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Asymmetrical basal delphinoid skull from the upper lower Miocene Yamato Formation of Hokkaido, northern Japan: implications on evolution of cranial asymmetry and symmetry in Odontoceti

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Abstract. We describe an asymmetrical basal delphinoid skull from the upper lower Miocene Yamato Formation of Hokkaido, northern Japan. The skull shows clear cranial asymmetry: the nasal process of the left premaxilla is longer than that of the right one; the mesethmoid and frontals are left skewed 2.9°; and the right nasal is larger than the left one. Evaluation of the deformation of the fossil based on the carbonate content of the matrix indicates that the concretion in which the skull was found formed in an early stage of diagenesis and that the present specimen was not affected by compaction during diagenesis. A cladistic analysis including the new specimen shows cranial asymmetry among Delphinoidea extends back to the late early Miocene in the fossil record, and supports the hypothesis that cranial asymmetry in basal delphinoids is more common than previously thought. On the other hand, trait analyses suggest that the common ancestor of Delphinoidea had a symmetrical skull. We hypothesize that some extinct odontocetes that had symmetrical crania were able to produce narrow-band high-frequency clicks to avoid predation, as in extant symmetrical cranial species.

Key words: Cetacea, cranial asymmetry and symmetry, Delphinoidea, early Miocene, evolution

Introduction

It has been suggested that Kentriodontidae (Cetacea, Odontoceti, Delphinoidea) is a stem delphinoid group that includes the ancestors of modern delphinoids (Barnes, 1978). Generally, the family is divided into Kentriodontinae, Lophocetinae, and Pithanodelphininae (Muizon, 1988a; Dawson, 1996a; Kazár and Grigorescu, 2005). However, Kentriodontidae has long been considered a paraphyletic group (e.g. Muizon, 1988a; Ichishima *et al*., 1994), although no computer-assisted phylogenetic analysis was performed. The paraphyly of Kentriodontidae was supported quite recently with phylogenetic analyses (Murakami *et al*., 2012a, b; hereafter we used "Kentriodontidae" or basal delphinoids instead of Kentriodontidae). "Kentriodontidae" are traditionally considered to have symmetrical skulls (Barnes, 1978). In contrast, most odontocetes, including more basal taxa and derived Delphinoidea (i.e., Delphinidae, Phocoenidae, and Monodontidae) have cranial asymmetry (matrices of Murakami *et al.*, 2012a, b; but see Barnes, 1985a). These cranial and facial asymmetries are related to their echolocation ability (Mead, 1975; Heyning, 1989; Cranford *et al*., 1996). Mead (1975) and Huggenberger *et al.* (2009) reviewed the history of research on cranial asymmetry in Odontoceti. According to them, Pouchet (1886) described asymmetrical skulls in odontocetes. Several authors (Beddard, 1900; Abel, 1902; Howell, 1930) noted that asymmetry of the skull is correlated with the development of a complex nasal apparatus and its asymmetry. Then, the sonar system of Odontoceti was discovered in the 1950s (e.g. Kellogg *et al.*, 1953). Subsequently, Norris (1964) and Wood (1964) discussed the role of cranial asymmetry in relation to sound production. Mead (1975) proposed that development and asymmetry of the nasal sac systems are related to their function as air reservoirs, as reflecting elements, or to direct involvement in sound production. The skull plays an important role in echolocation; it acts as an acoustic reflector to guide the sound to the melon, which is a fatty tissue, and is the pathway for sounds transmitted to the water column (Evans and Maderson, 1973; Aroyan *et al.*, 1992; Aroyan, 1996; Cranford *et al.*, 2008). Cranford *et al.* (1996) suggested that the phonic lips in odontocetes were the source of biosonar signals, a function that was confirmed by Cranford (2000) using high-speed video endoscopy.

If the common ancestor of Delphinoidea had a symmetrical skull, is the asymmetrical skull of crown Delphinoidea a secondarily acquired character? If so, why have they undergone such a complex evolutionary scenario? Interestingly, the skulls of pithanodelphinines and a few basal delphinoids are reported to be asymmetrical to some degree (Barnes, 1985b; Kazár and Grigorescu, 2005; Lambert *et al.*, 2005). Furthermore, many late middle Miocene asymmetrical basal delphinoid skulls have been reported from Japan (Jimbo, 1897; Kimura *et al.*, 2003; Kohno *et al.*, 2007). Thus, it is possible that certain asymmetrical basal delphinoids might be the direct ancestors of derived delphinoids with an asymmetrical skull, this feature having been retained throughout the intervening course of evolution. In other words, basal delphinoids with symmetrical skulls might be collateral lines which secondarily lost asymmetrical skulls. Here, we report an asymmetrical kentriodontid skull from the upper lower Miocene Yamato Formation of Hokkaido, northern Japan. The new specimen supports the hypothesis that cranial asymmetry among basal delphinoids is more common than previously thought and suggests a broad variation in this feature.

Institutional Abbreviations.—**CMM**, Calvert Marine Museum, Maryland, USA; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **LACM**, Los Angeles County Museum, Los Angeles, California, USA; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **NMV**, Nakagawa Museum of Natural History, Hokkaido, Japan; **UBFG**, Faculty of Geology and Geophysics, University of Bucharest, Romania; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Anatomical Terms.—The anatomical terminology of the skull and ear bones follows Mead and Fordyce (2009).

Systematic paleontology

Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Superfamily Delphinoidea Gray, 1821
Delphinoidea gen. et sp. indet.

Figures 2–3

Material.—NMV-72; a partial skull.

Locality and Age.—NMV-72 was collected as a calcareous concretionary float by Kohei Abe from the Wakkawenbetsu River, Nakagawa, Hokkaido, Japan (44°36′13.64″N, 142°02′39.57″E; Figure 1). The specimen was attributed to the upper lower Miocene Yamato Formation, because (1) other Neogene formations distributed in the Wakkawenbetsu River do not contain calcareous concretions; and (2) the fine sandstone grain size of the matrix is compatible with the Yamato Formation but not with other nearby formations (Hikida *et al.*, 1999). The Yamato Formation comprises shallow marine deposits that are characterized by hummocky cross-stratification (Matsuda *et al.*, 1999). To rigorously estimate the age of the specimen, we thrice attempted to obtain diatom fossils from the matrix of the specimen. However, no diatom fossils have yet been obtained. The Yamato Formation is considered to correspond to the lower part of the Chikubetsu Formation in the Haboro area, northern Hokkaido (e.g. Osanai *et al.*, 1960). The Chikubetsu Formation corresponds to the late early Miocene to early middle Miocene according to its North Pacific diatom biohorizon (17.5–15.5 Ma; *Actinocyclus ingens* Zone and *Denticulopsis lauta* Zone *sensu* Yanagisawa and Akiba, 1998; Sagayama, 2000).

