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New fossil lipotid (Cetacea, Delphinida) from the Upper Miocene of Japan

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Abstract. Two specimens of fossil lipotid have been recovered from the Upper Miocene of Gunma and Tochigi prefectures, Japan. The specimens consist of crania including periotic and tympanic bullae. We describe and diagnose the specimens as a new genus and species of the family Lipotidae, *Eolipotes japonicus*, gen. et sp. nov. The paratype of *E. japonicus*, GMNH-PV-1011, was found stratigraphically between two tuff layers and a well constrained age interval (11.29–11.25 Ma) can be proposed, indicating that *E. japonicus* is the oldest precisely dated lipotid species yet described. Phylogenetic analysis revealed that *E. japonicus* is more closely related to *Parapontoporia* spp. than to the recently extinct Yangtze river dolphin, *Lipotes vexillifer*. Given the phylogenetic relationships and parsimonious distribution of the event to fluvial invasion in Lipotidae, it is suggested that at least two independent invasions to the freshwater habitat occurred in Lipotidae.

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Keywords: Cetacea, Delphinida, *Eolipotes japonicus* gen. et sp. nov., Lipotidae, Miocene, Odontoceti

Introduction

The Yangtze river dolphin, *Lipotes vexillifer*, also known as baiji, is an odontocete that exclusively dwelt in the Yangtze River and its tributaries in China. It was the only modern species in the family Lipotidae. *Lipotes vexillifer* was formally described by G. S. Miller in 1918 based on a specimen caught by C. M. Hoy at Tung Ting Lake, China, in 1916 (Miller, 1918). For a long time, it has been regarded as one of the rarest and most threatened cetacean species. In 2006, extensive acoustic and systematic visual surveys in its historical range failed to provide any evidence of its survival, and it is now believed to be extinct (Turvey *et al.*, 2007). Only 90 years have passed between its first modern scientific recognition and possible extinction, although it has been mentioned in ancient literature published more than 2000 years ago (Zhou, 2018).

Molecular phylogenetic analyses revealed that Lipotidae diverged early in the evolution of the Delphinida, and the emergence of their lineage dates to late Oligocene or Early Miocene (McGowen *et al.*, 2009, 2020; Zurano *et al.*, 2019). However, regarding fossil relatives, only three species within a single genus have been formally described, and their evolutionary history is poorly known (Muizon, 1988; Fordyce and Muizon, 2001), though the taxonomically questioned fossil taxon has also been described (Zhou *et al.*, 1984). Most known fossil lipotids were discovered in Messinian (Late Miocene) or Pliocene deposits, with a few uncovered in Tortonian deposits (Late Miocene). There is a large gap between the age of the oldest known lipotid fossil and their divergence age estimated by molecular analyses. Therefore, Lipotidae can be regarded as one of the most enigmatic cetacean families.

Two fossil specimens of Lipotidae were recovered from the Upper Miocene of Gunma and Tochigi prefectures, north Kanto District, Japan. The purpose of the present paper is to describe the specimens and diagnose a new species and expand the knowledge of the evolutionary history of the Lipotidae.

Methods

Anatomical terminology generally follows Mead and Fordyce (2009). The surface mesh of the fossil specimens were created by capturing surface details using the Artec Spider handheld 3D scanner (Artec Group, Luxembourg). Captured data were processed via a standard workflow (manual alignment, global registration, and model fusion) with Artec Studio 13 and then exported to Geomagic Sculpt v2022.0.34 (3D Systems, Inc., Valencia, CA, USA).

Institutional Abbreviations.—AMNH, American Museum of Natural History, New York, USA; GMNH, Gunma Museum of Natural History, Tomioka, Gunma, Japan; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; SDSNH, San Diego Natural History Museum, San Diego, California, USA; TPM, Tochigi Prefectural Museum, Utsunomiya, Tochigi, Japan.

Systematic paleontology

Cetacea Brisson, 1762
Neoceti Fordyce and Muizon, 2001
Odontoceti Flower, 1867
Delphinida Muizon, 1984
Lipotoidea Muizon, 1988
Lipotidae Zhou, Qian and Li, 1978 sensu Geisler *et al.*, 2011
Eolipotes gen. nov.

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Type and Only Known Species.—*Eolipotes japonicus* sp. nov.

Diagnosis.—As for the type and only species.

Etymology.—*Eolipotes* derived from the Latin for *eo* meaning early plus *lipotes* for the genus name of their recently extinct relative, *Lipotes vexillifer*. *Lipotes* is from Greek *lipos* for fat and *tes* suffix for action and agency (Brownell and Herald, 1972).

Eolipotes japonicus sp. nov.

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Figures 2–4, 5C, 6, 8

Holotype.—TPM7847-1, cranium; found by Yukinori Hamada and recovered by the students of the Geology Club of the Kaijo Junior & Senior High School with the staff of TPM in 2012. The cranium was found with several skeletal elements, including tympanic bullae, isolated teeth and fragments of postcranial bones, which were scattered around the cranium (Kashiwamura *et al.*, 2013). However, three tympanic bullae (two right and one left) were recovered with the cranium, which clearly indicates that the bones originated from at least two individuals. It is difficult to convincingly identify the origin of the tympanic bulla(e) originating from the same individual as the cranium. Moreover, the possibility that the cranium and other bones originated from different individuals or even different species cannot be discarded. Thus, we conservatively restricted the holotype to the cranium (TPM7847-1) here. In the TPM catalog, all skeletal elements found with the cranium were assigned the same parent number (TPM7847) and branch numbers were assigned for each skeletal part: e.g. TPM7847-2 was assigned for all three tympanic bullae.

Type Locality.—TPM7847-1 originated from the riverbed of the Kinugawa River, Utsunomiya, Tochigi Prefecture, Japan (latitude 36°35′48″N, longitude 139°58′2″E; Figure 1A).

Type Horizon.—Upper part of the Ogane Formation or lower part of the Tanokura Formation, Arakawa Group, Late Miocene, Tortonian. The holotype, TPM7847-1, was recovered from diatomaceous siltstone corresponding to the upper part of the Ogane Formation or lower Tanokura Formation, Arakawa Group (Hayashi *et al.*, 2008; Kashiwamura *et al.*, 2013; Kimura *et al.*, 2014).

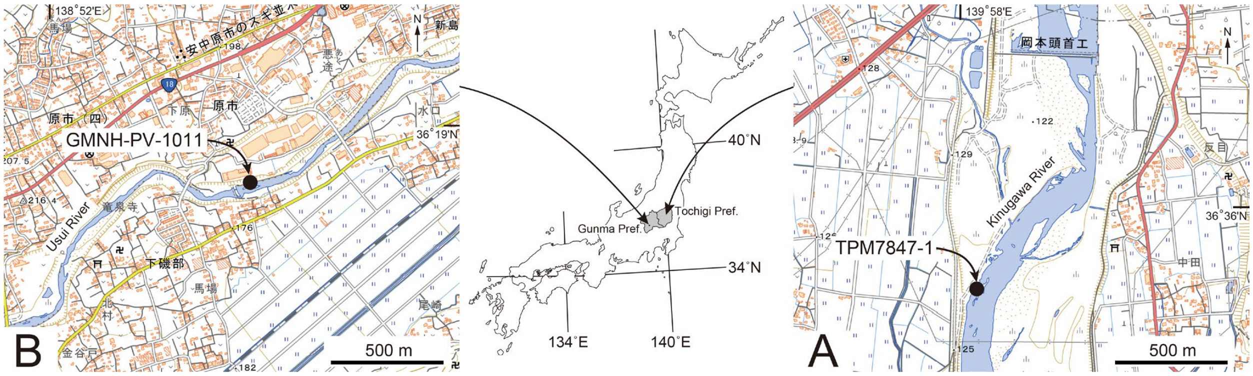

Figure 1. Localities of the holotype and the paratype of *Eolipotes japonicus* gen. et sp. nov. **A,** locality of the holotype (TPM7847-1), Utsunomiya, Tochigi Prefecture; **B,** locality of the paratype (GMNH-PV-1011), Annaka, Gunma Prefecture. The base map was produced using a GSI map issued by the Geospatial Information Authority of Japan.

The horizon from which TPM7847-1 was recovered is correlated with the planktonic foraminiferal Zone N. 16 of Blow (1969) (Hayashi *et al.*, 2008).

Paratype.—GMNH-PV-1011, a partial cranium with detached right periotic and both tympanic bullae; collected by Hajime Nakajima.

Locality of the Paratype.—GMNH-PV-1011 was collected from an outcrop along the Usui River, Haraichi, Annaka, Gunma Prefecture, Japan (latitude 36°18′52″N, longitude 138°52′35″E; Figure 1B). GMNH-PV-1011 was found nearby the locality of the paratype of *Norisdelphis annakaensis* (GMNH-PV-3464: Kimura and Hasegawa, 2020).

Horizon and Age of the Paratype.—Haraichi Formation, Annaka Group, earliest Late Miocene, Tortonian, *ca.* 11.29–11.25 Ma. The horizon from which the paratype was recovered is stratigraphically located between the Baba and Mizuguchi tuffs (Takahashi and Hayashi, 2004) and is located a few tens of centimeters stratigraphically above the Baba tuff (Miyazaki, 1988; Kimura and Hasegawa, 2020). The geologic age of Baba tuff was estimated as 11.26 ± 0.09 Ma (biotite) and 11.29 ± 0.12 Ma (sanidine) by ^{40}Ar/^{39}Ar dating (Odin *et al.*, 1997). Though the geologic age of the Mizuguchi tuff has not been estimated by radiometric or fission-track dating, it can be estimated *ca.* 11.25 Ma based on the sedimentation rate (Takahashi and Hayashi, 2004: fig. 13).

Etymology.—Named for Japan, where the holotype and the paratype were found.

Diagnosis.—*Eolipotes* differs from other Lipotidae, *Lipotes* and *Parapontoporia*, by having the posterior extremity of the premaxilla directly contacting the anterolateral angle of the nasal, and anteroposteriorly shorter pterygoid sinus fossa, whose anterior extremity is not anteriorly extended beyond the level of the antorbital notch, lower maxillary crest posterolateral to the maxillary eminence, and broader anterior incisure of periotic; further differs from *Lipotes* by having anteroposteriorly elongated frontal in cranial vertex, and by lacking salient anteroposterior ridges on the dorsal surface of anterior process of periotic.

Remarks.—*E. japonicus* is placed in the Lipotidae by having the following combination of morphological characters: rostrum constricted transversally at the level of posterior end of alveolar groove (Barnes, 1985; Muizon, 1988), swollen frontals on vertex (Muizon, 1988), retention of a well-defined anterior bullar facet, styloid apex of the anterior process of the periotic (Muizon, 1988) (= anterior spine of Boessenecker, 2013), and anteromedial tubercle on the medial surface of the anterior process of the periotic (Barnes, 1985; Boessenecker, 2013, but see Boessenecker and Poust, 2015).

Zhou *et al.* (1984) described a fossil from the possible Miocene deposit of China as a new genus and species of Lipotidae, *Prolipotes yujiangensis*. However, as mentioned later, *P. yujiangensis* is regarded incertae sedis and several authors questioned their affinity to the Lipotidae (Muizon, 1988; Fordyce and Muizon, 2001; Pyenson, 2009).

Description

The cranium of the holotype, TPM7847-1, lacks the anterior part of the rostrum and most of the cranium ventral to the facial region (Figures 2, 3, S1, and S2). The cranium of the paratype, GMNH-PV-1011, preserves part of the cranial vertex, the roof of right temporal fossa, and ear bones (Figure 4). Unless otherwise mentioned, the following description of the cranium is based on the holotype. Measurements are shown in Table 1.

The cranium is relatively small. The anteroposterior length of the facial part of the cranium and the transverse width of the cranium at the postorbital process of the frontal are *ca.* 118 mm (base of the rostrum to the preserved posterior extremity of the supraoccipital) and 144 mm (estimated by doubling the left half width) in the holotype, respectively.

