts of the formation (Suto *et al.*, 2005, and literature cited therein). Some avian taxa from the formation, including two sulid species (*Morus* sp. and *Sula* sp.) and anatine and anserine anatids, also seem to be known from the early Oligocene and the later ages (Koda *et al.*, 1991). However, Tsubamoto *et al.* (2015) recently reevaluated a small mammal assemblage from the upper part of the Iwaki Formation and suggested that the formation is correlated to the late Eocene Ergilian (=Priabonian) Asian Land Mammal Age (Russel and Zhai, 1987). As noted above, the ages of the early plotopterids in U.S.A. and Japan are also not definitive.

Here we report two plotopterid specimens, a right femur from the Itanoura Formation (latest Eocene to earliest Oligocene), and a distal portion of the right tibiotarsus, from the Kakinoura Formation (early Oligocene), both from the lower part of the Nishisonogi Group, Saikai, Nagasaki Prefecture, Kyushu, Japan (Figure 2A). The femur (SM–SKT–940) is one of the oldest plotopterid specimens known from the U.S.A. and Japan, but it is not similar to those of any other plotopterid taxa. The tibiotarsus (SM–SKT–1153) is slightly younger and is referable to *Olympidytes*, a plotopterid genus previously unknown from Japan. They suggest the early Oligocene Plotopterid diversity in Japan was higher than previously reported.

Plotopterids in western Japan

The northern part of Kyushu Island (i.e. Fukuoka, Saga, and Nagasaki prefectures) and Yamaguchi Prefecture, western Japan, are known for several important records of plotopterid diversity from the Ashiya, Kishima and Nishisonogi groups (Figure 2A; Hasegawa *et al.*, 1979; Olson and Hasegawa, 1996; Okazaki, 2009; Ohashi *et al.*, 2011; Matsuoka *et al.*, 2014; Ando, 2017; Ohashi, 2017; Ando and Fukata, 2018). Among many plotopterid specimens from this region, the specimens from the Ashiya Group are particularly well documented (Hasegawa *et al.*, 1979; Olson and Hasegawa, 1996; Ando, 2017; Ohashi, 2017; Ando and Fukata, 2018). Indeed, only two taxa, *Copepteryx hexeris* and *C. titan*, are formally described from Kyushu and Yamaguchi Prefecture (Olson and Hasegawa, 1996), based on postcranial material including femora from the several localities of the Yamaga Formation, the basal part of the Ashiya Group, Fukuoka Prefecture. Other remains of *Copepteryx hexeris* (a tarsometatarsus and a coracoid) were also reported from the early Oligocene Shioda Formation, upper part of the Nishisonogi Group, Saikai, Nagasaki Prefecture (Hasegawa *et al.*, 1979; Olson and Hasegawa, 1996). The Yamaga Formation of Ashiya Group yielded a skull and a mandible each of unnamed species (Olson and Hasegawa, 1996; Kawabe *et al.*, 2014). Although the fission-track age of the Yamaga Formation was previously reported as 31.7 ± 2.3 Ma (Ozaki and Hamasaki, 1991), the calcareous nannoflora of the formation is assigned within the subzone CP19a (Okada, 1992), which extends late early to early late Oligocene (29.62–26.84 Ma; Vandenberghe *et al.*, 2012). Besides, some plotopterid specimens were described from the Jinnobaru Formation of the Ashiya Group that are stratigraphically above the Yamaga Formation. Olson and Hasegawa (1996) reported a coracoid tentatively assigned to *Tonsala* sp. from the Jinnobaru Formation, Hikoshima Island, Yamaguchi Prefecture. Recently, the cranial end of a plotopterid scapula was described from the same locality (Ando and Fukata, 2018).

A furcula of *Copepteryx* sp., found in the Kishima Formation of the Kishima Group (Okazaki, 2009), is one of the oldest plotopterid specimens in western Japan, and is probably coeval with the plotopterid femur (SM–SKT–940) described here. According to Okada (1992), the calcareous nannoflora of the Kishima Formation belongs to the CP16a, which is currently estimated to range between 34.44 and 33.43Ma (latest Eocene to earliest Oligocene; Vandenberghe *et al.*, 2012). Although not formally described, one plotopterid cranium was reported from the Yukiaino Formation (late Oligocene) of the Kishima Group (Hasegawa *et al.*, 1979; Olson and Hasegawa, 1996).

Unlike in the North America, small Oligocene plotopterid materials have been rarely reported in Japan. For example, *Copepteryx* mentioned above is the largest plotopterid genus (Olson and Hasegawa, 1979, 1996), and the coracoid and furcula reported from Hikoshima, Yamaguchi Prefectures are intermediate in size between *Copepteryx* and the American *Tonsala* material (Olson and Hasegawa, 1996; Ando and Fukata, 2018). Exceptions are relatively small plotopterid specimens from the Iwaki Formation, Fukushima, which are not formally reported. Our new specimens are comparable to North American plotopterids in size, thus contribute to our understanding of early plotopterid diversity in Japan.

Methods

The newly discovered materials were directly compared and described with other plotopterid materials (*Copepteryx titan*, KMNH-VP.200.006; *C. hexeris*, KMNH-VP.200.001 [femur], cast of NSMT-PV-15035; *Hokkaidornis abashiriensis*, cast of AMP 44; *Plotopterum* sp., cast of MFM 18000). Other specimens in the