Description

Skull

The skull lacks the rostrum, the basicranium and several portions of the facial surface as a result of weathering (Figures 2, 3). Although the nasals, frontals, and distal tips of the nasal processes of the premaxillae are preserved, their surfaces are also affected to some extent by weathering.

Premaxilla.—The right premaxilla seems to be distinctly wider than the left premaxilla, but this feature could be overestimated due to the bad preservation because some part of the left premaxilla in the facial area has been damaged by weathering (Figures 2A, 3A). The lateral edge of the right premaxilla does not overhang either the right premaxilla or maxilla (Figures 2B, 3B). The anteromedial, posteromedial, and posterolateral sulci cannot be observed because of weathering. The premaxillae around the external bony nares are convex dorsally, the premaxillary eminences (*sensu* Murakami *et al.*, 2012b:1182; Figures 2A–C, 3A–C). The tops of the eminences are wide and flat. The greatest dorsoventral thickness of the right premaxillary eminences is 15.5 mm, but

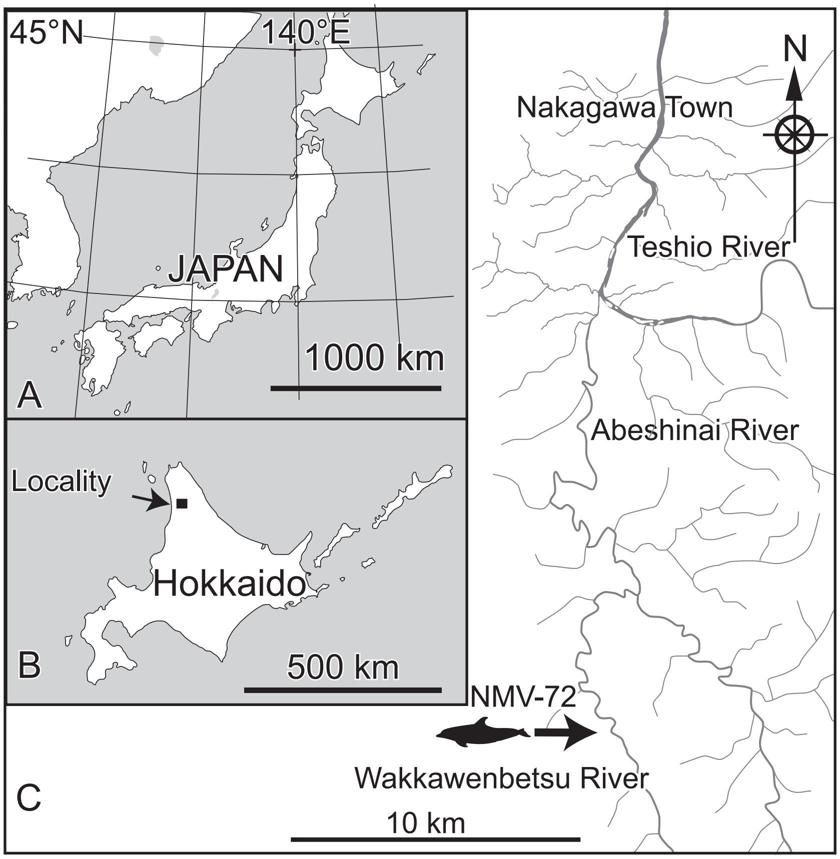


Figure 1. Locality of NMV-72.

they were originally thicker. The premaxillary sac fossa is very shallow and its surface is smooth. Both the right and left nasal processes of the premaxillae contact the lateral edges of the nasals widely (Figures 2A, 3A). The right and left processes are asymmetrical: the distal tip of the left nasal process is 4 mm longer than the right one and extends beyond the anterior half of the nasal. The distal tip of the right nasal process of the premaxilla is divided into a posterolateral plate and a posteromedial splint by a shallow premaxillary cleft (Figures 2A, 3A).

Maxilla.—The mediolateral inclination of the ascending process of the maxilla around the vertex is gentle (Figures 2A, C, 3A, C). The right maxilla appears dorsally between the right premaxilla and the ossified mesethmoid cartilage anterior to the external bony nares. Both maxillae also appear at the posterolateral edges of the external bony nares and are surrounded by the mesethmoid, premaxillae, and nasals. Neither maxilla approaches nor reaches the sagittal line posterior to the nasals (Figures 2A, 3A).

Mesethmoid.—The mesethmoid is skewed leftward 2.9° (Figures 2A, C, 3A, C). The mesethmoid ridge is well developed and divides the external bony nares into right and left parts (Figures 2A, C, 3A, C). The right and left external bony nares are the same size. The external bony nares are relatively long anteroposteriorly (33 mm long and 29 mm wide) and are V-shaped. The anteroposterior inclination of the mesethmoid is gentle rather than steep. The mesethmoid cartilage is well ossified and tightly fills the mesorostral groove perhaps posterior to the antorbital notch (Figures 2A, C, 3A, C). The mesethmoid is moderately well developed dorsally, although its top cannot be seen from the lateral view (Figures 2B, 3B).

Nasal.—The nasals are anteroposteriorly elongated (Figures 2A, 3A). The lateral margins of the nasals are convex, consequently the nasals are widest at their midpoints. The nasals are asymmetrical, with the right nasal larger than the left one. The greatest width of the right nasal (24 mm) is clearly wider than that of the left nasal (21 mm). Moreover, the posterior edge of the right nasal becomes narrow, whereas the left nasal widens posteriorly. The anterolateral angle of each nasal extends more anteriorly than does the anteromedial edge (Figures 2A, 3A). However, it is uncertain whether the anterolateral sulcus of the nasal was present or just absent due to weathering. The posterior edge of each nasal is convex posteriorly.