The anteroposterior axis of the rostrum is shifted to the left with respect to the sagittal axis of the facial part of the cranium in dorsal view. The transverse width of the rostrum gradually widens posteriorly from the preserved anterior extremity of the rostrum. The rostrum exhibits a constriction at its base in dorsal view. When viewed dorsally, the curvature of the outline of the rostrum changes at the level of the posterior end of the alveolar groove (indicated by white arrows in Figure 2A, C). Then, at *ca.* 25 mm posterior from the level of the end of the alveolar groove, the rostrum abruptly widens as the maxillary eminence develops. The cranial vertex, which is predominantly formed by nasals and frontals, displays an asymmetry and is clearly shifted to the left side.

Premaxilla.—The premaxillae meet medially and roof over the mesorostral groove dorsally at the anterior part of the preserved rostrum. The left and right premaxillae are separated from the level of the posterior end of the alveolar groove to the level of the base of the rostrum, with a maximum opening of the mesorostral groove of 3 mm. The dorsal surface of the premaxilla is convex dorsally in the anterior part of the preserved rostrum. At the base of the rostrum, the dorsal surface of the premaxilla slopes medially to form a shallow depression (central basin of Barnes, 1985). The central basin ranges from the anterior to the level of the base of the rostrum to the posterior to the level of the posterior end of the alveolar groove as in other lipotids (*Lipotes* and *Parapontoporia*). The depth of the central basin is of about 7 mm from the dorsal-most surfaces of the maxillary eminence. In the genus *Para-*

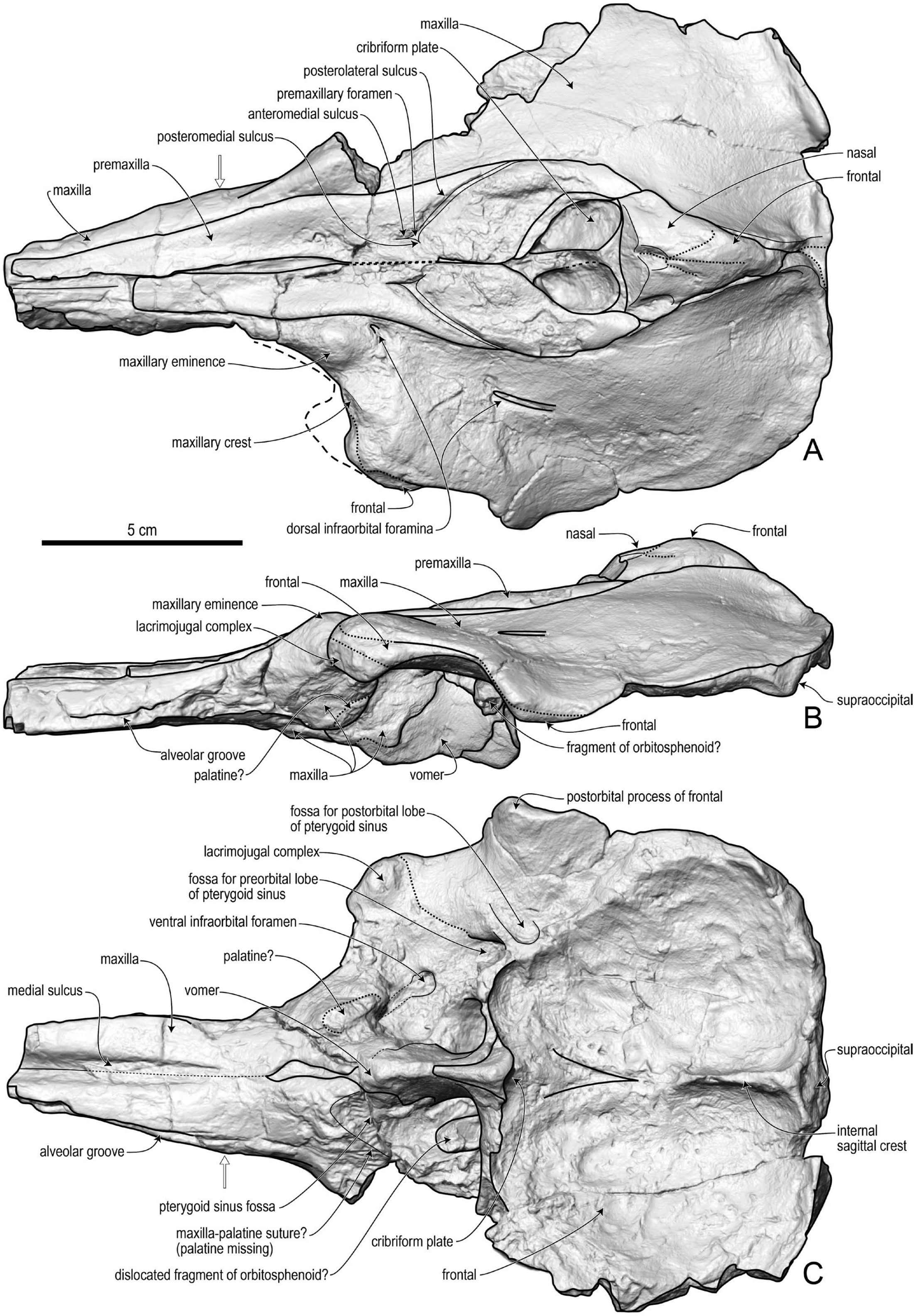

Figure 2. 3D models with line drawings of the cranium of the holotype, *Eolipotes japonicus*, gen. et sp. nov. (TPM7847-1). **A,** dorsal view; **B,** left lateral view; **C,** ventral view. White arrow indicates a point of curvature change in the lateral margin of the rostrum. Scale bar equals 5 cm.

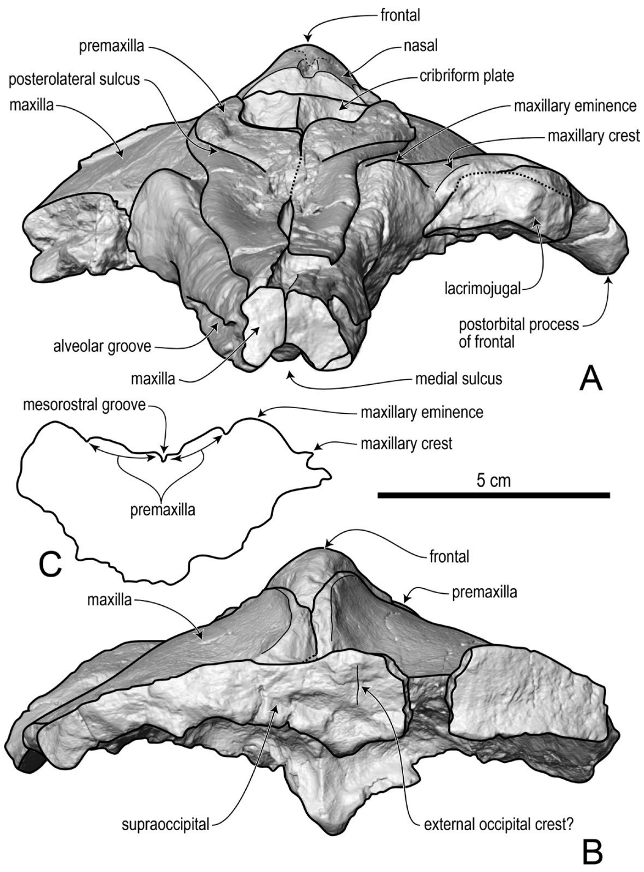

Figure 3. 3D models with line drawings of the cranium of the holotype, *Eolipotes japonicus*, gen. et sp. nov. (TPM7847-1). **A,** anterior view; **B,** posterior view; **C,** cross section at the base of the rostrum. Scale bar equals 5 cm.

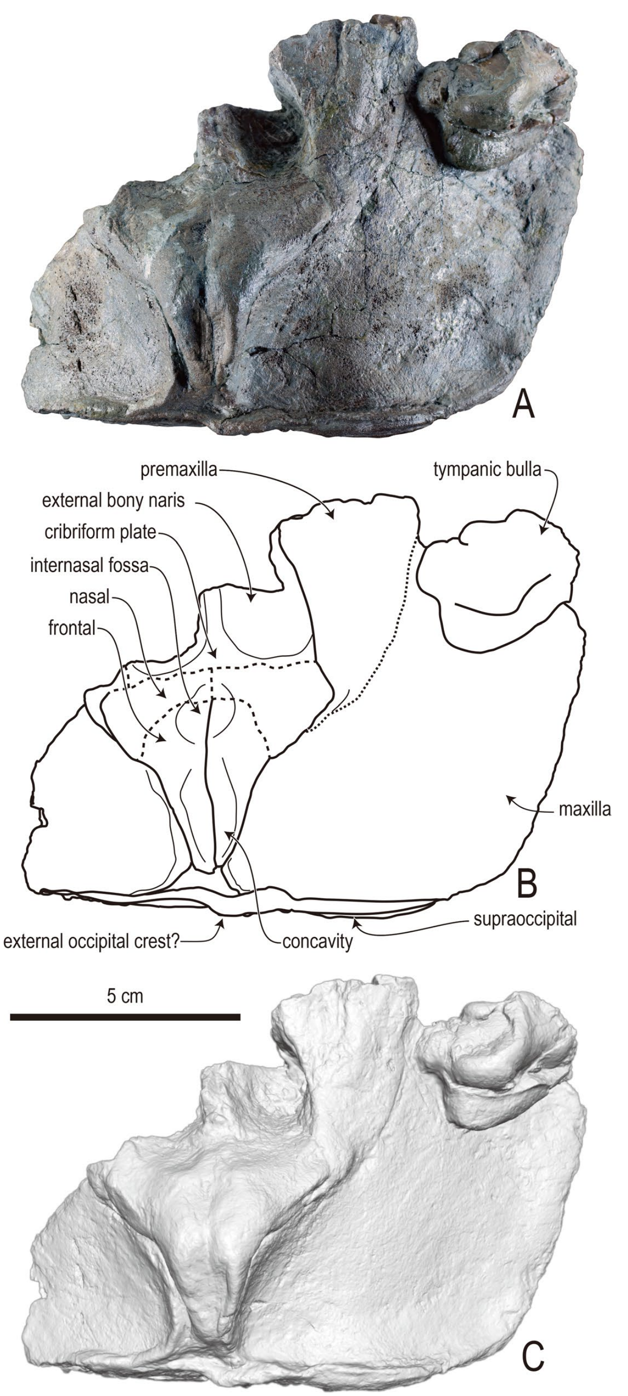

Figure 4. Cranium of the paratype of *Eolipotes japonicus*, gen. et sp. nov. (GMNH-PV-1011) in dorsal views. **A,** photograph; **B,** line drawing; **C,** 3D model of the cranium. Scale bar equals 5 cm.

pontoporia, *P. wilsoni* has a similarly deep central basin, whereas *P. sternbergi* has a shallower central basin and *P. pacifica* lacks such a central basin (Barnes, 1985). The right premaxilla is transversely wider than the left at the level of the central basin.

A marked constriction of the lateral margin of the premaxilla occurs at the level of the base of the rostrum. This constriction displays an asymmetry, being more developed in left premaxilla. Each premaxilla is perforated by a small premaxillary foramen. Three sulci, the anteromedial, posteromedial and posterolateral sulci, are connected to the premaxillary foramen. The anteromedial and posteromedial sulci are short and narrow, whereas the posterolateral sulcus is relatively wide and extends posterolaterally to the level of the anterior end of the external bony nares. Unlike the condition seen in other lipotids (*Lipotes* and *Parapontoporia*), each premaxilla contacts with the anterolateral corner of the corresponding nasal (Figure 5). This might be interpreted as a primitive character for the Lipotidae. Immediately anterior to the external bony nares, the premaxillary sac fossa displays asymmetry and the right premaxillary sac fossa is wider than the left. The dorsal surface of each fossa is more or

Table 1. Measurements of the specimens.