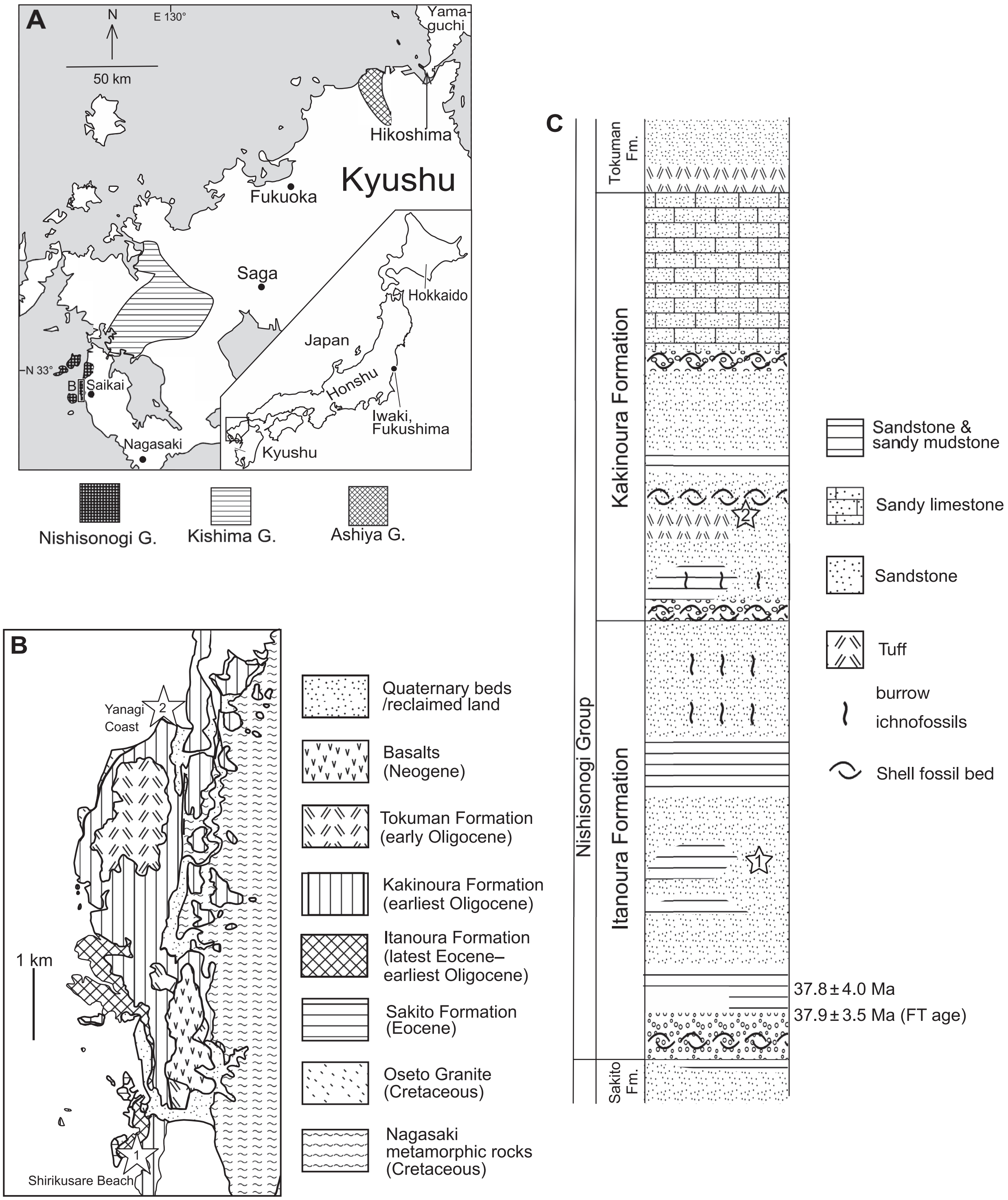

Figure 2. Local stratigraphy and geology. **A,** Plotopterid–bearing strata (stratigraphic group level) in Kyushu and Yamaguchi, western Japan; **B,** geological map of the region; **C,** stratigraphic column based on Hattori *et al.* (1993; fig. 20) showing the fossil horizons. The star marks 1 and 2 represent the localities and horizons for the femur (SM–SKT–940) and tibiotarsus (SM–SKT–1153), respectively.

text were cited from the literature as mentioned below. Measurements were made with a digital caliper (Bigman, Miki, Japan) to the nearest 0.1 mm for the newly discovered specimens, and a measurement tape (Topman, Miki, Japan) were also used for *Copepteryx* specimens housed in Kitakyushu Natural History Museum to the nearest 1 mm. For description and direction, we followed the terminology from Baumel and Witmer (1993).

X-ray computed tomography scanning

To better understand bone microanatomy and the fossil preservation, we scanned the femur (SM-SKT 940) on a microfocus X-ray computerized tomography (CT) system, TXS320-ACTIS (TESCO Co., Yokohama, Japan), at the Fukui Prefectural Dinosaur Museum, Katsuyama, Fukui, Japan. Stacks of the CT images were used to produce virtual renderings (voxel resolution: 0.0476 mm × 0.0476 mm × 0.1 mm) by the software VGStudio Max 2.1 (Volume Graphics, Heidelberg, Germany). To analyze the femoral shaft, its cross-section views were reproduced from the renderings with VGStudio Max 2.1 after the coordination of the axes.

The cross-sectional views of the femoral shaft were analyzed using Bone Profiler (ver. 4.5.8; Girondot and Laurin, 2003) to estimate cortico-diaphyseal index (CDI, thickness of the bone cortex divided by the radius of shaft; Castanet *et al.*, 2000) and compactness (a measure of the distribution of bone presence; Girondot and Laurin, 2003). We followed Ksepka *et al.* (2015) for the image preparation. CDI and compactness values were compared with those of Sphenisciformes and volant birds reported in De Margerie *et al.* (2005) and Ksepka *et al.* (2015). The CDI values reported by De Margerie *et al.* (2005) includes that of great cormorant (*Phalacrocorax carbo* Linnaeus, 1758), a volant bird that is capable of marine diving.

Abbreviations.—AMP, Ashoro Museum of Paleontology, Ashoro, Japan; CDI, cortico-diaphyseal index; KMNH, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; MFM, Mizunami Fossil Museum, Mizunami, Japan; NSMT-VP, National Science Museum, Tokyo, Japan; SM-SKT, Sakito History and Folklore Museum, Saikai, Japan; WGS, world geodetic system.

Systematic paleontology

Class Aves Linnaeus, 1758
Family Plotopteridae Howard, 1969
Plotopteridae gen. et sp. indet.

Material.—SM–SKT–940, a right femur (Figure 4, 5).

Localities and geological settings.—The femur (SM–SKT–940) was discovered from the Shirikusari Beach, Setofukushima, Saikai City. 32°55’36” N, 129°38’16” E (WGS 84 datum), middle part of the Itanoura Formation, latest Eocene or earliest Oligocene. It was found in a medium-grained sandstone, about 40 m above the bottom of the Itanoura Formation (about 90 m in total thickness), from the basal part of the Nishisonogi Group (Figure 2BC). The Itanoura Formation is mainly composed of cross-laminated sandstones and yields numerous marine molluscan fossils reflecting shallow marine depositional environments (e.g. Nagao, 1928; Mizuno, 1964; Hattori *et al.*, 1993). Miyachi and Sakai (1991) reported the fission track dating (37.8±4.0 Ma and 37.9±3.5 Ma) of the tuff and tuffaceous layers interbedded in the basal part of the Itanoura Formation, which supports the correlation to the late Eocene in age. In addition, Okada (1992) assigned the calcareous nannoflora from the lower part of the Itanoura Formation to the CP16a subzone (*ca.* 34.44-33.43 Ma, the latest Eocene to earliest Oligocene; Vandenberghe *et al.*, 2012) and the upper part of the formation to the following early Oligocene CP16b subzone (*ca.* 33.43-32.92 Ma). These fission track and nannofloral ages support that the Eocene–Oligocene boundary is potentially positioned within the lower half of the Itanoura Formation; thus, the horizon of SM–SKT–940 in the middle part of the formation should be viewed as close to the Eocene–Oligocene boundary. However, no evidence clarifies the position of