Frontal.—In dorsal view, the frontal only appears at the vertex as a narrow, acutely angled, triangular area (11 mm width). The anterior edges of the frontals are wedged into the posterior edges of the nasals (Figures 2D, 3D). The suture line between the right and left frontals is skewed leftward 2.9° in dorsal and 2.8° in ventral view (Figures 2A, D, 3A, D). The anterodorsal wall of the braincase is formed by the frontals.

Pterygoid.—The hamular fossa of the pterygoid is considered to be narrowed by the space between the lateral lamina of the palatine (Figures 2B, D, 3B, D).

Orbitosphenoid.—The frontal groove on the orbitosphenoid slopes nearly vertically and is narrow (9 mm in anteroposterior width; Figures 2B, D, 3B, D).

Materials and methods

Evaluation of deformation

Concretionary carbonate is usually precipitated in the pore spaces of sediments. Consequently, the volume of the concretion-forming minerals can be roughly considered equal to the sediment porosity at the time of carbonate precipitation (e.g. Raiswell, 1976). For this reason, Murakami *et al.* (2012a) proposed that the deformation of a fossil can be evaluated from the degree of sediment porosity, estimated from the carbonate content. Here, we evaluated the deformation of the present specimen with this method.

We estimated the carbonate content of the concretion that included the present specimen as follows. (1) Several pieces of the concretion were reduced to powder with an agate mortar and pestle. We pick up six samples from the matrix of the concretion in close vicinity to the specimen (Figure 3): (α), left bony nares; (β), right bony nares; (γ), left choana; (δ), right choana; (ε), right lateral lamina of the palatine; (ζ), anteroventral wall of braincase. (2) The powdered sample was weighed with a gravimeter (AB304-S, Mettler Toledo International Inc.). (3) The powdered concretion was acidified with a 6 M solution of HCl in a 300 mL beaker and heated at 50°C for two hours on a hotplate to decompose the carbonate. The solution was stirred for 10 seconds every 15 minutes. (4) The beaker was covered with a sheet of Parafilm after it had been cooled for 15 minutes. The solution was further reacted at room temperature for 24 hours. (5) The solution was transferred to a centrifuge tube, which was weighed with the same gravimeter as the sample. (6) To neutralize the solution, the tube was centrifuged four times at 3500 rounds/minute for 10 minutes and four times at the same speed for six minutes in a Kubota Tabletop Centrifuge 4000 (Kubota Co.). When the solution had been neutralized, the supernatant was discarded. (7) The remaining moist powder was placed in a centrifuge tube and dried in a drying oven (Drying Oven Kosumosu SSN 111S: Isuzu Seisakusho Co., Ltd.) for 24 hours. (8) The powder in the centrifuge tube was further dried in a vacuum oven (Model 285A: Fresh Scientific Ltd.) for three hours. After drying, the centrifuge tube and the remaining dried powder was weighed with a gravimeter.

Cladistic analysis

In order to estimate the phylogenetic position of NMV-72, a cladistic analysis was performed with TNT 1.1 (Goloboff *et al.*, 2008). *Georgiacetus vogtlensis* Hulbert *et al.*, 1998 is used as the outgroup. The phylogenetic tree was based on a reanalysis of the comprehensive data matrix (74 ingroup taxa, 282 characters) of Murakami *et al.* (2012b). Character state scoring of NMV-72 is shown in Appendix 1. We add state (2) to character 69 and state (3) to character 94 of the matrix: (69-2) widening medial exposure of the maxilla and the premaxilla not forming the external nares; (94-3) greatest width of the frontal at the vertex less than 1/3 of the greatest width of the nasals. Other revisions, the complete character list and the data matrix are provided in Appendix 2. All characters were treated as unweighted and unordered. The heuristic searches were employed with Sectional search and Tree fusing option with 1000 replicates.

Trait analysis

Heyning (1989) noted that the asymmetry of the skull has basically two easily quantifiable components: the deviation of the medial suture from the midline of the skull and the size and/or shape difference between corresponding bilateral structures. Two characters (character 97 and 73, respectively; see below) used in the cladistic analysis correspond respectively to these components. In order to understand the evolution of cranial asymmetry of the skull in Delphinoidea, we traced the evolution of these two characters (characters 73 and 97) on a phylogenetic tree, using the parsimony algorithm implemented in Mesquite Version 2.73 (Maddison and Maddison, 2010). The phylogenetic tree was based on a reanalysis of the present cladistic analysis, with characters 73 and 97 excluded to avoid circular reasoning (Felsenstein, 1985). The method of the cladistic analysis was the same as the present analysis. The two characters related to cranial asymmetry are defined as follows. Character (73) is the ratio of width of right premaxilla to width of left premaxilla in line with midpoint of external nares: <1.10