Cranium	holotype TPM7847-1	paratype GMNH-PV-1011
Total length of cranium	205+	88+
Length of rostrum	83+	–
Width of the rostrum at its base	56	–
Width of the premaxillae at rostrum base	28	–
Preorbital width of the cranium	114e	–
Postorbital width of the cranium	144e	–
Anteroposterior length of bony nares	20	–
Transverse width of bony nares	25	–
Anterior transverse width of nasals	30	47
Minimum distance between maxille across vertex	9	12
Anteroposterior length of bony orbit	37	–

Periotic	paratype GMNH-PV-1011
Total length	34+
Length of anterior process	13+
Width at pars cochlearis	21
Length of posterior bullar facet	12
Length of pars cochlearis	15

		TPM7847-2		
Tympanic bulla		Fig. 7A–B	Fig. 7C	Fig. 7D–E
Total length	35+L/34+R	32	28+	32+
Total width	18+L/22+R	20+	16+	21
Width of inner posterior prominence	7L/7R	7	9	8
Dorsoventral height at sigmoid process	26+L/18+R	18+	–	–

Abbreviations: e, estimated by doubling half-width; L, left side; R, right side; +, less than original value.

less flattened. A salient bump delimits the lateral edge of the right premaxillary sac fossa. Although the bump is also found in left premaxilla, it is much lower than that of right premaxilla.

Maxilla.—As stated above, the lateral margin of the right maxilla displays a constriction in the proximal part of the rostrum in dorsal view. The alveolar groove is preserved on the lateral surface of the maxillae, opening ventrolaterally. Each individual alveolus is difficult to recognize, possibly due to the preservation. In ventral view, the maxillae meet medially and form the ventral surface of the palate. A deep medial sulcus (Barnes, 1984) on the midline of the palate extends posteriorly to the level of the posterior end of the alveolar groove that becomes shallower and narrower posteriorly (Figure 2C). The cross-sectional outline of the maxilla is inverted U-shaped in anterior view owing to the development of the deep medial sulcus (Figure 3A). The development of the deep medial sulcus is also observed in other cetaceans, which have extremely elongated rostrum (e.g. *Parapontoporia* spp., eurhinodelphinids). This may imply that the additional surface area allows this structure to strengthen the elongated rostrum.

The maxilla bears an elliptical eminence at the level of the base of the rostrum, which we interpret as the maxillary eminence of Barnes (1985) (= boss-like rostral crest of Mead and Fordyce, 2009 and Boessenecker, 2013). The right maxillary eminence is larger than and positioned slightly anterior to the left maxillary eminence. In accordance of the development of the maxillary eminences, the maxillae abruptly widen transversely in dorsal view. This widening is clearly indicated in the right maxilla, whereas the lateral surface of the corresponding part of the left maxilla is damaged. Lateral to the left maxillary eminence, the anterior and dorsal surface of the maxilla and lacrimojugal complex are damaged and some parts of the bones are missing (the estimated original outline is indicated by a dashed line in Figure 2A). The antorbital notch was possibly formed by the maxilla and lacrimojugal complex and more medially placed than in *Parapontoporia*, however, the shape and location of the antorbital notch is unknown owing to bone damage.

A low oblique ridge is present just posterolateral to

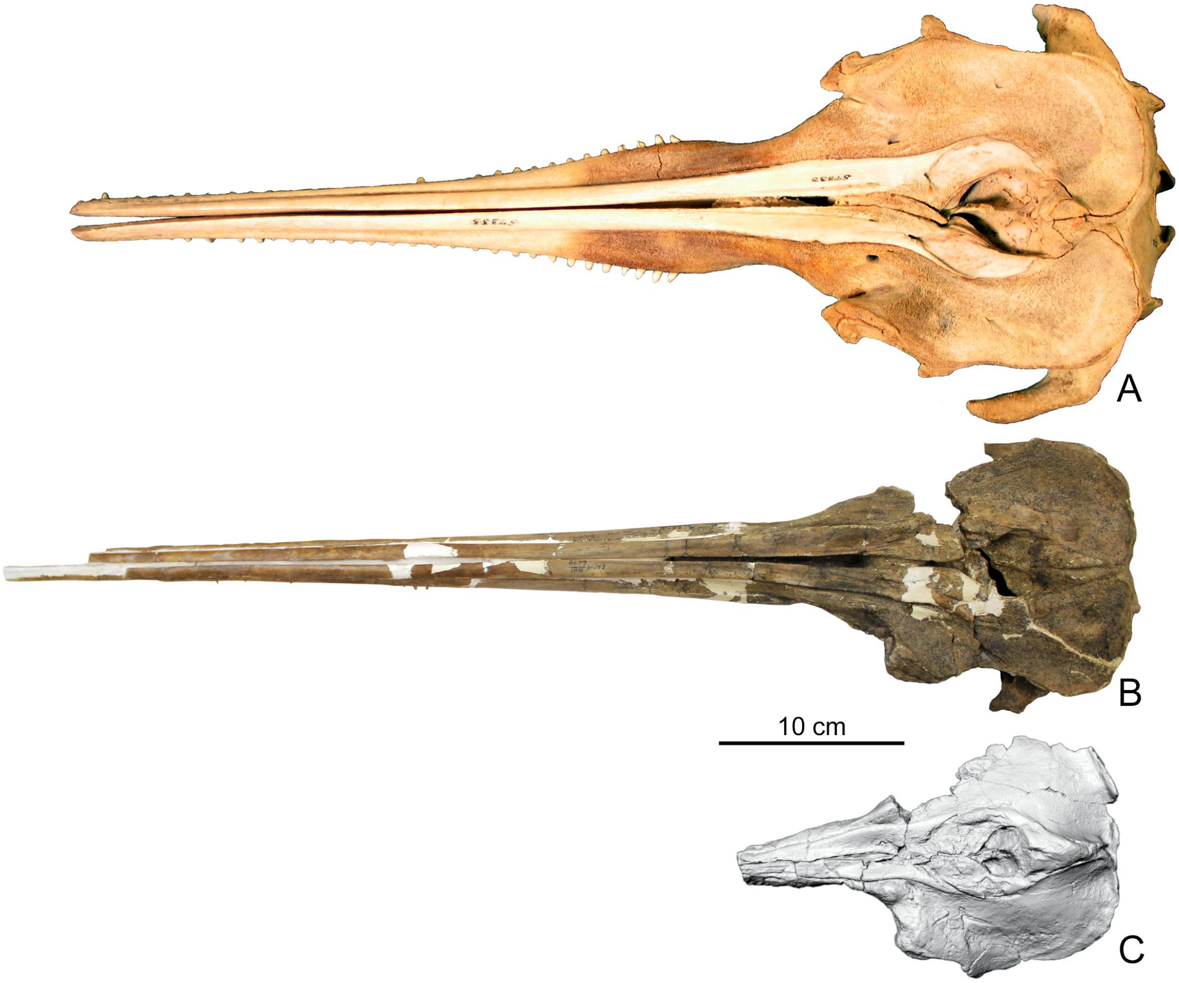

Figure 5. Lipotid crania in dorsal view. **A,** *Lipotes vexillifer* (AMNH M-57333, O'Leary *et al.*, 2007), Tung Ting Lake, Hunan Prov., China; **B,** *Parapontoporia sternbergi* (LACM6238, courtesy of J. H. Geisler), San Diego Formation, Early Pliocene to Early Pleistocene, California, USA; **C,** *Eolipotes japonicus*, gen. et sp. nov. (TPM7847-1, holotype), Upper part of the Ogane Formation or lower part of the Tanokura Formation, Arakawa Group, Late Miocene, Utsunomiya, Tochigi, Japan. Scale bar equals 10 cm. A, B, photograph; C, 3D model.

the maxillary eminence on the dorsal surface of the left maxilla. We interpret this structure as an incipient maxillary crest (Figure 2A). This crest does not clearly extend posteriorly to the level of the orbit, but it continues to the smoothly convex dorsal surface of the lateral part of the supraorbital region of the maxilla. Therefore, the dorsal surface of the maxilla is shallowly depressed between the premaxilla and the elevated lateral part of the supraorbital process at the level of the orbit. In *Lipotes* and *Parapontoporia*, the maxillary crest is anteromedially oriented as in *Eolipotes japonicus*, but it is more sharply elevated than that of *E. japonicus*.

Two dorsal infraorbital foramina are preserved on the left maxilla. The anterior dorsal infraorbital foramen is located close to the lateral margin of the premaxilla just anterior to the level of the premaxillary foramen. The relative position of the anterior dorsal infraorbital foramen is similar in *Lipotes* (Miller, 1918; Peixun, 1989) but unlike that in *Parapontoporia* spp., in which the anterior dorsal infraorbital foramen is located posterior to the level of the premaxillary foramen (Barnes, 1985; Figure 5). The posteromedial extremities of left and right maxillae approach each other closely and are elevated against the corresponding frontal.

In ventral view, a possible sutural surface for the palatine is preserved at the posterior end of the rostral part of the right maxilla, which may indicate the position of the maxillary-palatine suture. The position of this suture indicates the possible anterior limit of the pterygoid sinus fossa which appears to be short anteriorly, ending at or posterior to the level of the antorbital notch, unlike those in *Lipotes* and *Parapontoporia*.

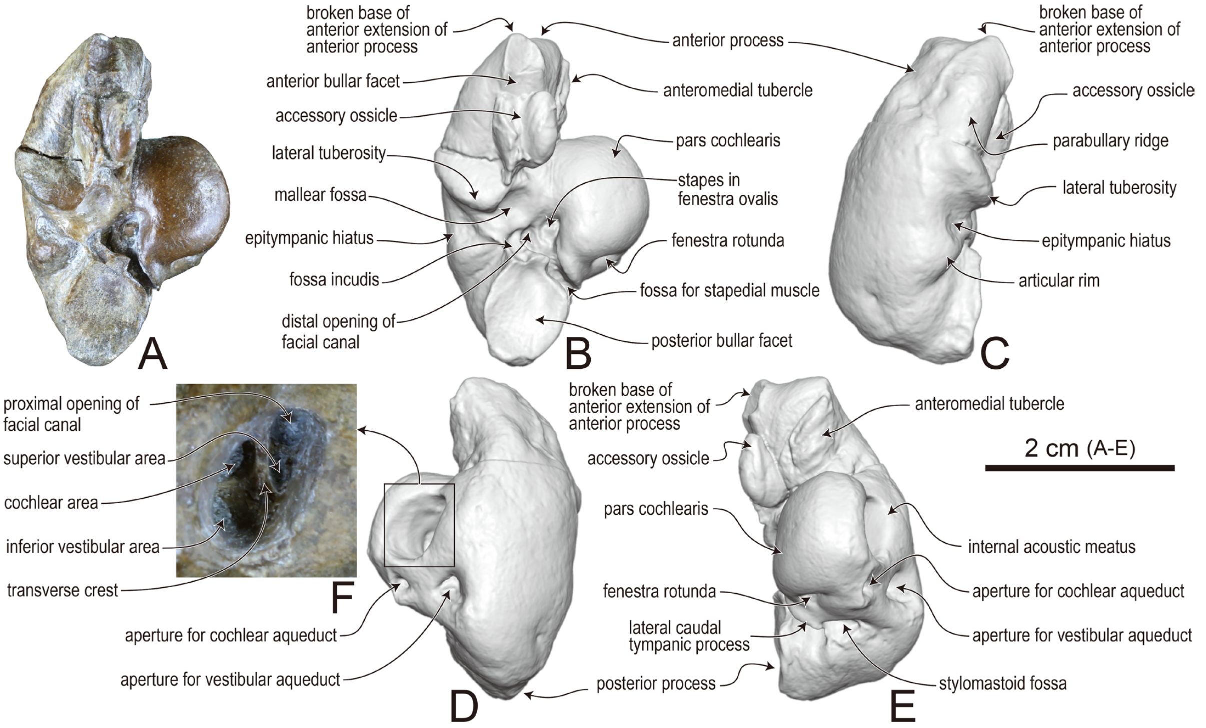

Figure 6. Photographs and 3D models of the right periotic of the paratype of *Eolipotes japonicus*, gen. et sp. nov. (GMNH-PV-1011). **A, B,** ventral views; **C,** lateral view; **D,** dorsal view; **E,** medial view; **F,** fundus of internal acoustic meatus. Scale bar equals 2 cm for A–E.