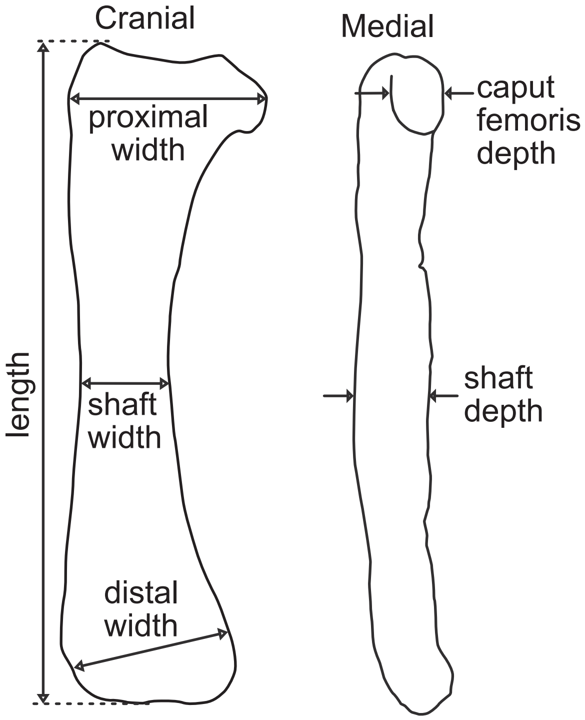

Figure 3. Measured loci for the femur (SM–SKT–940).

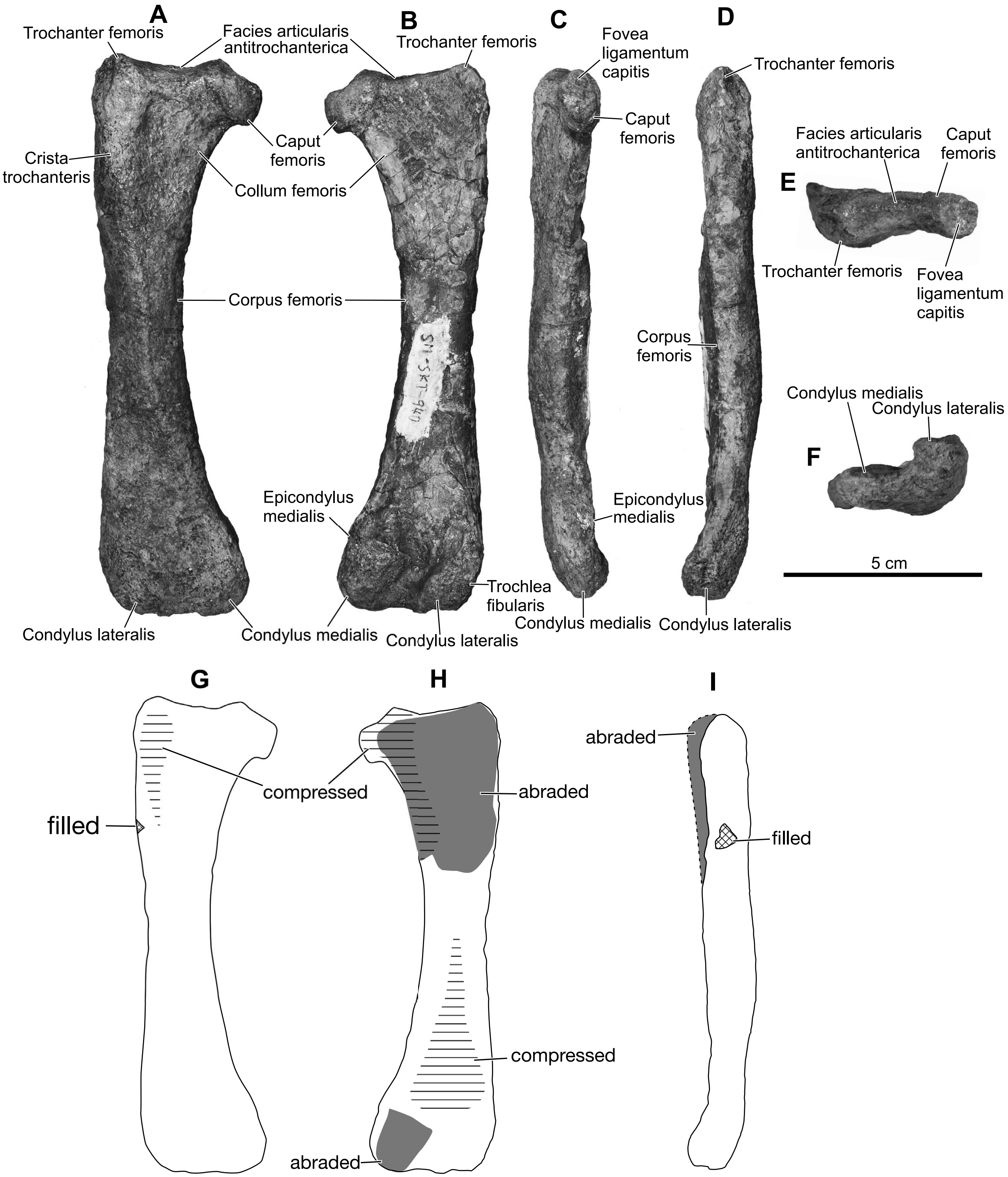

Figure 4. Photograph SM–SKT–940, a right femur of Plotopteridae gen. et sp. indet. Cranial (**A**), caudal (**B**), medial (**C**), lateral (**D**), proximal (**E**) and distal (**F**) views. Breakage of the specimen in cranial (**G**), caudal (**H**), and lateral (**I**) views.