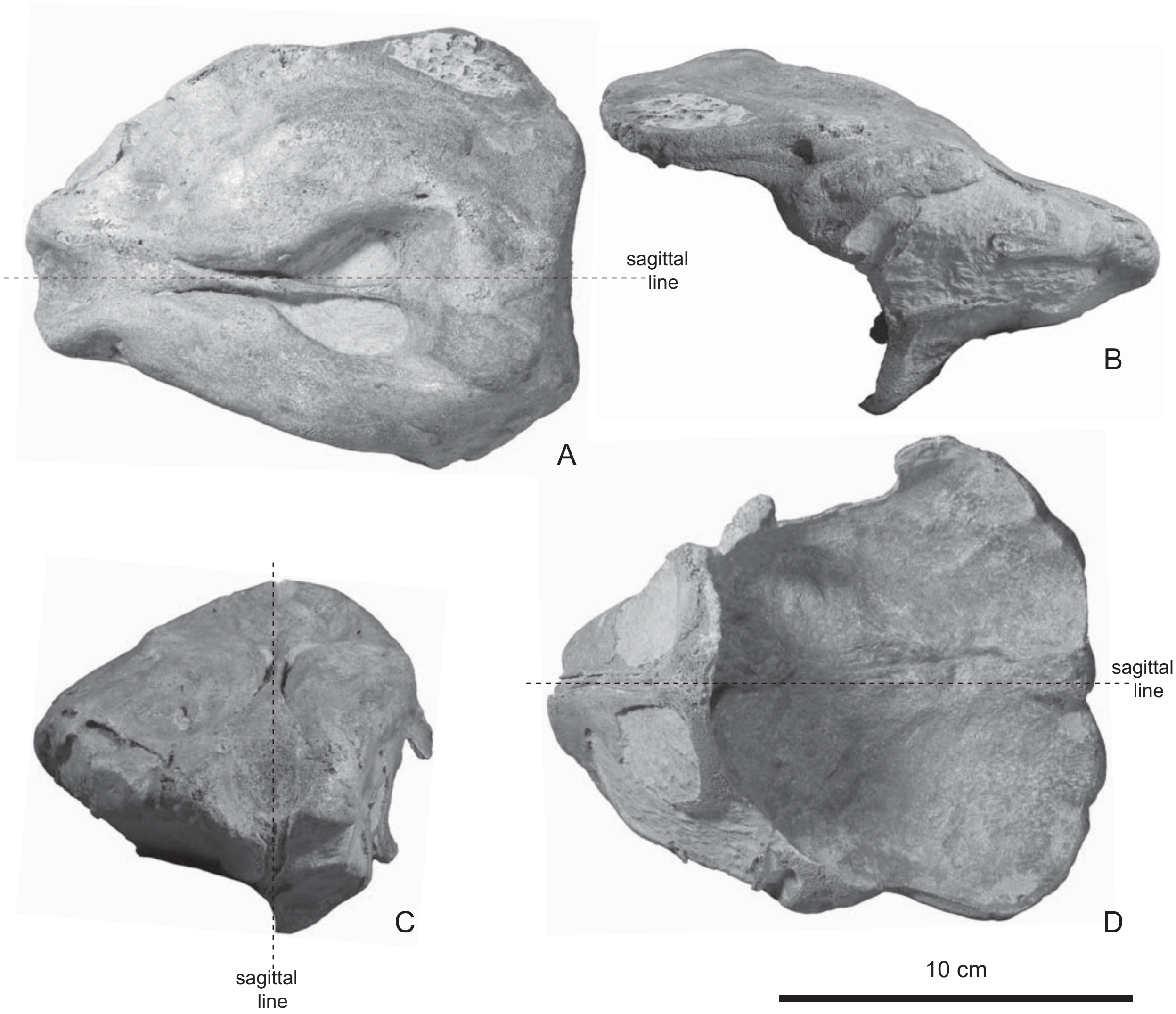


Figure 2. Photograph of the skull of NMV-72. **A**, dorsal view; **B**, right lateral view; **C**, anterior view; **D**, ventral view.

(0); 1.10–1.50 (1); 1.50> (2) (modified from Murakami *et al.*, 2012a, b). Character (97) Cranial vertex skewed asymmetrically to left side: absent (0); present (1) (e.g. Barnes, 1990).

Results and discussion

Evaluation of deformation

The carbonate content (*Cwet*) was calculated as follows:

$$Cwet\ (\%) = (1 - (RPw - Tw) / Pw) \times 100$$

where RPw is the weight of the centrifuge tube + the remaining powder, Tw is the weight of the centrifuge tube, and Pw is the weight of the original powder. Analyses of samples (α)–(ζ) yielded.

$$Cwet(\alpha)\ (\%) = (1 - (13.20 - 13.12) / 0.32 \times 100 = 75.0\%$$
$$Cwet(\beta)\ (\%) = (1 - (13.53 - 13.44) / 0.21 \times 100 = 57.8\%$$
$$Cwet(\gamma)\ (\%) = (1 - (13.18 - 13.09) / 0.26 \times 100 = 65.4\%$$
$$Cwet(\delta)\ (\%) = (1 - (13.24 - 13.19) / 0.16 \times 100 = 68.7\%$$
$$Cwet(\varepsilon)\ (\%) = (1 - (13.60 - 13.43) / 0.46 \times 100 = 63.0\%$$
$$Cwet(\zeta)\ (\%) = (1 - (14.49 - 13.46) / 2.79) \times 100 = 63.1\%$$

The grain size of the matrix surrounding the specimen is that of fine sandstone. The original porosities of marine sandy sediments are estimated to be 55–69% (Bouma and Moore, 1975), and the porosity of the matrix of the concretion that yielded the specimen was in this