Palatine.—The ventral side of the cranium is damaged, and most of the palatine is missing. A possible palatine fragment could be preserved, attached to the posteriormost part of the ventral surface of the left maxilla (Figure 2C).

Nasal.—The nasals are transversely wide (anterior transverse width of both nasals: 30 mm) anteriorly and narrow posteriorly. The nasals are almost fused with the frontals posteriorly and the sutures between the nasals and the frontals are nearly obliterated in both the holotype and paratype. The posterior tips of the left and right nasals are separated medially by the frontals. Together with the frontals, the nasals constitute a dorsally inflated cranial vertex. In dorsal view, the cranial vertex is in the form of an anteroposteriorly elongated triangle, and the dorsal surface of the nasal is swollen and transversely convex. An internasal fossa (*sensu* Muizon, 1988) occupies the area of the joined anteromedial corners of the nasals. The nasal is triangular and elongated posterolaterally in dorsal view. The vertex of the cranium of the paratype is larger than that of the holotype (anterior transverse width of both nasals in paratype: 47 mm).

Ethmoid.—The cribriform plate contributes to the posterior wall of the bony nares. The dorsal margin of cribriform plate extends dorsally to the level of the dorsal surface of the posterior extremity of the premaxilla, which is apparently lower than the level of the dorsal margin of the nasals. The bony nares are anteroventrally directed (*ca.* 45 degrees with respect the rostrum). This contrasts with the condition of *P. sternbergi*, which has nares that pass into the cranium more steeply (Barnes, 1985; Boessenecker, 2013).

Lacrimojugal complex.—As stated above, the anterior part of the lacrimojugal complex was damaged. The antorbital notch was probably formed by the lacrimojugal complex and the maxilla. However, the original morphology is unclear caused by damage to the bone surface.

Vomer.—In ventral view, the vomer appears as a narrow stripe between the maxillae at the level of the base of the rostrum, however, this is probably due to the damage of the maxillae.

Frontal.—The dorsal surface of the supraorbital process of the frontal is almost fully covered by the maxilla, except at the orbital edge. In dorsal view, the lateral margin of the orbit is slightly laterally concave, and the orbit is directed slightly anterolaterally. In lateral view, the orbit is shallowly arched dorsally, and the preorbital process is dorsoventrally thick. The postorbital process is small and does not extend ventrally, unlike that observed in *Lipotes* (Miller, 1918; Zhou, 2009). On the ventral surface of the supraorbital process, the infratemporal crest is a well-defined ridge, and deep concavities are present immediately anteromedial and posterolateral to the crest. The former and latter are interpreted as the fossae for the preorbital and postorbital lobe of the pterygoid sinus, respectively.

At the vertex, the frontal is dorsally swollen and forms the highest part of the vertex. The transverse pinching of the frontals at the cranial vertex is developed similar to that in *Lipotes* and *Parapontoporia* (Figure 5). But it should be noted that similar pinching also appears in some "kentriodontids" (e.g. *Pithanodelphis* and *Liolithax*), and to a lesser extent the inioids, *Brujadelphis*, *Isthminia*, *Scaldiporia*, *Pontistes* and *Brachydelphis*. At the vertex, the frontals are asymmetrical in dorsal view; the right frontal is slightly wider. An anteroposteriorly elongated concavity is present between the frontals at the cranial vertex in the paratype, but this concavity is not present in the holotype. In ventral view, the internal surface of the frontal preserves the extensive cerebellar juga.

Interparietal.—In ventral view, the interparietal is present between the frontals to form an internal sagittal crest, but the suture between the interparietal and frontal is unclear.

Supraoccipital.—Only part of the dorsal margin of the supraoccipital is preserved in the holotype and paratype. The preserved portion of the supraoccipital suggests that *Eolipotes* had a nearly vertical occipital shield. The nuchal crest is transversally straight. The external occipital crest is low. A shallow concavity is present lateral to the external occipital crest in the paratype. The external occipital crest is unclear in the holotype caused by damage to the bone surface.

Periotic.—No periotic was found in the holotype; the following description is based on the right periotic of the paratype, GMNH-PV-1011 (Figure 6). The anterior process is bent slightly anteromedially and slightly narrowed transversely. Although the anterior extremity of the anterior process is missing, the remains indicate that the anterior process had an anterior bullar facet and a slender anterior extension at the anteroventral angle (Figure 6B, C, E). We interpreted this anterior extension as anterior spine of Boessenecker (2013). Muizon (1988) described this morphology as "styloid apex of anterior process of periotic". The anterior bullar facet is a key character of Lipotidae (*Lipotes* and *Parapontoporia*) that differs from the other delphinidans. The anterodorsal part of the anterior process makes a distinct angle, and the anterior process consequently represents a rectangular outline in lateral view. This contrasts with that in other lipotids: the anterodorsal angle of the anterior process is rounded in *Lipotes*, and much less developed in *Parapontoporia*. The medial surface of the anterior process bears a tubercle. We interpreted this tubercle as being homologous to the anteromedial tubercle of Boessenecker (2013) and Boessenecker and Poust (2015). Boessenecker (2013) suggested this to be a key character of Lipotidae (but, see Boessenecker and Poust, 2015). A narrow groove, immediately dorsal to the anteromedial tubercle, is possibly a groove for the tensor tympani muscle. The fovea epitubaria is occupied by the accessory ossicle and a fragment of the base of the anterior pedicle of the tympanic bulla.

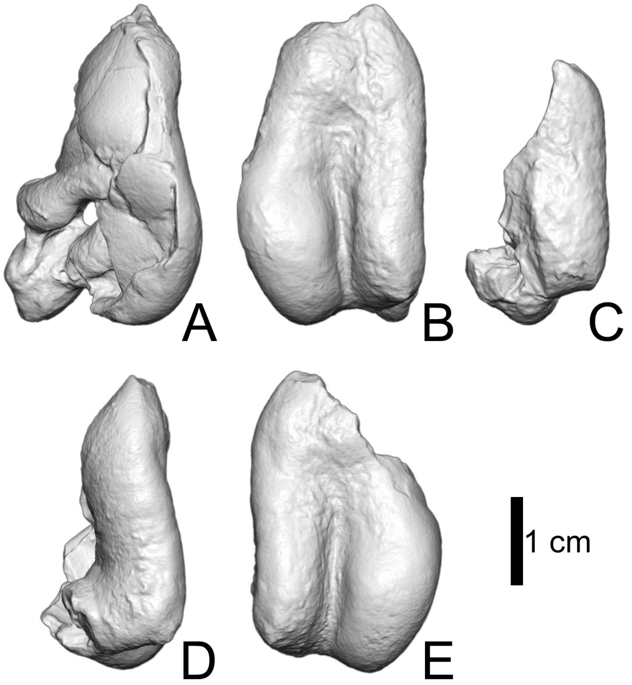

Figure 7. Delphinida aff. Lipotidae, tympanic bullae, TPM7847-2, which are recovered from the matrix around the cranium of the holotype of *Eolipotes japonicus*, TPM7847-1. **A,** lateral view of right tympanic bulla; **B,** ventral view of right tympanic bulla; **C,** ventral view of the other right tympanic bulla; **D,** medial view of left tympanic bulla; **E,** ventral view of left tympanic bulla. Scale bar equals 1 cm. Three tympanic bullae (two right and one left) were recovered with the cranium of the holotype (TPM7847-1), which indicates that the bones originated from at least two individuals. It is difficult to convincingly identify the origin of the tympanic bulla(e) originating from the same individual as the cranium. Thus, we conservatively restricted the holotype to the cranium (see details in main text).

The mallear fossa is large, relatively shallow and circular in outline. Lateral to the mallear fossa is a lateral tuberosity, which is well developed and continues anteriorly to the rounded and low parabullary ridge. Posterior to the lateral tuberosity is a wide epitympanic hiatus, which is divided into anterior and posterior parts by the round tuberosity on its ventral surface. We interpret this tuberosity as low, rounded articular rim (*sensu* Fordyce, 1994). The fenestra ovalis is situated at the lateral edge of the pars cochlearis. The stapes is preserved in the fenestra ovalis. Lateral to the fenestra ovalis is the proximal

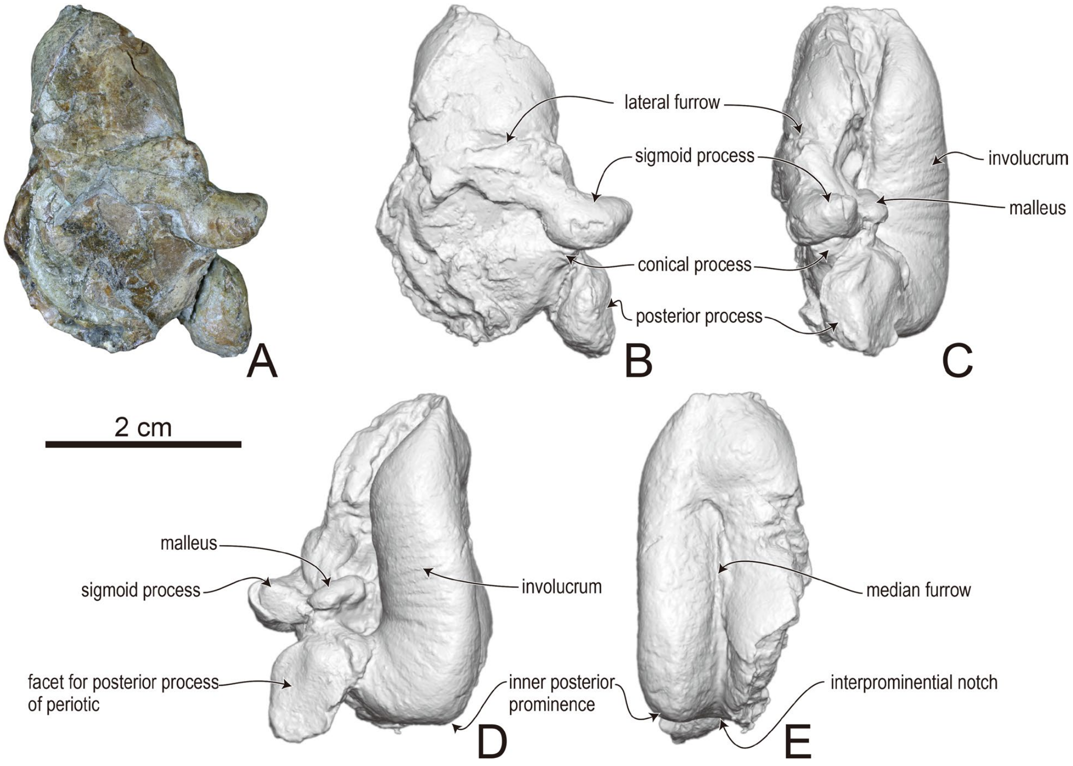

Figure 8. Photograph and 3D models of the left tympanic bulla of the paratype of *Eolipotes japonicus*, gen. et sp. nov. (GMNH-PV-1011). **A, B,** lateral views; **C,** dorsal view; **D,** medial view; **E,** ventral view. Scale bar equals 2 cm.

opening of the facial canal, which continues posteriorly to the facial sulcus. The fossa incudis is outlined by distinct medial and lateral crests. The fossa for the stapedial muscle is deep and anteroposteriorly elongated.