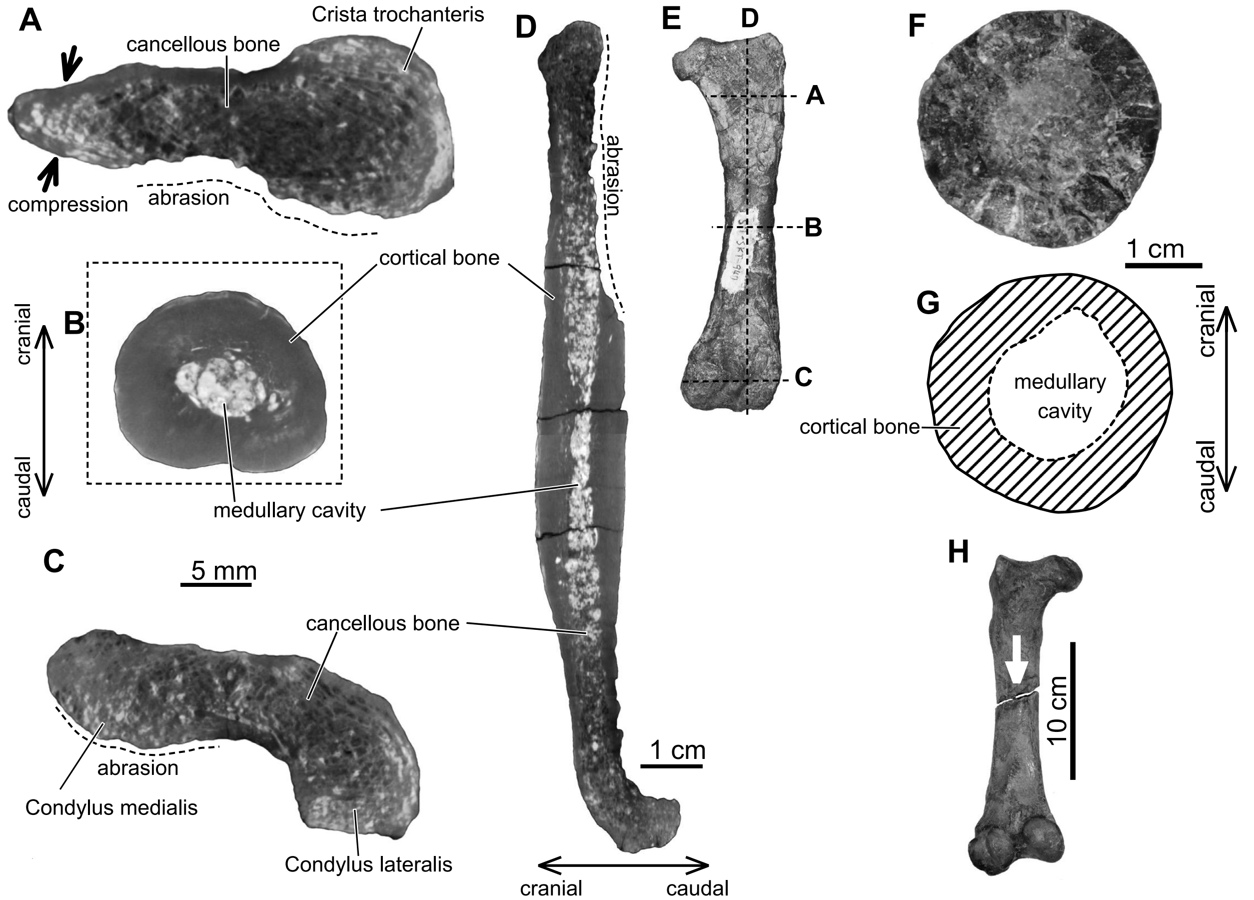

Figure 5. CT images of SM–SKT–940, a right femur of Plotopteridae gen. et sp. indet. (A, B, C, D, E), compared with the left femur (KMNH-VP-200.004) of *Copepteryx titan* (F, G, H). Horizontal sectional views at proximal (**A**), middle (**B**), distal (**C**) parts, and vertical sectional view of the whole (**D**). **E,** portions of the CT images of SM–SKT–940. Note that the proximal part shows both a partial compression (a pair of black arrows) and abrasion (A, D), whereas the mediocaudal surface of the distal condyle show essentially the abrasion. **F,** the cross section of the middle shaft in KMNH-VP-200.004 with its interpretation (**G**). The position of F and G is indicated in **H** (the white arrow).

the Eocene–Oligocene boundary in the formation, and some workers believe the Itanoura Formation is younger than the Eocene–Oligocene boundary without reasonable geochronological evidence (cf. Yamaguchi, 2004; Yamaguchi *et al*., 2006).

Measurements.—Length = 136.5 mm; Proximal width = 41.5 mm; Caput femoris depth = 11.3 mm; Shaft width = 18.4 mm; Shaft depth = 14.8 mm; Distal width = 35.9 mm (see Figure 3 for the loci).

Description and comparison.—When discovered, the caudal surface of the specimen was completely exposed and partially worn. The specimen is craniocaudally compressed and abraded (Figure 4G–I). Particularly, the caudal surface of the proximal region and the condylus medialis is severely abraded and/or compressed, so that these regions are presumably half as thick as the original condition. However, our CT scanning images (Figure 5A–D) show these deformations mostly affected the craniocaudal axis, and based on our observation, many bone trabeculae are distorted parallel to the bone surface (Figure 5AC). Coupled with the fact the specimen was found with its caudal surface facing up, we assume that its outline in the transverse section is more or less preserved, and thus described it primarily based on the observations on the cranial and caudal view.

SM–SKT–940, about 14 cm in length, is smaller than *Copepteryx* and *Hokkaidornis* femora. The genus *Copepteryx* is remarkable for their large body sizes as diving avian taxa; the femora of *C. hexeris* and *C. titan* are 19 and 22 cm in length, respectively, almost twice as long as that of the largest living diving bird, the Emperor penguin (Olson and Hasegawa, 1996). Also, *Hokkaidornis abashiriensis* from Hokkaido Island, northern Japan, is the second-largest plotopterid genus ever described, with its femur being 17.9 cm long (Sakurai *et al*., 2008). Instead, SM–SKT–940 is comparable to those of medium-

Table 1. Comparison of plotopterid femora. [a] Measured by authors; [b] after Olson and Hasegawa (1996); [c] after Sakurai *et al.* (2008); [d] after Dyke *et al.* (2011); [e] after Mayr and Goedert (2016); [f] after Olson and Hasegawa (1985); For the specimen measured by the authors, see Figure 3 for the measured loci. For other specimens, corresponding lengths were cited from the literature.

Taxon	Length	Proximal width	Shaft width	Shaft depth	Distal width	Femoral neck
SM–SKT–940[a]	136.5	41.5	18.4	14.8	35.9	Yes
Copepteryx titan (KMNH-VP.200.004)[b]	223	65.5	32	31	66.5	No
C. hexeris (KMNH-VP.200.001)[b]	190+	56	–	–	–	No
C. hexeris (NSMT-VP-15035)[b]	198	60	26.5	27.5	56	No
Hokkaidornis abashiriensis (AMP 44)[c]	178.9	–	22.8	25	51.5	No
Tonsala hildegardae (UWBM 86873)[d]	106.5	24.2	11	–	23.6	Yes
'T.' buchanani (UWBM 86870)[d]	135.1	31.2	14.4	–	25.2	Yes
Olympidytes thieli (right, SMF Av 608)[e]	111.2	28.6	–	–	27.1	Yes
Klallamornis abyssa (SMF Av 610)[e]	~143	–	–	–	~34	?
Plotopterum sp. (MFM 1800)[f]	70.5	17.5	7.2	6.8	17.5	Yes

sized North American plotopterids, *'Tonsala' buchanani* and *Klallamornis abyssa*, and is somewhat larger than that of holotype *Olympidytes thieli* (Table 2). However, Mayr and Goedert (2016) stated that the femoral lengths of *'Tonsala' buchanani* were overestimated due to the intervening matrix. Therefore, only *Klallamornis* reliably matches the size of SM–SKT–940. Despite its size, the shaft and distal end of SM–SKT–940 are wide, being as stout as in large Japanese plotopterids (*Copepteryx* and *Hokkaidornis*), and stouter than the small to medium–sized North American plotopterids (*Tonsala*, and *Klallamornis*), with *Olympidytes* being an intermediate of these two groups. Nevertheless, this stoutness is partly attributable to the deformation.