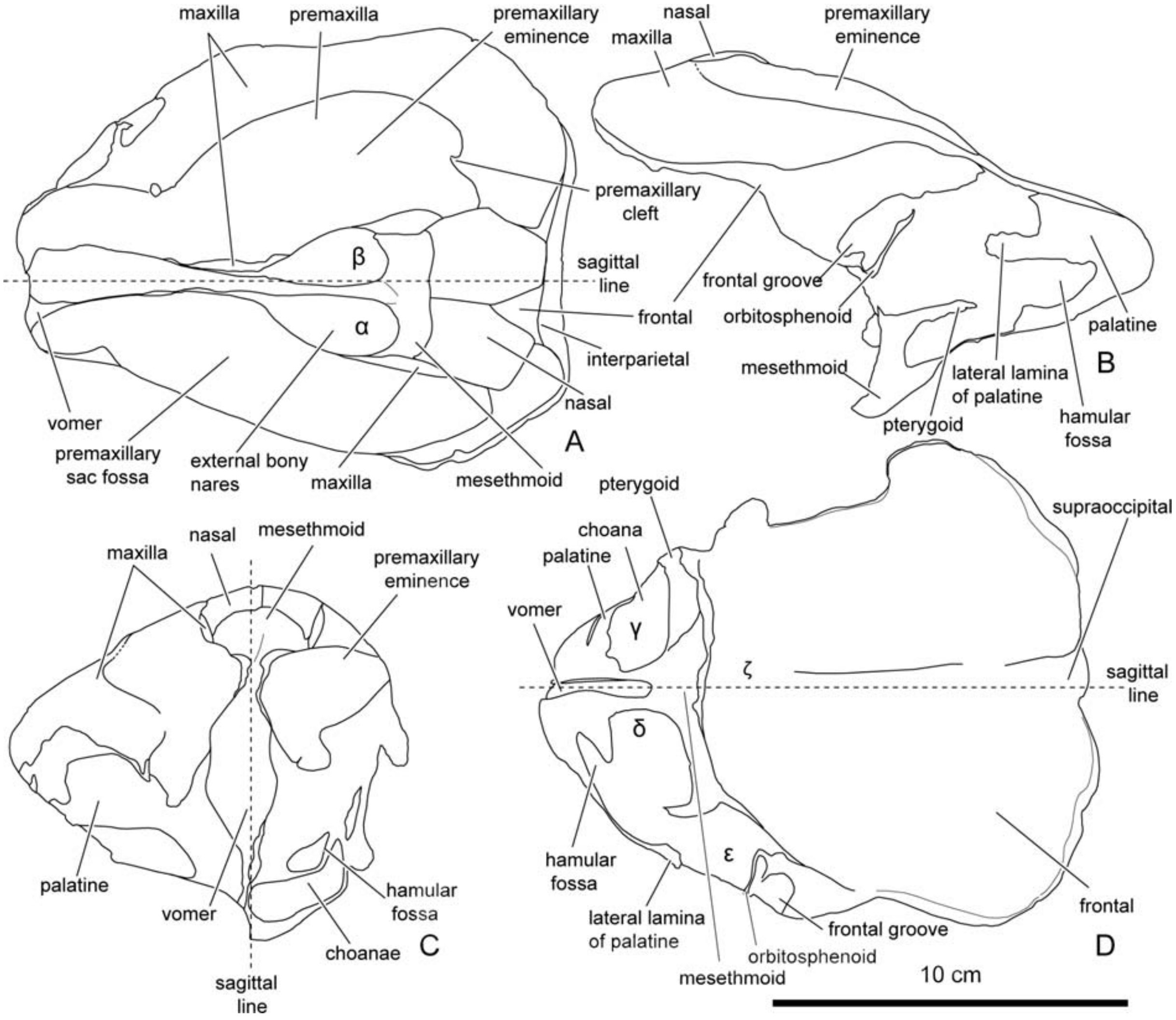


Figure 3. Corresponding line drawings for Figure 2 (the skull of NMV-72). **A**, dorsal view; **B**, right lateral view; **C**, anterior view; **D**, ventral view. (α), (β), (γ), (δ), (ε), and (ζ) are sampling points of the analysis for carbonate content (see text).

range. Although Murakami *et al*. (2012a) estimated the porosities of marine sandy sediments to be 70–80%, those values were actually muddy marine sediments. Results for five of six samples show values within the range of sandy sediment. Only one sample (sample α) showed a value within the range of muddy sediment, and this sample may have been affected by biological activity of the benthos. The values estimated for the carbonate content indicated that the fossil-bearing calcareous concretion that contained the present specimen formed early in the process of sediment burial. Therefore, the cranial asymmetry of the present specimen is real and was not affected by deformation arising from compaction during diagenesis. This method can be used elsewhere to evaluate whether a fossil yielded by a calcareous concretion has been deformed or not.

Cladistic analysis

The cladistic analysis found 18 most parsimonious trees with a length of 1720 steps. The general topology of the consensus tree supports the phylogenetic hypotheses of Murakami *et al.* (2012a, b; 2014; see their discussion about interfamilial relationship within Delphinoidea). Several synapomorphies indicate that NVM-72 locates the sister taxa of *Atocetus iquensis* (Figure 4), although only 26 of 282 characters were coded in NMV-72. NMV-72 shares one of seven synapomorphies with Delphinida (121-1, presence of the lateral lamina of

Figure 4. Phylogenetic position of NMV-72 among Odontoceti. The strict consensus of 15 most parsimonious trees, found by tree-bisection-reconnection. Decay indices are indicated above the nodes.

the palatine (Muizon, 1988a)), while the other six characters cannot be scored (89-1, 127-1 151-3, 164-0, 186-1, 224-1). NMV-72 share three of nine synapomorphies of Delphinoidea: 69-1, presence of the medial maxilla-premaxilla suture or accessory ossicles anterior to external nares (Muizon, 1984); 90-2, transverse width of either of nasals as percent maximum length of nasals: Width > 70% of the maximum length of the nasals (Murakami *et al.*, 2012b); 279-1, presence of the mesorostral groove diverging anteriorly from posterior to antorbital notch (Murakami *et al.*, 2012b). The other six characters in NMV-72 cannot be coded (25-1, 47-2, 116-0, 193-0, 203-1, and 207-0). NMV-72 does not have two synapomorphies of derived Delphinoidea (67-1, U-shaped bony nares (Muizon, 1984); 81-1, mesethmoid expanded dorsally (Muizon, 1984)): 12 other synapomorphies cannot be coded (1-0, 32-1, 33-2, 34-1, 125-2, 131-0, 138-0, 158-1, 171-1, 176-2, 177-1, 200-0). On the other hand, six synapomorphies (3-1, 86-2, 99-2, 104-2, 110-2, and 139-1) of a clade (*Kentriodon pernix* + (*Atocetus iquensis* + NMV-72)) cannot be coded in NMV-72. However, the sister relationship between *Atocetus iquensis* and NMV-72 is supported by one synapomorphy (94-3, the greatest width of the frontal at the vertex less than 1/3 of the greatest the width of nasals). Thus, the present cladistic analysis indicates that NMV-72 belongs to the basal delphinoids.

Affinity of the specimen.—The present cladistic analysis indicates that NMV-72 is a basal delphinoid. Generally, basal Delphinoidea is divided into Kentriodontinae, Lophocetinae, and Pithanodelphininae (Muizon, 1988a; Dawson, 1996a; Kazár and Grigorescu, 2005). NMV-72 lacks the posterolateral projection of the nasal, a synapomorphy of Kentriodontinae (Muizon, 1988a; Lambert *et al.*, 2005; Figure 5A, B), although this character shows intraspecific variability (Lambert *et al.*, 2005). NMV-72 differs from all Lophocetinae, except *Liolithax pappus*, in lacking an extremely elevated vertex. Moreover, in NMV-72 the nasals are not highly compressed laterally by the maxillae, a synapomorphy of Lophocetinae (Dawson, 1996a; Figure 5C, D). However, both NMV-72 and Pithanodelphininae show cranial asymmetry (Figure 5F–I), the frontal exposure of the vertex considerably narrower than that of the nasals (Kazár and Grigorescu, 2005), and presence of the anterior margin of frontals wedged between the posterior edges of the nasals (Muizon, 1988a), although this last character also occurs in *Liolithax pappus* and the morphology of the nasal of Pithanodelphininae is similar to that of *Liolithax* (see Kazár and Grigorescu, 2005, p. 929) and *Lophocetus repenningi*.