The outline of the pars cochlearis is rounded posteromedially, whereas the roughly straight anterior margin makes a more distinct angle with the medial margin in ventral view. The caudal tympanic process (lateral caudal tympanic process of Lambert *et al.*, 2017b) is small and extends posteriorly. The small fenestra rotunda, situated at the posterior face of the pars cochlearis, is slightly extended dorsomedially by a short and narrow fissure. Dorsal to the fenestra rotunda is the aperture of the cochlear aqueduct, which bears a pointed small tuberosity on its posterior margin. A similar small pointed tuberosity is also found in *Lipotes*. The aperture for the vestibular aqueduct is situated lateral to the aperture for the cochlear aqueduct, the former being larger than the latter. The aperture for the vestibular aqueduct has a relatively close alignment with the aperture for the cochlear aqueduct. The internal acoustic meatus is oval and deep in dorsal view. The transverse crest is relatively low and separates the proximal opening of the facial canal and superior vestibular area laterally from the cochlear area and inferior vestibular area medially.

The posterior process is short and directed ventrally. The posterior bullar facet is relatively small, smooth and shallowly concaved. In lateral view, the dorsal margin of the posterior process is well convex. This shape is similar to that in *Parapontoporia* but different from the less convex outline in *Lipotes*. There is a small fossa between the base of the posterior process and the pars cochlearis, interpreted as the stylomastoid fossa. A similar structure is also found in *Lipotes*.

Tympanic bulla.—As stated above, three tympanic bullae (TPM7847-2) were recovered with the cranium of the holotype (TPM7847-1), which clearly indicates that the bones found with the cranium originated from at least two individuals (Figure 7). The three tympanic bullae are almost identical in size, with no clear morphological difference. The tympanic bullae of TPM7847-2 are slightly smaller in size than those of the paratype (GMNH-PV-1011) (Figure 8). Except for the size difference, no clear morphological differences are observed between the tympanic bullae of TPM7847-2 and the paratype. However, as stated above, the tympanic bullae (TPM7847-2) are not regarded as being part of the holotype (TPM7847-1) here. The following description of the tympanic bulla is based on that of the paratype (GMNH-PV-1011), unless otherwise mentioned.

Figure 9. Delphinida aff. Lipotidae, isolated teeth, TPM7847-5, which were recovered from the matrix around the cranium of the holotype of *Eolipotes japonicus*, TPM7847-1. It is unclear whether the teeth originated from the holotype. Scale bar equals 1 cm.

The paratype includes both tympanic bullae (Figures 4 and 8). The left bulla is isolated, and the right one is firmly appressed to the dorsal surface of the maxilla. The following description is mainly based on the left tympanic bulla. Both tympanic bullae are deformed by mediolateral compression, particularly on the posterior part of the lateral lobe. In ventral view, the medial margin of the tympanic bulla is almost straight in outline (Figure 8). Although it is unclear due to postmortem deformation, the remains suggests that the outer posterior prominence was transversely wider and more posteriorly extended than the inner posterior prominence, as typical in Lipotidae. The interprominential notch is deep and continues to the deep median furrow anteriorly. The median furrow is slightly longer than that of *Lipotes* and extends to the level of the anterior 1/3 of the length of the tympanic bulla. The anterior end of the tympanic bulla is slightly damaged and no apparent anterior spine is preserved in the paratype. In TPM7847-2, the apex is pointed and triangular in ventral and lateral views (Figure 7A, B). In lateral view, the sigmoid process is located slightly posteriorly to the middle of the tympanic bulla and is tilted posterodorsally. The conical process is relatively small and partly obscured by the sigmoid process. The posteroventral angle of the tympanic bulla is well rounded in outline in lateral view. In medial view, the dorsoventral thickness of the involucrum is almost the same from posterior to anterior end, as in *Lipotes*.

Teeth.—No teeth are preserved in the paratype. More than 50 isolated teeth (TPM7847-5) were recovered from the matrix around the cranium of the holotype (Figure 9). However, as mentioned above, the teeth (TPM7847-5) are not considered a part of the holotype in this study. The teeth are small, slender and single-rooted with recurved apices of the crown. No accessory cusp is present. The apical part of the root is also recurved. The neck does not represent an apparent swelling.

Body length estimation.—Body length of the holotype of *E. japonica* is estimated to be 2.17 m. To estimate the body length, we used the calculation formula for stem Delphinoidea of Pyenson and Sponberg (2011). Since the holotype and paratype lack the zygomatic process of the squamosal, we are unable to know the bizygomatic width of the cranium. Instead, we used the postorbital width of the cranium for the estimation. In general, postorbital width is not so different from bizygomatic width in Delphinida (e.g. Perrin, 1975), even though, the estimation requires caution.

Discussion

Phylogenetic analysis

We have decided to place the two specimens (TPM7847-1 and GMNH-PV-1011) in the same species because the specimens do not show any distinct differences of the anatomical features and share the combination of the following anatomical features: the posterior extremity of the premaxilla directly contacts to the anterolateral corner of the corresponding nasal; the posteromedial extremities of right and left maxillae approach each other very closely and are elevated against the corresponding frontal; the cranial vertex, which is predominantly formed by nasals and frontals, displays a swollen triangular outline in dorsal view; the frontals are transversely narrow and anteroposteriorly elongated in cranial vertex; the occipital shield is nearly vertical and the nuchal crest is transversally straight in dorsal view.

We conducted a phylogenetic analysis using data from the supermatrix of Kimura and Hasegawa (2019) to investigate the phylogenetic relationships of *Eolipotes japonicus*. The supermatrix of Kimura and Hasegawa (2019) is a modified version of the supermatrix of Lambert *et al.* (2017a) and Peredo *et al.* (2018), which originated from Geisler and Sanders (2003) for morphology and McGowen *et al.* (2009) for molecular data. We have added one operational taxonomic unit (*E. japonicus*) and the resulting supermatrix consists of 324 morphological and 60,851 molecular characters. Phylogenetic analyses were conducted with TNT (Goloboff *et al.*, 2008) using the New Technology Search with and without implied

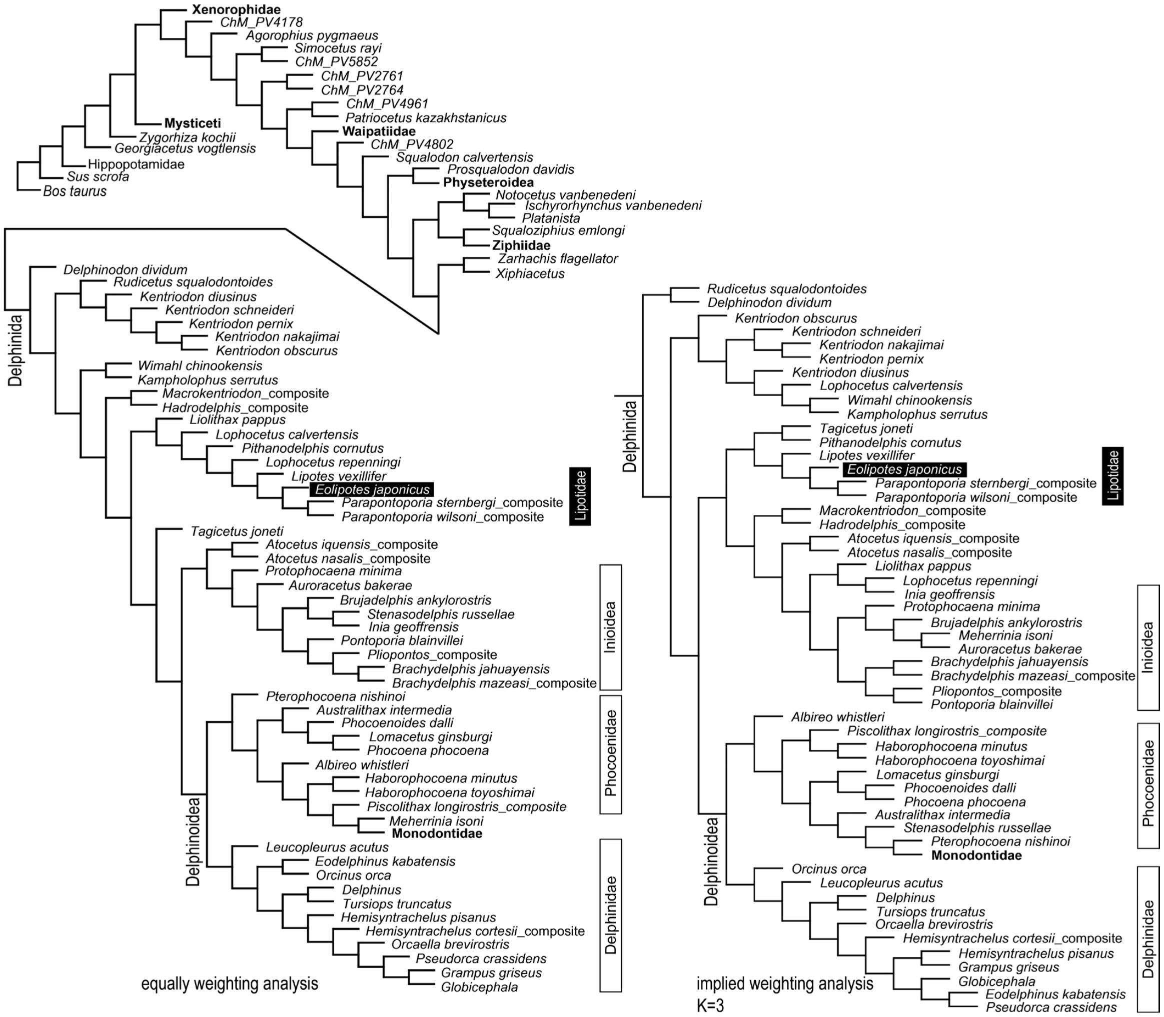

Figure 10. Single most parsimonious tree resulting of equal and implied (K = 3) weighting analysis of a supermatrix (324 morphological and 60,851 molecular characters) modified from Lambert *et al.* (2017a), Peredo *et al.* (2018) and Kimura and Hasegawa (2019), which originated from Geisler and Sanders (2003) for morphology and McGowen *et al.* (2009) for molecular data. Basal nodes are omitted in the resulting tree of implied weighting analysis. Clades in bold were collapsed. The full results of the phylogenetic analyses are shown in supplementary material.

(K = 3, 6, 9) weighting to evaluate the stability to the results (Goloboff, 2013; Sanders and Geisler, 2015). Each analysis was tasked with the shortest tree 1,000 times.

Each phylogenetic analysis with and without implied weighting resulted in one parsimonious tree. Figure 10 presents the results of both equal and implied (K = 3) weighting analysis, and full results of the analysis are presented in the supplementary material (Figure S4). The results were essentially identical to those of previous studies (Lambert *et al.*, 2017a; Peredo *et al.*, 2018; Kimura and Hasegawa, 2019). The monophyly of the superfamily Delphinoidea and the closer relationship of Monodontidae with Phocoenidae than Delphinidae was suggested in all analyses, except for the phylogenetic position of *Meherrinia* in equal and *Stenasodelphis* in implied (K = 3, 6) weighting analyses. The ambiguity in their phylogenetic position might be owing to many unknown states in the matrix of their morphological characters: i.e., 67% and 73% of the morphological characters were scored "?" for *Meherrinia* and *Stenasodelphis*, respectively. This might also partly be owing to the lack of molecular data of the extinct species. The phylogenetic position of Lipotidae within Delphinida was not clearly resolved in our analyses. Equal weighting analysis suggested that the Lipotidae was included in the sister clade of Delphinoidea + Inioidea, and Lipotidae clustered with some "kentriodontids". This clade is supported by following characters: the suture between the maxilla and the premaxilla on the rostrum is fused at the anterior quarter of the rostrum with the remaining portions is unfused (char. 11); the posterior region of the rostral edge bowed far outward forming a deep U-shaped antorbital notch (char. 12); at least one third of the mandibular symphysis is fused (char. 41); the posterolateral sulcus from the premaxillary foramen present and extends to the level equivalent to the middle of the nasal openings (char. 73); the anterior edge of the nasal is dorsoventrally thick (char. 116); the anterior edge of the supraoccipital is triangular with pointed anteriorly in dorsoposterior view (char. 153); the superior lamina of the pterygoid is completely absent from the orbital region (char. 168). Whereas in implied weighting analyses, Lipotidae formed a monophyletic group with Inioidea + some "kentriodontids", sister clade of the Delphinoidea. This clade was commonly supported in all implied analyses by the absence of the swelling on the lingual side of the posterior lower teeth (char. 30).