There are some plotopterid femora in the collection from the Iwaki Formation (Iwaki City, latest Eocene), reported by Koda *et al.* (1991). Among these, a right femur (I-416049) is comparable to SM–SKT–940 in size and stoutness of the shaft (the shaft width is 17 mm, and the total length is estimated to be *ca.* 150 mm). However, this femur is incomplete, missing both proximal and distal ends. Therefore, further comparison with the materials from the Iwaki Formation cannot be made.

The caput femoris of SM–SKT–940 is craniocaudally compressed; its fovea ligamentum capitis is oval, not circular as in other plotopterid femora, but it is most likely due to postmortem compression. In craniocaudal view, it resembles those of *Tonsala* and *Olympidytes* (Figure 6C–E), in that it is short and wide, and not bulbous as in *Copepteryx titan* (Figure 6G). The ventral margin of the caput femoris extends more medioventrally than the ventral margin of the collum femoris, forming a characteristic constriction, femoral neck. The constriction is well developed in smaller species (i.e., *Tonsala* and *Olympidytes*, Figure 6C–E), whereas it is not seen in larger species (*Copepteryx* and *Hokkaidornis*, Figure 6F–H). The presence of a femoral neck in *Klallamornis* is not clear because of the breakage (G. Mayr, personal communication). The collum femoris of SM–SKT–940 is medioventrally wide, but this is likely attributable to the deformation, based on our observation on the CT images (Figure 5A). The trochanter femoris is well developed, with its proximal end is proximodistally at about the same level as the proximal edge of the caput femoris, as in *Olympidytes*, *Copepteryx*, and *Hokkaidornis* (Figure 6E–H). The trochanter femoris is less developed in *Plotopterum* and *Tonsala* (Figure 6B–D). In contrast, SM–SKT–940 is similar to *Plotopterum*, *Tonsala*, and also *Olympidytes* (Figure 6A–E) in that the contour of the facies articularis antitrochanterica is straight, in contrast to the deeply concave facies articularis antitrochanterica in *Copepteryx* and *Hokkaidornis* (Figure 6F–H). The shaft of the femur is straight and cylindrical. As in *Copepteryx hexeris*, SM–SKT–940 lacks a bulge on its lateral edge, seen in some of the plotopterid taxa (Figure 6B–E, G). SM–SKT–940 differs from any other plotopterids in that its sulcus patellaris intercondylaris is inconspicuous. As in *Tonsala buchanani*, the condylus medialis of SM–SKT–940 extends distally so that its distal edge is proximodistally at the same level with the condylus lateralis, although this is probably because its distal end is strongly compressed.