In conclusion, NMV-72 shows an affinity to Pithanodelphininae rather than to Kentriodontinae or Lophocetinae. NMV-72 could be a basal pithanodelphinine because it does not have two other synapomorphies of Pithanodelphininae: maxillae approaching or reaching the sagittal line posterior to the nasals, and large nasals (Kazár and Grigorescu, 2005; Figure 5F–I). However, we tentatively regard NMV-72 as Delphinoidea gen. et sp. indet. because of the fragmentary nature of the specimen. When it is compared with members of Pithanodelphininae, the right premaxilla of NMV-72 is much wider and more convex than that of all members of Pithanodelphininae. The distal tips of the right nasal processes of the premaxillae are somewhat similar to those of the left nasal processes of *Sarmatodelphis*, in that both of them are divided into a posterolateral plate and a posteromedial splint (Figure 5E, G). The external bony nares are longer than those of any other pithanodelphinines (Figure 5E–I) and the anteriorly wedged frontals between the posterior edges of the nasals are wider than those of other pithanodelphinines (Figure 5E–I).

Trait analysis

The cladistic analysis resulted in 15 most parsimonious trees of 1718 steps (Figures 6, 7), giving rise to a strict consensus tree identical to that obtained in the present analysis with the exception of a few branches. One of the most parsimonious possibilities for evolution of the left skewed cranial vertex is that the character was obtained at the common ancestor of all extant odontocetes (clade A, Figure 6). In this scenario, the symmetrical cranial vertex reappeared at the common ancestor between Delphinoidea and *Squaloziphius emlongi* (clade B). Then, the left skewed cranial vertex was re-obtained independently at Lipotidae, Iniidae, *Brachydelphis mazeassi*, NMV-72, and derived Delphinoidea; however, this scenario requires that the left skewed cranial vertex evolved independently up to 11 times. In either case, the common ancestor of Delphinoidea had the symmetrical vertex and the left skewed cranial vertex evolved independently in NMV-72 and derived Delphinoidea.

Asymmetry of the premaxillae (width of each premaxilla at the midpoint of the external nares) appeared a minimum of four times and a maximum of eight times in the analysis (Figure 7). In all case, asymmetry of the premaxillae has been obtained independently between Delphinoidea and other Odontoceti (e.g. Physeteroidea and Ziphiidae). Asymmetry of the premaxillae weakened stepwisely in Phocoenidae as discussed in Murakami *et al.* (2012b). Two relatively early diverged delphinids, "*Stenalla*" *kabatensis* and the killer whale *Orcinus orca*, also have secondarily obtained moderate asymmetry of the premaxillae. Thus, the present analyses suggest that the presence of symmetrical skulls in several basal delphinoids are the result of reversal, as in Pontoporiidae