All analyses recovered a monophyletic group including *Lipotes*, *Parapontoporia* and *Eolipotes* and showed that *E. japonicus* formed a clade with *Parapontoporia* spp. This clade is recognized as family Lipotidae, because it includes the last common ancestor and all its descendant of *Lipotes* and their fossil relatives. This clade was commonly supported by following characters in all analyses: the presence of a small articular rim that forms a ridge anterolateral to articulation surface of the posterior process of the periotic (char. 240); the posterior process of the periotic and tympanic bulla has a smooth articular surface (char. 242); the medial portion of the maxilla faces mainly dorsolaterally at the vertex (char. 308); and tooth diameter is less than 10% of the nares width (char. 314). Regarding the character of the tooth diameter (char. 314), no teeth were preserved in situ in the cranium of *Eolipotes*. But, the diameter of the alveolar groove of the cranium of the holotype clearly indicates that the tooth diameter is less than 10% of the bony nares width. The diameter of the isolated tooth found with the holotype (TPM7847-5) is less than 10% of the nares width, although it may not have been derived from the same individual/taxon. Because in recovering the clade of some kentriodontids with the Lipotidae in all analyses, the results suggest the paraphyly of the Kentriodontidae as in previous studies (e.g. Peredo *et al.*, 2018; Kimura and Hasegawa, 2019).

Pattern of the adaptation to freshwater habitat in the Lipotidae

Cetaceans have adapted to a fully aquatic life from their terrestrial ancestors. Fossil and stable isotopic studies document their habitat transition from terrestrial/freshwater to marine during the Eocene (Thewissen *et al.*, 1994, 2001; Roe *et al.*, 1998; Clementz *et al.*, 2006; Marx *et al.*, 2016). Some cetacean species have reinvaded fluvial environments. Lipotidae was previously included in the Platanistoidea together with Iniidae, Pontoporiidae and Platanistidae (e.g. Simpson, 1945), and collectively referred to as "river dolphins" as a reflection of the modern species, which, with the exception of *Pontoporia blainvillei*, inhabit fluvial environments (Jefferson *et al.*, 2015). Each modern genus of "river dolphins" has a fossil relative that dwelt in a marine environment and each has independently adapted to the fully fluvial habitat (Geisler *et al.*, 2011; Marx *et al.*, 2016; Aguirre-Fernández *et al.*, 2017). Their fluvial invasion has been suggested to be driven by the global sea-level change and/or competitive niche overlap with delphinoids (Cassens *et al.*, 2000; Hamilton *et al.*, 2001; Marx *et al.*, 2016; Benites-Palomino *et al.*, 2020). Previous studies have suggested that the fluvial invasion has occurred multiple times, including outside of the traditional "river dolphin" groups (e.g. Fordyce, 1983; Cassens *et al.*, 2000; Benites-Palomino *et al.*, 2002; Hulbert and Whitmore, 2006; Bianucci *et al.*, 2013; Pyenson *et al.*, 2015; Boersma and Pyenson, 2016). However, the pattern of their invasion of freshwater habitat within each lineage is unclear.

In Lipotidae, only the recently extinct representative, *L. vexillifer*, had an exclusively riverine habitat (Zhou, 2009). Since the recovery of the fossil lipotid *Parapontoporia* spp. from marine deposits, they had been believed to inhabit marine environment (Barnes, 1985; Pyenson, 2009; Boessenecker and Poust, 2015). Recently, Boessenecker and Poust (2015) described a Late Pliocene/Pleistocene periotic of *Parapontoporia* sp. from lacustrine/fluviodeltaic deposits (Tulare Formation), suggesting their adaptation to the nonmarine habitat as an obligate or facultative freshwater species (Smith and Reeves, 2012). Because the specimens of *Eolipotes japonicus* were found from the marine deposits, they are considered to have inhabited marine environments.

Results of our phylogenetic analyses suggest that *Eolipotes* is more closely related to *Parapontoporia* than to *Lipotes*. Given this phylogenetic relationship and the distribution of freshwater taxa in our most parsimonious trees, it is suggested that the invasion of Lipotidae into freshwater environments occurred at least twice independently: i.e., the fluvial invasion occurred respectively in the lineage of *Parapontoporia* and the lineage leading to *Lipotes* (Boessenecker and Poust, 2015). But, this interpretation needs some caution, because an alternative scenario is also possible: the common ancestor of Lipotidae had adapted into fluviodeltaic habitat as seen in many extant delphinoid populations (e.g. Amano, 2018; Flores *et al.*, 2018; Smith, 2018), followed by further specialization for a strictly freshwater habitat in the lineage of *L. vexillifer*. Future discoveries of fossils that are early members of the Lipotidae and/or species more closely related to *Lipotes* than *Eolipotes* and *Parapontoporia* will more clearly illuminate the pattern of their adaptation to freshwater habitat.

Fossil record of the Lipotidae

Molecular studies have suggested that the Lipotidae emerged early in the evolution of the Delphinida and have a long independent evolutionary history (McGowen *et al.*, 2009, 2020; Zurano *et al.*, 2019). However, in terms of the paleodiversity, our knowledge of their evolutionary history is quite limited. Only three species in a single genus, *Parapontoporia*, have been recognized as the fossil members of the family Lipotidae. Fossil Lipotidae have been found exclusively on both sides of the North Pacific. *Parapontoporia* spp. is widely known from the Neogene of eastern North Pacific (Boessenecker, 2013). *Parapontoporia* spp. is also numerically common, and in some rock units like the Purisima Formation, is the single most common odontocete (Boessenecker, 2013). Boessenecker (2013) reviewed 13 fossil occurrences of *Parapontoporia* spp. in the appendix, and then Boessenecker and Poust (2015) described another specimen of *P. sternbergi* from a nonmarine deposit of California, USA. Most specimens from the eastern side of the North Pacific have been recovered from Messinian and Pliocene deposits, and only two specimens (*P. pacifica* from the Almejas Fm. and *Parapontoporia* sp. from the San Mateo Fm.) possibly date to Tortonian (Barnes *et al.*, 1981; Barnes, 1984, 1985, 1998; Boessenecker, 2013; Boessenecker and Poust, 2015). The geologically youngest known occurrence of *Parapontoporia* is the Tulare Fm. (Boessenecker and Poust, 2015).

Whereas the only sub-Recent species of the family, *L. vexillifer*, inhabited the western side of the North Pacific, the fossil record of the family Lipotidae in this area remains scarce. There are only two specimens of fossil Lipotidae reported from Japan. Oishi (1992) reported the occurrence of *Parapontoporia* sp. from the Pliocene Tatsunokuchi Formation, Iwate, Japan. Ishimaru (2002) mentioned a cranium found from the Pliocene Tastsunokuchi Formation, Miyagi, Japan and suggested affinities with the Lipotidae. Both specimens were mentioned in the abstract of an oral presentation and have not been formally described yet. Zhou *et al.* (1984) described a fossil from the possible Miocene deposit of Yujiang River, China as a new genus and species of Lipotidae, *Prolipotes yujiangensis*. However, it only consists of a fragment of the mandible, which is considered undiagnostic for the Lipotidae. Thus, *P. yujiangensis* is regarded incertae sedis and several authors questioned their affinity to the Lipotidae (Muizon, 1988; Fordyce and Muizon, 2001; Pyenson, 2009). Therefore, *Eolipotes japonicus* is the first formally described fossil lipotid from Japan and the only species recovered from the western side of the North Pacific.

As stated above, both specimens described here are from the Upper Miocene. The paratype of *E. japonicus*, GMNH-PV-1011, was found stratigraphically between the tuff layers and geologic age is convincingly dated as 11.29–11.25 Ma (Odin *et al.*, 1997; Takahashi and Hayashi, 2004). All previously known fossil lipotids found from the western side of North Pacific are from the Pliocene. The oldest fossil lipotid in the eastern North Pacific is dated as early as *ca.* 10 Ma (*Parapontoporia* sp. from San Mateo Formation) (Barnes *et al.*, 1981; Boessenecker, 2013). Therefore, the paratype of *E. japonicus*, GMNH-PV-1011, can be regarded as the geologically oldest fossil record of Lipotidae yet described. The holotype and the paratype of *E. japonicus,* with the Miocene lipotids from eastern side of North Pacific, suggest that lipotids were distributed on both sides of the North Pacific at least from the Late Miocene. *Eolipotes japonicus* expands our knowledge of the evolution of the Lipotidae. Future discoveries of fossil lipotids from both sides of the North Pacific may shed more light on their enigmatic evolutionary history.

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Author contributions

T. K. was primarily responsible for the description and taxonomic aspects. Y. H. discussed with T. K. Both authors contributed to writing the paper.

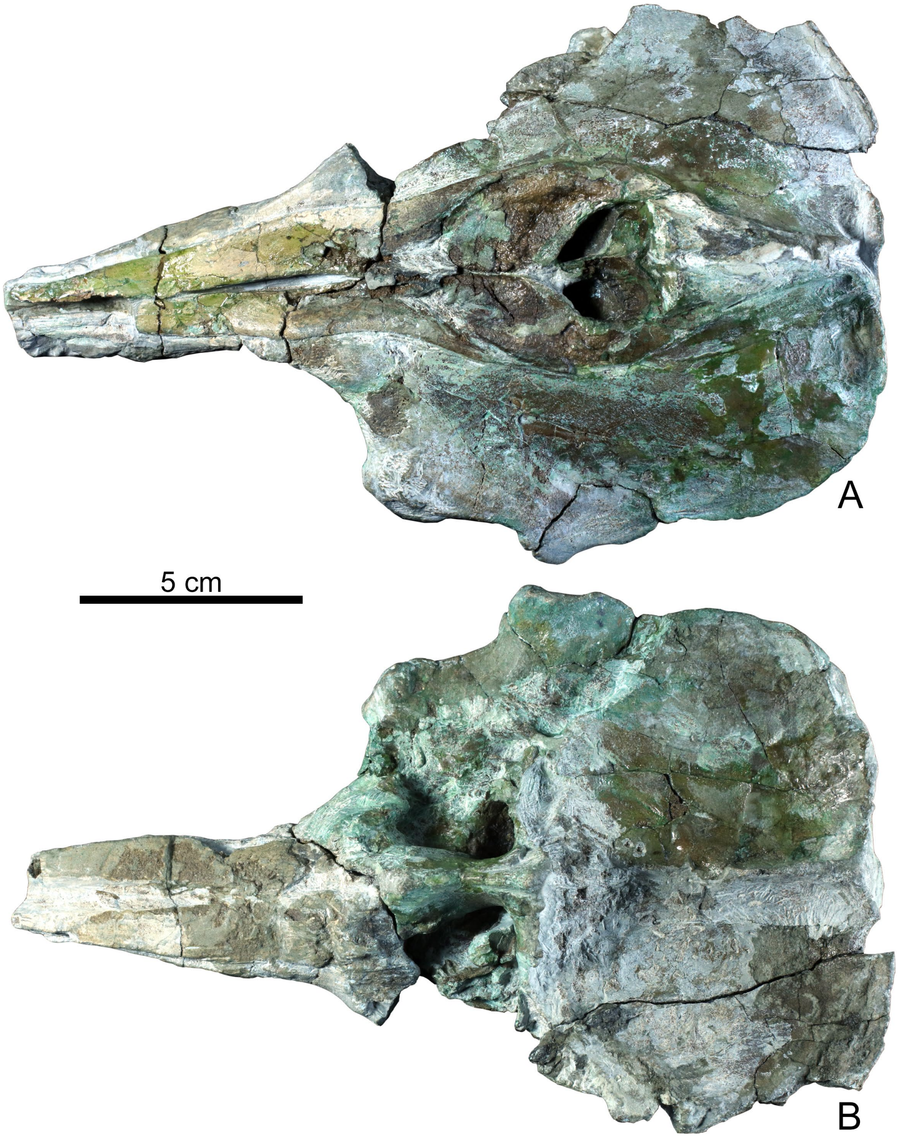

Figure S1. Cranium of the holotype, *Eolipotes japonicus*, gen. et sp. nov. (TPM7847-1). **A,** dorsal view; **B,** ventral view. Scale bar equals 5 cm.