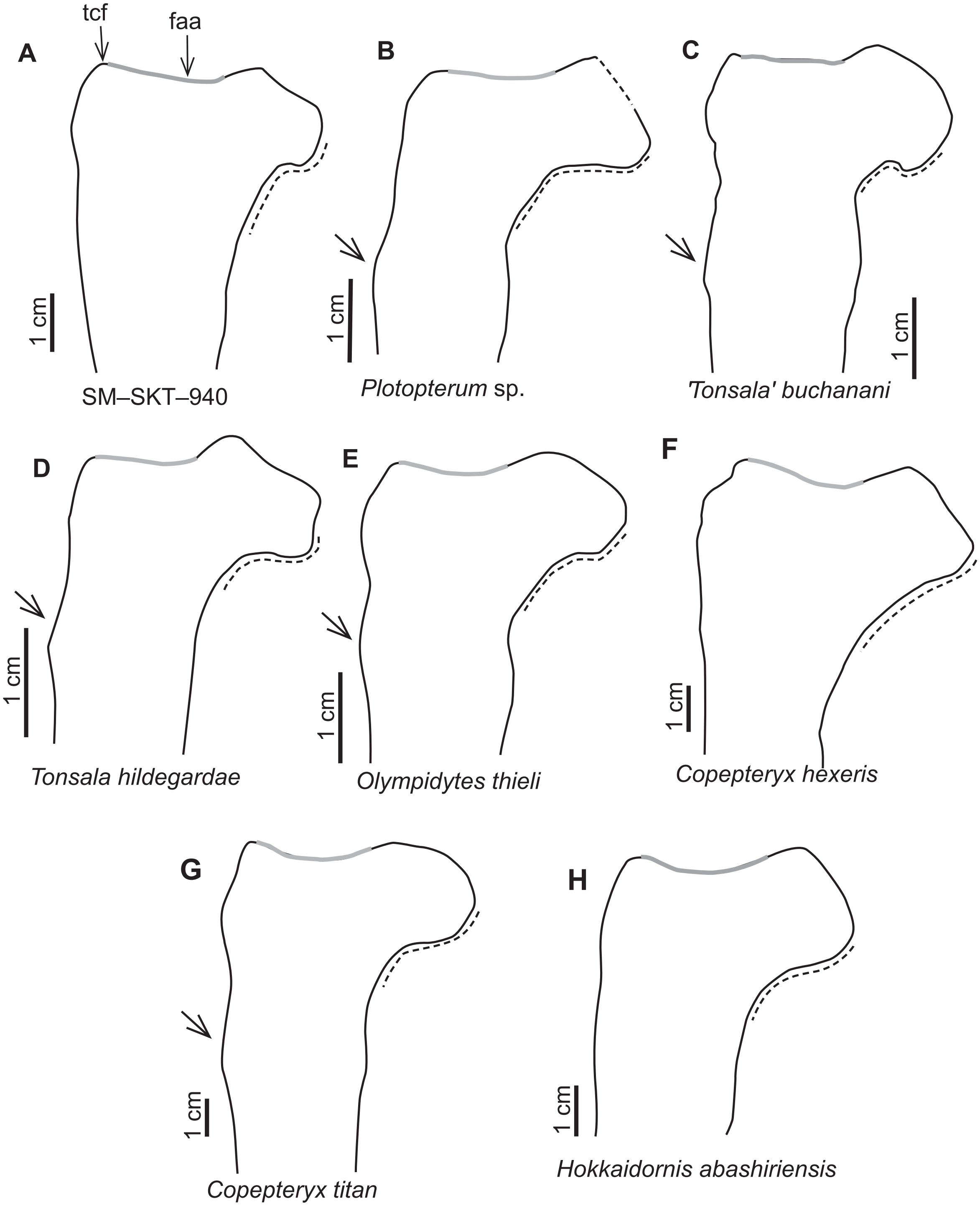

Figure 6. Morphological variety of the proximal femora of plotopterids. **A**, SM–SKT–940; **B**, *Plotopterum* sp. (MFM 1800, Olson and Hasegawa, 1996: fig. 1a, reversed); **C**, '*Tonsala' buchanani* (UWBM 86871, Dyke *et al.*, 2011: fig. 2p); **D**, *T. hildegardae* (UWBM86873, Goedert and Cornish, 2002: fig. 6d); **E**, *Olympidytes thieli* (SMF Av 608, Mayr and Goedert, 2016: fig. 2s); **F**, *Copepteryx hexeris* (NSMT-PV-15035); **G**, *C. titan* (KMNH-VP-200,004), and **H**, *Hokkaidornis abashiriensis* (AMP 44, Sakurai *et al.*, 2008; fig. 6b, reversed). B, C, D, E and H are drawn from the Figures of references. Note that A, B, C, D, and E each has a femoral neck, while F, G and H each lacks it. Also, in A, E, F, G, H each the trochanter femoris is well developed, and the facies articularis antitrochanterica is moderately concave, in contrast to B, C, D (see text). The arrows indicate the lateral bulge, seen in some of the plotopterid taxa but not in SM–SKT–940. Abbreviations: cfm, caput femoris; faa, facies articularis antitrochanterica; tcf, trochanter femoris.

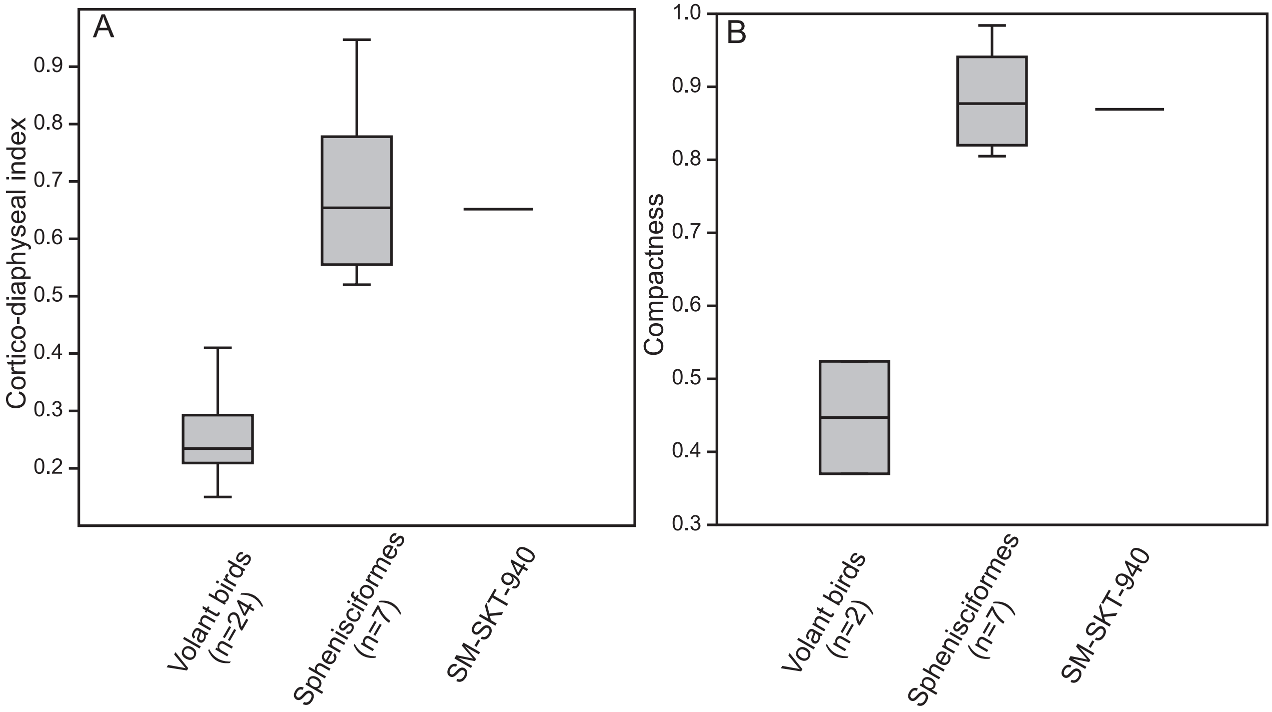

Figure 7. Box plots of the femoral mid-section cortico-diaphyseal index (CDI) (**A**), and compactness (**B**). The original data, beside SM–SKT–940, were from De Margerie *et al.* (2005) and Ksepka *et al.* (2015).

Microanatomical features.—A thick cortical bone and small medullary cavity were seen at the mid-section of the femur (Figure 5B). Similarly, a thick cortical bone is also seen in *Copepteryx titan* femur (KMNH-VP-200,004; Figure 5FG). At the mid-shaft of SM–SKT–940, the CDI and compactness are 0.65 and 0.87 respectively. Both the CDI and compactness are within the range of Sphenisciformes (0.52–0.95 and 0.81–0.98), and outside the range of volant birds (0.15–0.41 and 0.32–0.21) (Figure 7AB; De Margerie *et al.*, 2005; Ksepka *et al.*, 2015). The CDI value of the great cormorant, a diving and volant bird, is within the range of other volant birds. Thus, the high CDI and compactness of SM–SKT–940 imply its non-volant and diving behavior, as seen in extant penguins (i.e., Meister, 1962; Olson and Hasegawa, 1979; De Margerie *et al.*, 2005).

Remarks.—The femori of the families Plotopteridae, Phalacrocoracidae, Anhingidae, and order Sphenisciformes are characterized by robustness in the femoral head region when compared to other marine birds (e.g., albatross, auk, and Frigate birds). In addition, many plotopterids (Olson and Hasegawa, 1979, 1996; Mayr and Goedert, 2016) and penguins (Huxley, 1859; Wiman, 1905; Tambussi *et al.*, 2005; Clarke *et al.*, 2007, 2010; Ksepka and Clarke, 2010; Mayr, 2017) are known for their large size. The robustness and size of SM–SKT–940 are comparable to those of the plotopterids and penguins: although SM–SKT–940 is not the largest, but still larger than the femori of most birds and emperor penguins (~100–120 mm, see Ksepka *et al.*, 2015 and Mayr *et al.*, 2017). In addition, the thick cortical bone seen in SM–SKT–940 is a common feature of non-volant diving birds, and it is explained as an adaptation to reduce buoyancy (Olson and Hasegawa, 1979; Wall, 1983; Habib and Ruff, 2008). The presence of the thick cortical bone in the plotopterid femur has been reported in previous studies (Hasegawa *et al.*, 1979; Koda *et al.*, 1991) and regarded as a common character of plotopterids (Olson and Hasegawa, 1979; Mayr, 2005) and penguins (Meister, 1962; De Margerie *et al.*, 2005; Ksepka *et al.*, 2015). We also showed that *C. titan* femur had a thick cortical bone (Figure 5FG). However, large penguin femori can generally be distinguished from those of plotopterids and SM–SKT–940 in that they are even more massive and stout, and their articular heads/condyles are much well developed. Coupled with the fact that the penguin fossils are not known from Japan and northern Pacific, SM–SKT–940 is assigned to the family Plotopteridae.