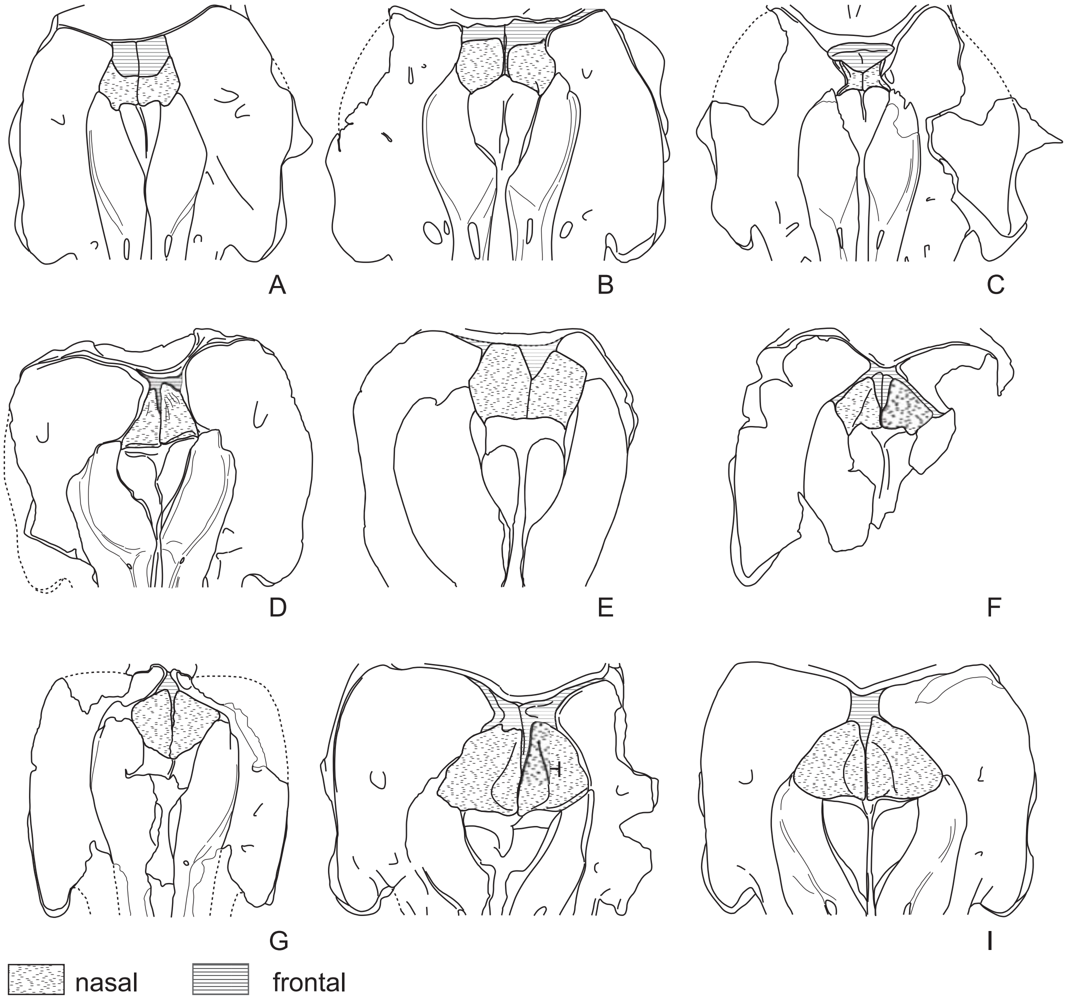
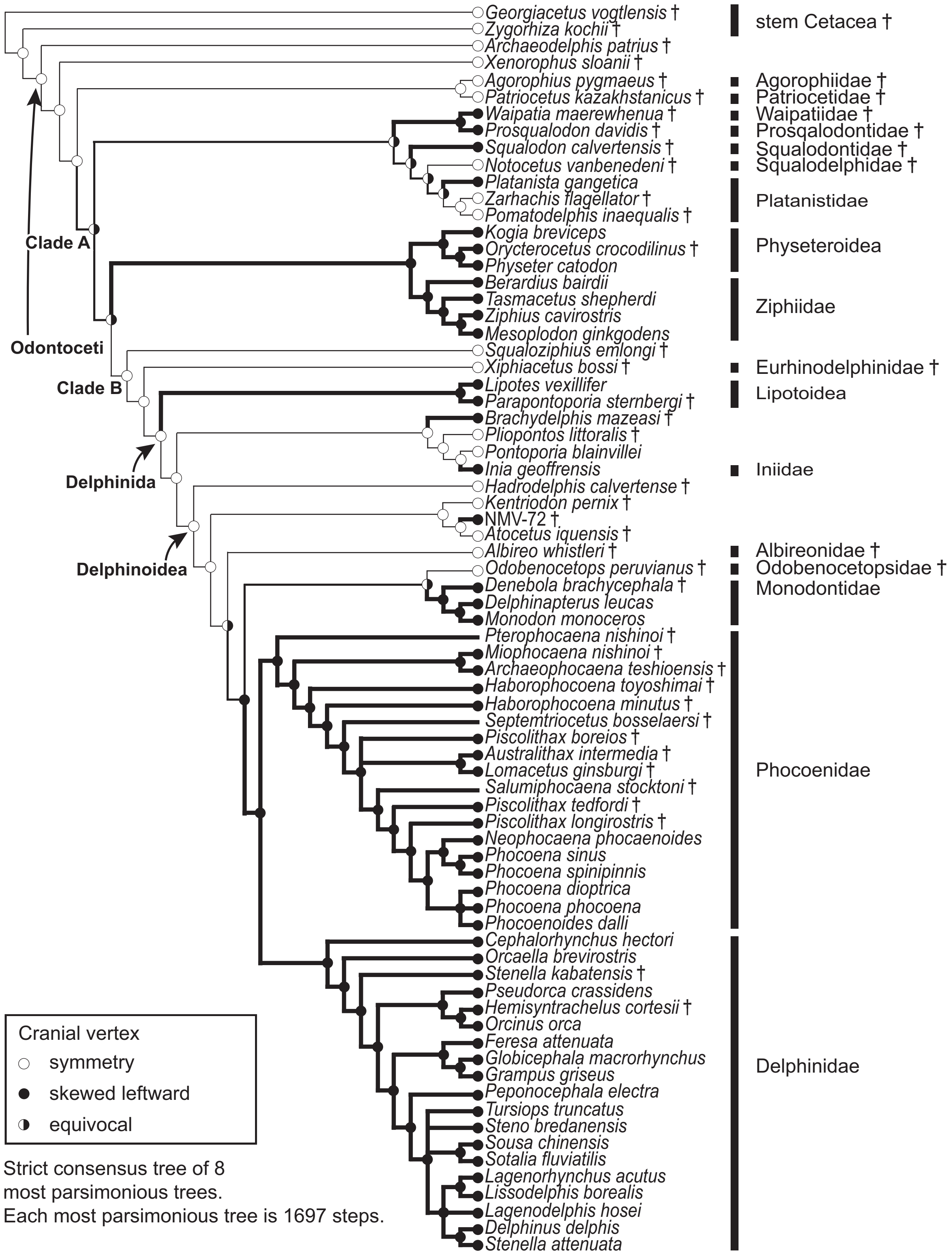


Figure 5. Comparisons of the facial area of the skulls of basal delphinoids. **A**, *Kentriodon pernix* Kellogg, 1927 (USNM 8060); **B**, *Macrokentriodon morani* Dawson, 1996b (CMM-V-15); **C**, *Hadrodelphis calvertense* (Kellogg, 1966; CMM-V-11); **D**, *Lophocetus repenningi* Barnes, 1978 (USNM 23886); **E**, NMV-72; **F**, *Pithanodelphis cornutus* Abel, 1905 (IRSNB 373); **G**, *Sarmatodelphis moldavicus* Kirpichnikov, 1954 (UBFG 628); **H**, *Atocetus nasalis* (Barnes, 1985b; LACM 26635); **I**, *Atocetus iquensis* Muizon, 1988b (NMNH PPI 113).