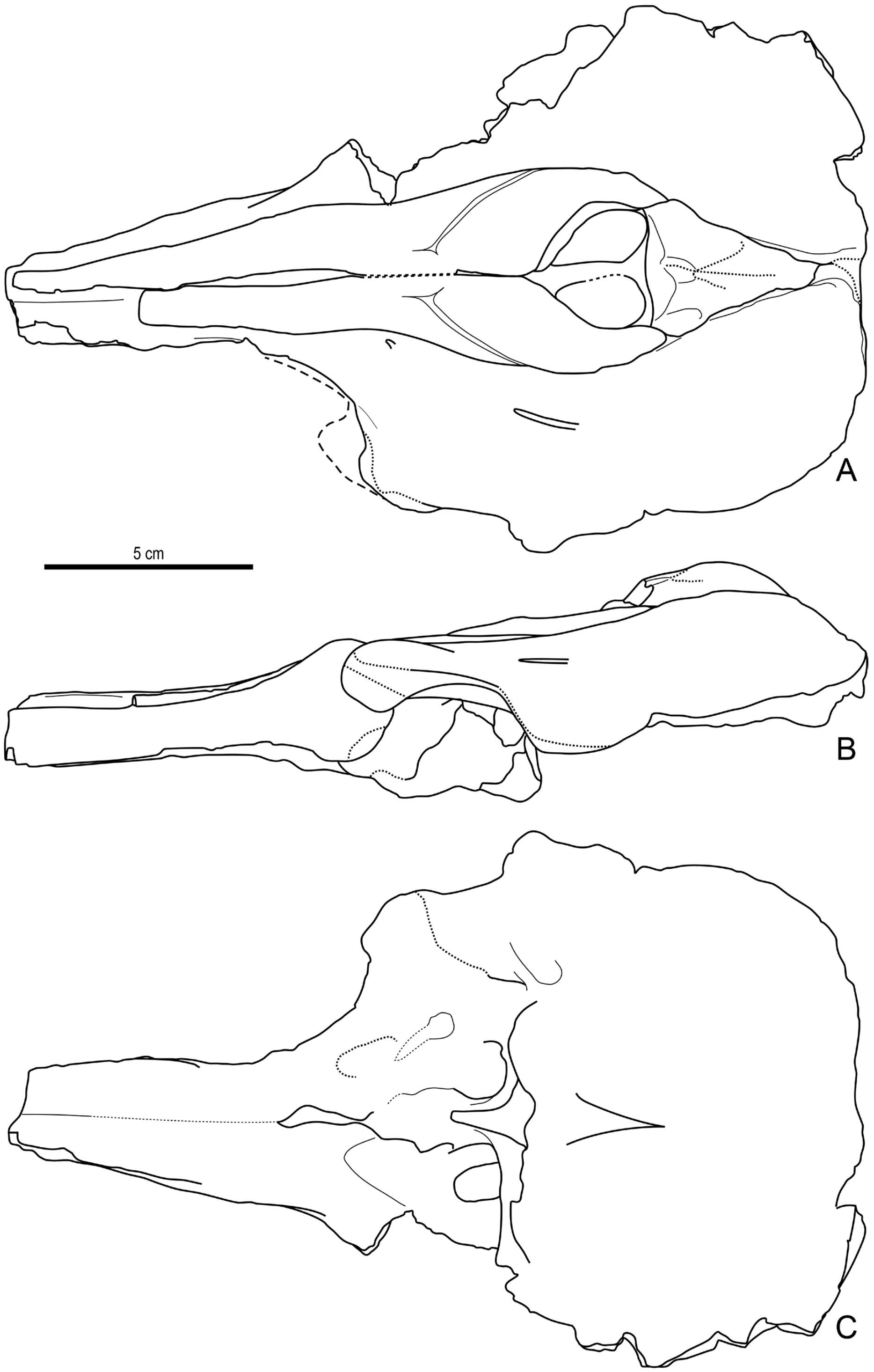

Figure S2. Line drawings of the cranium of the holotype, *Eolipotes japonicus*, gen. et sp. nov. (TPM7847-1). **A,** dorsal view; **B,** left lateral view; **C,** ventral view. Scale bar equals 5 cm.

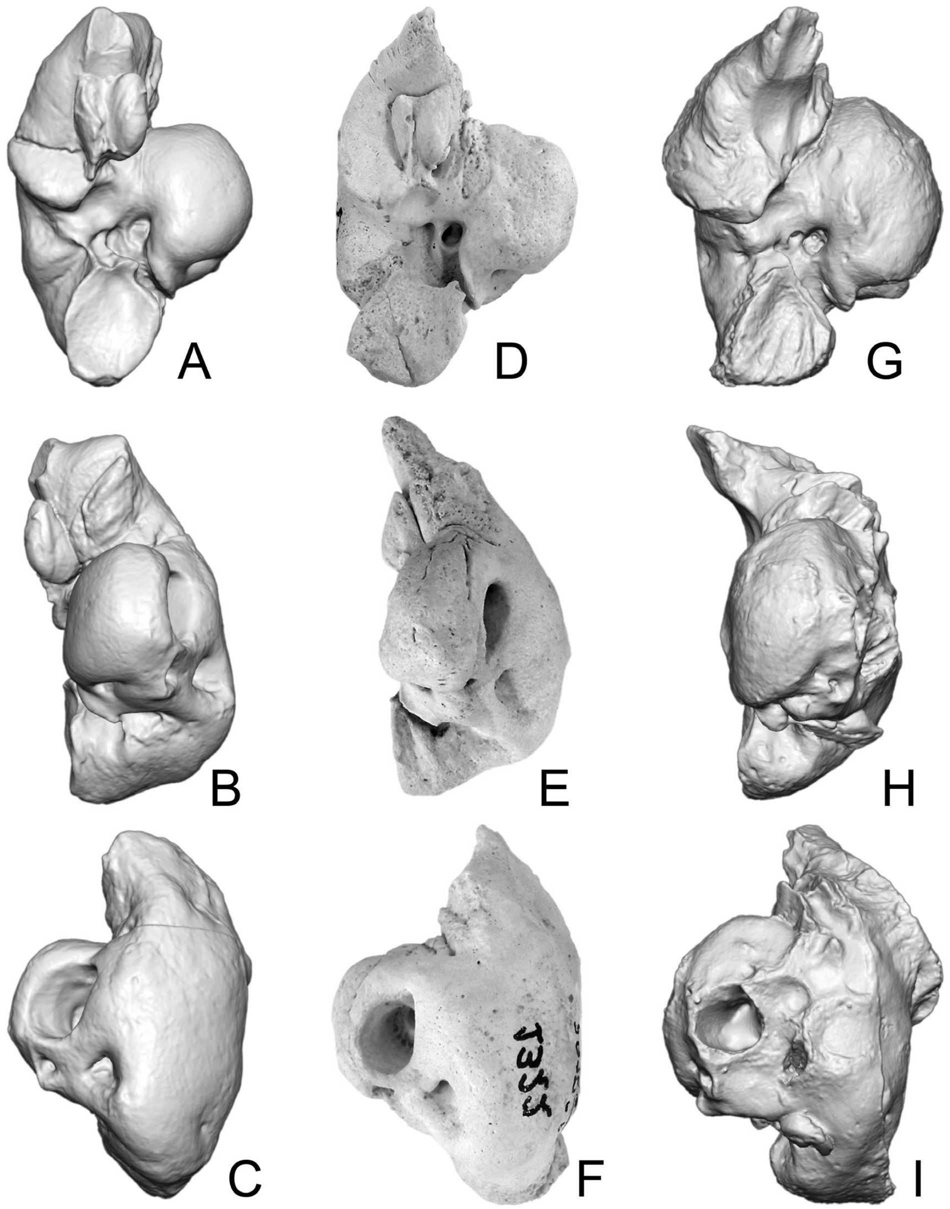

Figure S3. Comparison of the periotic in ventral, medial and dorsal views. **A–C,** *Eolipotes japonicus*, gen. et sp. nov. (3D model of GMNH-PV-1011); **D–F,** *Parapontoporia sternbergi* (photograph of SDSNH23630, mirrored for comparison, courtesy of M. Murakami); **G–I,** *Lipotes vexillifer* (3D model of USNM251644). Not to scale.

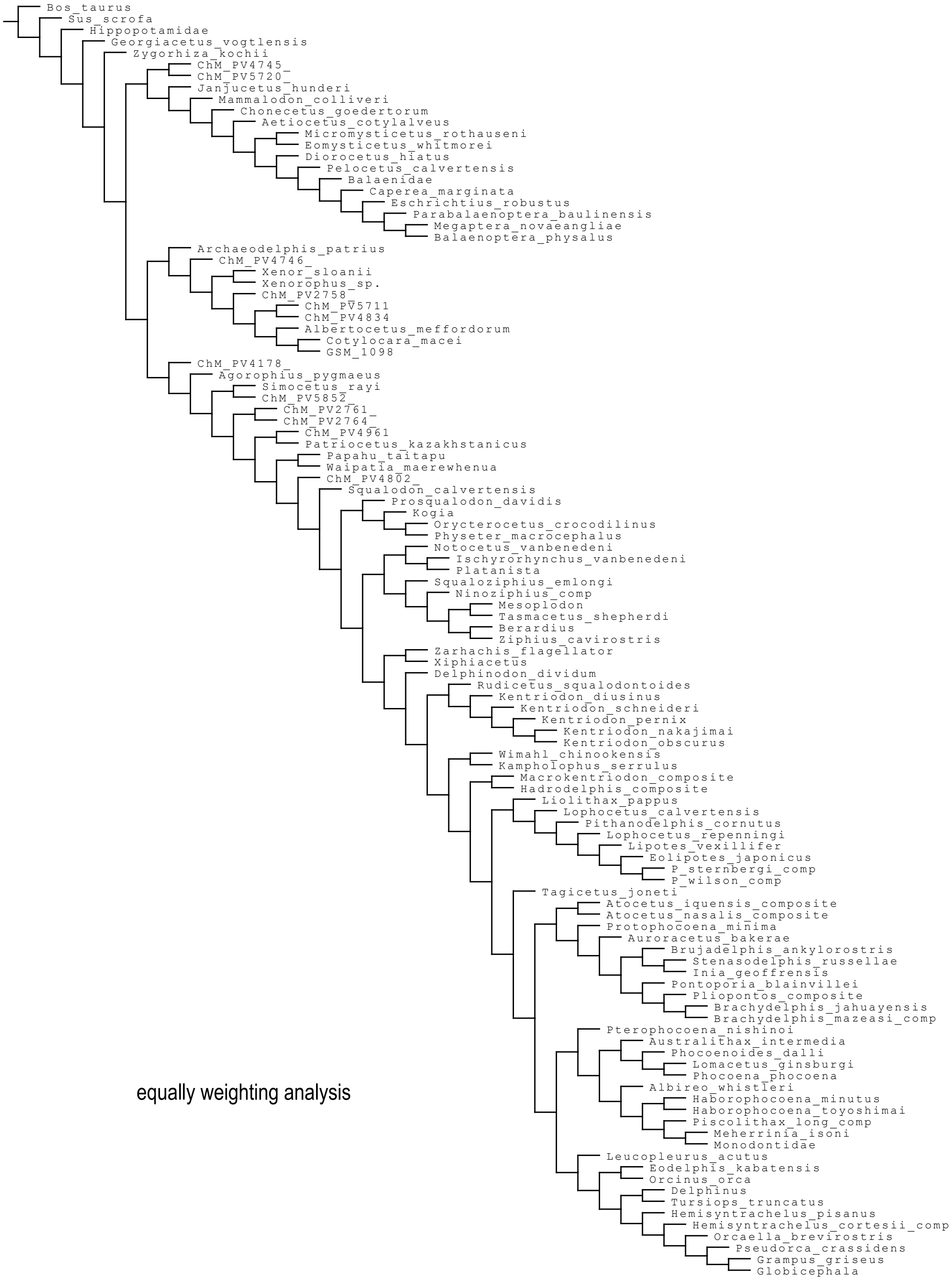

Figure S4. Most parsimonious trees resulting from the phylogenetic analyses.