SM–SKT–940 is distinct from *Copepteryx* and *Hokkaidornis*, two Oligocene plotopterid genera reported from Japan, in its smaller size, the short and wide caput femoris, straight edge of the facies articularis antitrochanterica, and having a femoral neck constriction. In these respects, it is similar to medium sized North American plotopterids, namely *'Tonsala' buchanani* and *Olympidytes*. Although SM–SKT–940 differs from these taxa in its stoutness, a taxonomically informative character for plotopterids (Mayr and Goedert, 2016, 2018), the deformed nature of SM–SKT–940 makes it difficult to confidently count it as a diagnostic character of the specimen. Among the North American plotopterids, SM–SKT–940 most resembles *Olympidytes* in that the trochanter femoris is well developed, straight facies articularis antitrochanterica. However, it cannot be distinguished from *Klallamornis*, because its femoral morphology is not well known, as it is damaged and partially covered by a rib and ilium. In addition, SM–SKT–940 differs from *Olympidytes* in that it lacks the lateral bulge (Figure 6E), which is a rather unique character among the family Plotopteridae, shared only with *Copepteryx hexeris* and *Hokkaidornis*. Therefore, at this point it is difficult to refer the specimen to any known plotopterid taxon.

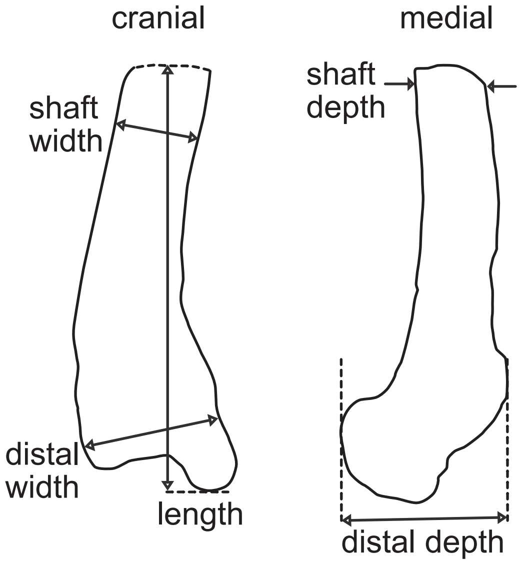

Figure 8. Measured loci for the tibiotarsus (SM–SKT–1153).

Family Plotopteridae Howard, 1969
Cf. *Olympidytes* sp. Mayr and Goedert, 2016

Material.—SM–SKT–1153, a distal portion of the right tibiotarsus (Figure 9).

Locality and geological setting.—The tibiotarsus (SM–SKT–1153) was discovered from the Yanagi Coast, Saikai City, Nagasaki Prefecture, lower part of the Kakinoura Formation (Nishisonogi Group, Figure 2BC). The specific horizon is a shell bed of *Ostrea lunaeformis*, reported by Hattori *et al.* (1993). Calcareous nannofossils of the Kakinoura Formation (Okada, 1992) are of CP16b-c (33.9-32.0 Ma; Anthonissen and Ogg, 2012), indicating the early Oligocene. This result is congruent with the detrital zircon age, 33.9±3.3 Ma, of a tuff layer of the Sari Formation (Kishima Group; Miyachi and Sakai, 1991), which correlates to the Tokuman Formation overlying the Kakinoura Formation.

Measurements.—length (as preserved) = 58.8 mm; shaft width = 11.5 mm; shaft depth = 7.9 mm (measured by a cast); distal width = 19.3 mm; distal depth = 21.3 mm (see Figure 8 for the loci).

Description.—The partial right tibiotarsus (Figure 9) is comparable to the smallest plotopterid tibiotarsi (Table 3). The specimen resembles *Olympidytes* in many aspects. The sulcus extensorius is proportionally narrow with a thick medial wall. The pons supratendineus is proportionally wider, and its lateral side is slightly narrower than in the medial side. The embossment located lateral to the pons supratendineus is large. In the cranial view, the incisura intercondylaris is deep. In these respects, the specimen does not differ from *Olympidytes*. However, SM–SKT–1153 lacks the deep sulcus lateral of the pons supratendineus, a diagnostic character of *Olympidytes*. Unlike in *Copepteryx hexeris*, the proximal part of the medial ridge does not show lateral inflection, and in this aspect, it is similar to in *Tonsala, Klallamornis*, and *Olympidytes*. The rostral edge of the condylus lateralis is damaged. On the caudal side, the trochlea cartilaginis tibialis is well developed; the sulcus inside it is concave, and its medial edge of the trochlea cartilaginis tibialis forms a high ridge and extends mediocaudally. The trochlea cartilaginis tibialis is variably developed in plotopterids; whereas in *Tonsala* and *Klallamornis*, the medial edge is low, and the sulcus is rather flat. In these respects, SM–SKT–1153 again resembles *Olympidytes*. Also, in SM–SKT–1153 and *Olympidytes*, the proximal edge of this ridge and caudal surface of the shaft form a relatively steep angle in medial view. The condylus medialis is larger than the condylus lateralis and extends more distally, which is a common character seen in plotopterids (Mayr and Goedert, 2016). Caudodistal part of the tibiotarsus is broken. The broken proximal shaft (Figure 9D) shows a very thick compact bone with a limited spongy bone zone.

Remarks.—The extended condylus medialis of SM–SKT–1153 and the dense bone histology both indicate the specimen belongs to the family Plotopteridae. Its size is comparable to small plotopterid genera, *Tonsala* and *Olympidytes*, reported in North America. Although SM–SKT–1153 is closer to that of *T. hildegardae* in size, morphologically it is most similar to *Olympidytes* as shown above. However, it differs from the holotype of *O. thieli*

Table 2. Comparative measurements of the plotopterid tibiotarsus. For the upper case letters, refer to Table 1. [a] Measured by authors; [b] After Olson and Hasegawa (1996); [c] after Sakurai *et al.* (2008); [d] after Mayr *et al.* (2015); [e] after Mayr and Goedert (2016). For the specimen measured by the authors, see Figure 8 for the measured loci. For other specimens, corresponding lengths were cited from the literature.

Taxon	Total length	Shaft width	Shaft depth	Distal width	Distal depth
SM–SKT–1153[a]	–	11.5	7.9	19.3	21.3
Copepteryx hexeris (KMNH VP 200,001)[b]	~300	23.6	17.7	~51	–
Hokkaidornis abashiriensis (AMP 44)[c]	–	24.4	18.4	45.3	–
Tonsala hildegardae (right, Av 601)[d]	~155.0	11.4	–	21	–
Olympidytes thieli (right, SMF Av 608)[e]	177.1	–	–	23.6	–

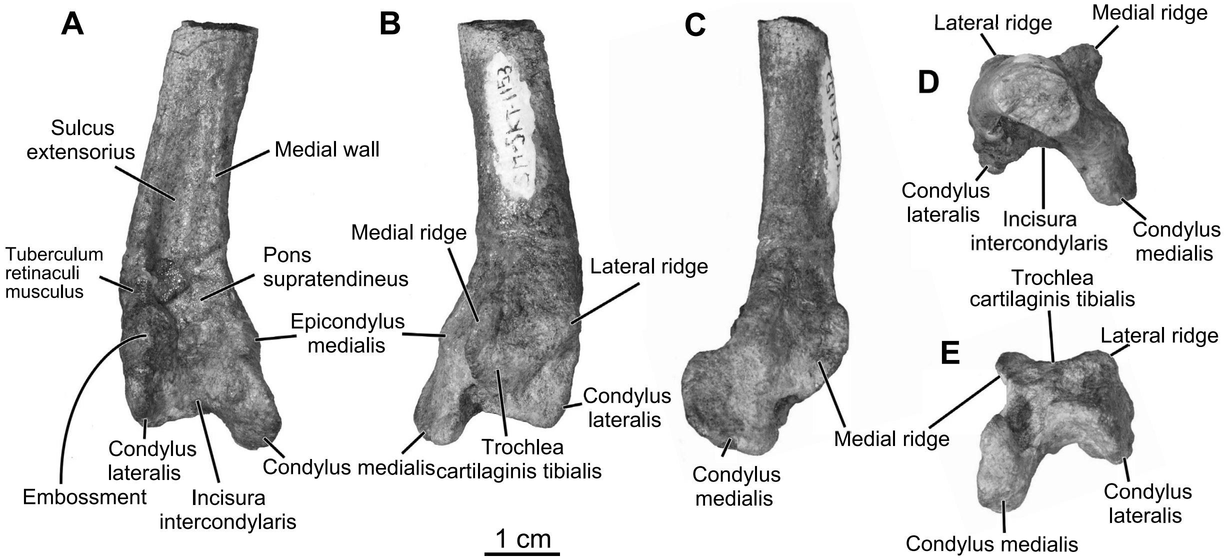

Figure 9. SM–SKT–1153, a distal portion of the right tibiotarsus of cf. *Olympidytes* sp. Cranial (**A**), caudal (**B**), medial (**C**), proximal (**D**), and distal (**E**) views.

in that it lacks the developed sulcus for tendon of musculus fibularis brevis lateral of pons supratendineus, a diagnostic character of *Olympidytes* (Mayr and Goedert, 2016). For this reason, we only tentatively refer the specimen to the genus *Olympidytes*.

Water birds generally have a variably developed trochlea cartilaginis tibialis with a deep sulcus and high ridges (Smith, 2010), and the specimens of *Olympidytes*, including SM–SKT–1153, are not an exception. The trochlea cartilaginis tibialis accommodates cartigo tibialis, on which tendons of musclus gastrochemius and superficial flexors ride (Baumel and Witmer, 1993). Therefore, the development of the trochlea cartilaginis tibialis is related to the plantar flexion movement of the distal hind limbs, which is crucial in the hindlimb-propelled diving or swimming. The trochlea cartilaginis tibialis is variably developed among the plotopterids: It was less developed in *Tonsala* and *Klallamornis*, but *Hokkaidornis* and *Olympidytes* had well-developed trochlea cartilaginis tibialis. This possibly suggests that *Hokkaidornis* and *Olympidytes* were using their hindlimbs for swimming in addition to their wing-propelled diving.

Discussion and conclusion

Up until now, only specimens of *Copepteryx* were reported from around the Eocene–Oligocene boundary in western Japan, or Saga (Okazaki, 2009) and Iwaki (Hasegawa *et al.*, 1979; Olson and Hasegawa, 1996). As shown above, SM–SKT–940 is not referable to *Copepteryx*, and SM–SKT–1153 resembles *Olympidytes.* These discoveries not only represent the western expansion of the plotopterid proliferation at the time, but also suggest the diversity of the family Plotopteridae around this time period was already high in Japan. The femur and tibiotarsus of cf. *Olympidytes* are significantly smaller than those of *Copepteryx*, which indicate the niche partitioning.

Recently, Mayr and Goedert (2016) revealed that the late Eocene-early Oligocene plotopterid diversity in North America was already high. The surge of plotopterid diversity might imply the association with the global cooling around the Eocene–Oligocene boundary (e.g. Shackleton and Kennett, 1975; Miller *et al.*, 1987, 2008, 2009; Zanazzi *et al.*, 2007), which was related to the enrichment of nutrients and phytoplankton diversity (e.g. Falkowski *et al.*, 2004; Finkel *et al.*, 2005; Katz *et al.*, 2005). Therefore, the coincidence of diversification/enlargement in the plotopterids and the Eocene-Oligocene cooling needs to be further studied in light of new discoveries of plotopterid material and the eustatic curve in the Pacific region. The high diversity of early plotopterids is probably reflected in the variably developed trochlea cartilaginis tibialis. It suggests that some plotopterids, such as *Olympidytes*, depended on their hindlimb to swim more than others, so swimming modes were more diverse among plotopterids. The difference in the mode of wing-propelled swimming of plotopterids has also been inferred by Ando and Fukata (2018) from their various shoulder girdle morphologies. Our speculation above also reinforces this, in terms of the variety of swimming modes in the family Plotopteridae. Nevertheless, more evidence is needed to confirm their hind limb swimming behaviors.

Acknowledgements

We thank H. Matsuoka (Kyoto University), Y. Hasegawa (Gunma Museum of Natural History) and Y. Okazaki (Kitakyushu Museum of Natural History) for their advice and helpful comments regarding Japanese plotopterid materials. Y. Hasegawa provided access to their specimens, including casts of MFM 1800 housed in Gunma Museum of Natural History. We thank Kengo Otsuki (Nagasaki Shimbun), who first discovered the SM–SKT–1153. We also thank G. Mayr (Senckenberg Research Institute and Natural History Museum Frankfurt) for providing morphological information of *Klallamornis* and improving the early manuscript of this paper, and P. S. Druckenmiller (University of Alaska Fairbanks) for proofreading. We thank the Saikai City Board of Education for providing photographs of the specimens.

This research was partly supported by JSPS KAKENHI Grant Number 16K05594 (to K. Miyata).

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Author contributions

Contents of this manuscript has not been published or submitted elsewhere. H. M. initiated the study and contributed to the description/comparison of the new specimens. K. M. contributed mainly to the X-Ray computed Tomography scanning. Both authors contributed to the writing of the paper.