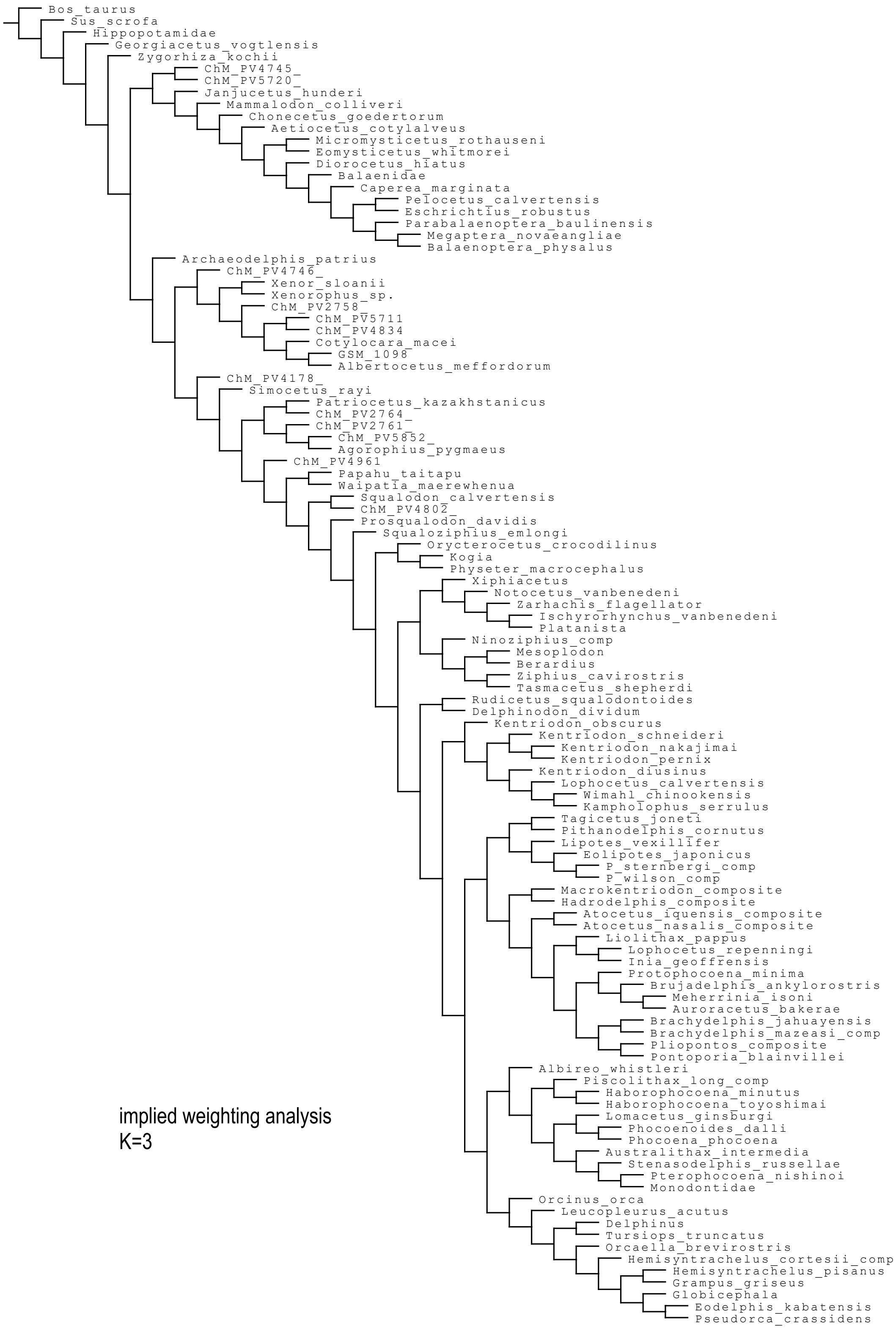

Figure S4. *Continued.*

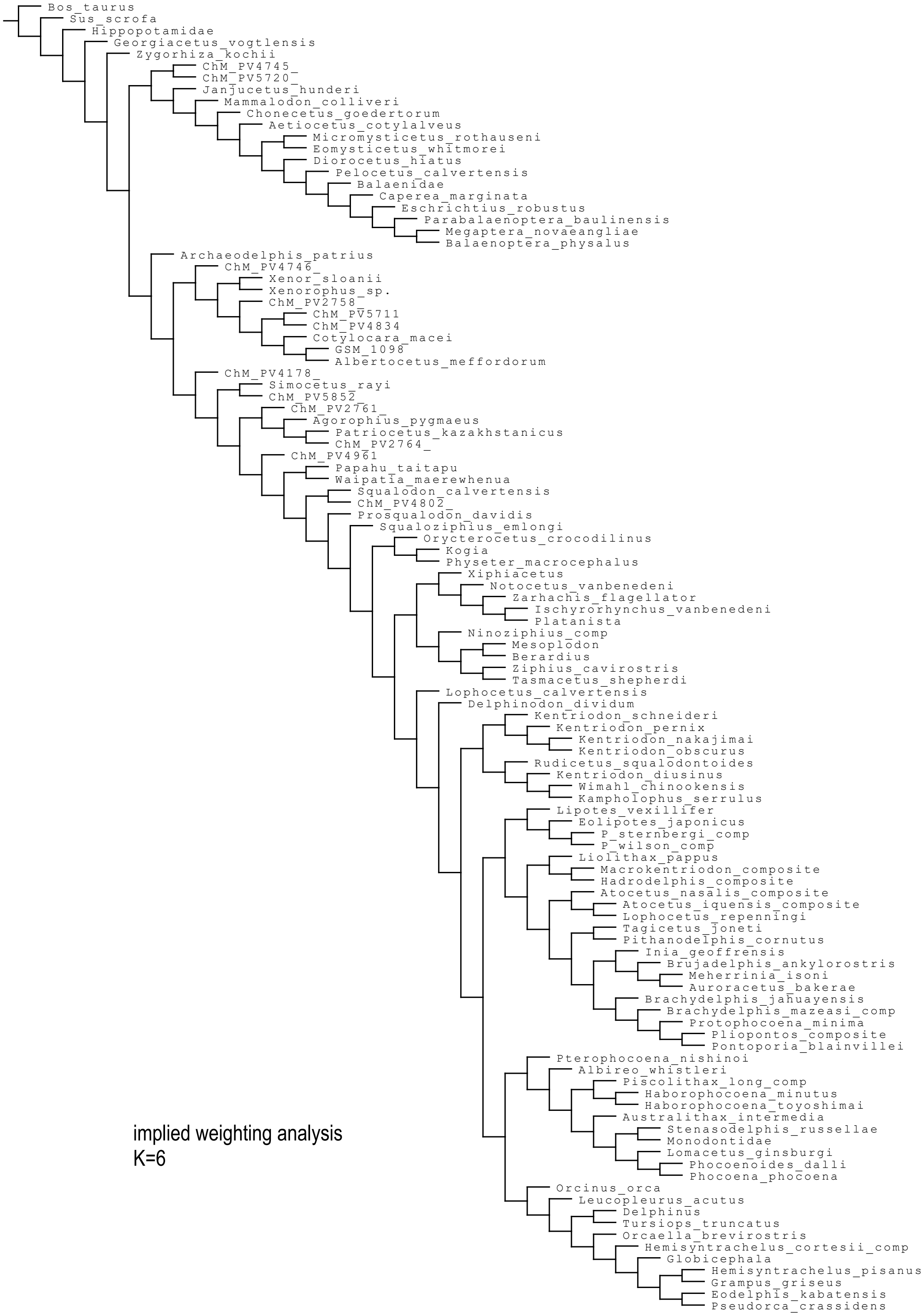

Figure S4. *Continued.*

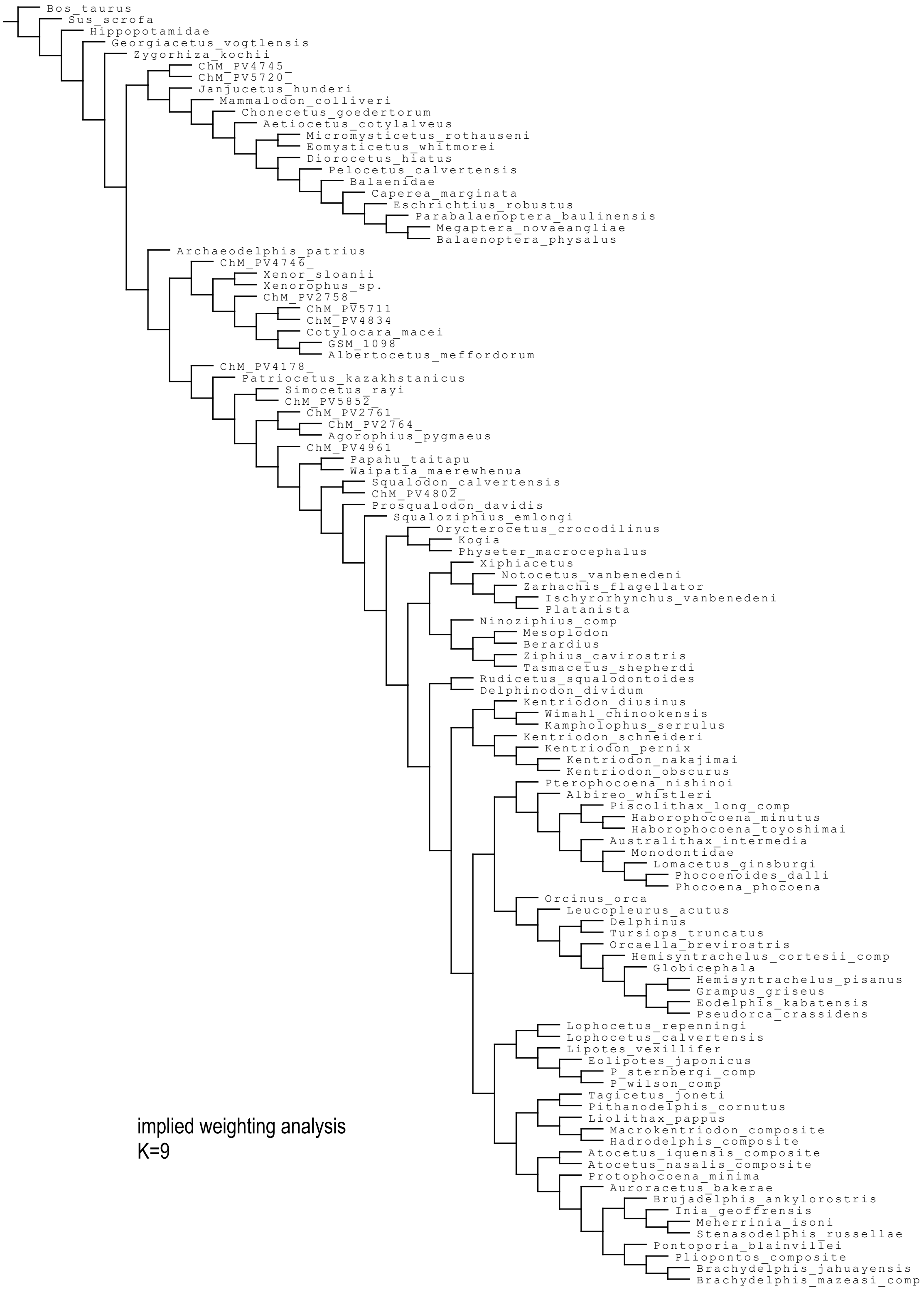

Figure S4. *Continued.*