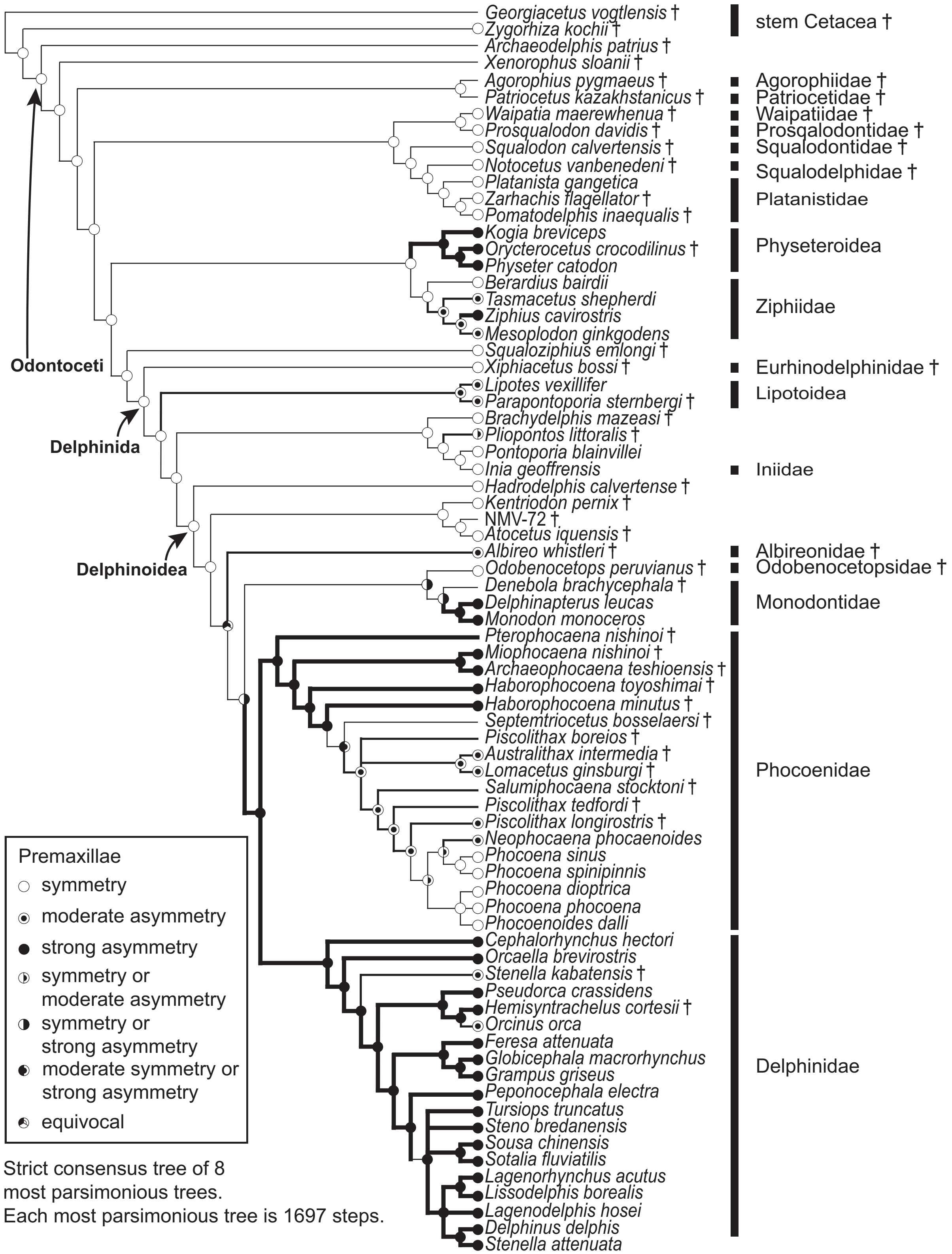
(Muizon, 1988a), Phocoenidae (Barnes, 1985a), and Albireonidae (Barnes and Furusawa, 2001).

Variety of cranial asymmetry.—One of the features of "Kentriodontidae", excluding Pithanodelphininae, was considered to be their symmetrical skulls (Barnes, 1978; Bianucci, 2001), although most odontocetes, including more basal taxa and derived Delphinoidea, have asymmetrical skulls, a feature related to their echolocation ability (e.g. Mead, 1975; Cranford *et al*., 1996). Actually, cranial asymmetry is also reported in other subfamilies of basal Delphinoidea, even though it excludes two characters in our trait analyses. In fact, the left external bony naris is wider than the right in *Tagicetus* (Lambert *et al.*, 2005; Figure 5B, C) and the right premaxilla is notably wider than the left in the basal area of the rostrum in *Hadrodelphis*, *Macrokentriodon*, and *Tagicetus*. Although Heyning (1989) stated that *Delphinodon*, *Lophocetus repenningi*, and *Liolithax pappus* have cranial asymmetry, it is difficult to detect slight degrees of asymmetry due to distortion of fossils. This type of cranial asymmetry is expressed in a wide variety (Muizon, 1988a; Kazár and Grigorescu, 2005; e.g. the relative lengths of the premaxillae, sizes of the nasals, and direction of the skewedness of the mesethmoid). For example, the cranial asymmetry of Pithanodelphininae includes the following features (Barnes, 1985b; Muizon, 1988a; Kazár and Grigorescu, 2005; Figure 5F–I): (1) greater development of the posterior lobe of the right maxilla (*Atocetus*,



Strict consensus tree of 8 most parsimonious trees.
Each most parsimonious tree is 1697 steps.

Figure 6. Evolution of the asymmetry of the vertex in Odontoceti.



Strict consensus tree of 8 most parsimonious trees.
Each most parsimonious tree is 1697 steps.

Figure 7. Evolution of the asymmetry of the premaxillae in Odontoceti.

Sarmatodelphis); (2) greater width of the right premaxilla and the maxilla at the level of the orbit (*Atocetus, Sarmatodelphis*) and the anterior extremity of the nares (*Sarmatodelphis*); (3) distal tip of the nasal process of the right premaxilla longer than that of the left premaxilla (*A. nasalis, Sarmatodelphis*); (4) right nasal higher than the left (*Atocetus, Pithanodelphis*); (5) narrow right external naris (*Sarmatodelphis*); (6) left-skewed internasal suture (*A. nasalis, Sarmatodelphis,* NMV-72); and (7) right-skewed sagittal crest formed by the maxillae (*A. nasalis, Sarmatodelphis*). Thus, we confirm that basal delphinoids display variety in their cranial asymmetry. Furthermore, our trait analyses indicate that the common ancestor of Delphinoidea lacked cranial asymmetry. Here, we are confronted with two questions: (1) what is the function of cranial asymmetry, and (2) if cranial asymmetry is functionally important, then why do many taxa lack or show weakened cranial asymmetry?

Role of cranial asymmetry in Odontoceti.—Recently, Fahlke *et al.* (2011) found very weak cranial asymmetry in protocetid and basilosaurid "archaeocetes" (rightward deviation of medial sutures from the midline of the skull, unlike in odontocetes). They concluded that (1) cranial asymmetry in these "archaeoceti" evolved for directional hearing in the water column; (2) Odontoceti evolved echolocation ability with modification of the nasal plug system and development of a leftward skewed and telescoping skull, after divergence from Mysticeti. Cranial asymmetry in Odontoceti was led by development of facial asymmetry for asymmetrical sound propagation enabling echolocation (Mead, 1975) and/or facial and cranial asymmetry evolved to avoid or minimize sound wave interference or cancellation due to two bilateral sound generators in echolocation (Heyning, 1989). Aroyan *et al.* (1992) and Aroyan (1996) demonstrated by means of simulations that in common dolphins, the skull around the right bony nares plays an important role as the sound reflector for forming a bioacoustic beam. Thus, cranial asymmetry is significant for echolocation in Odontoceti. However, weak cranial asymmetry or its absence does not necessarily indicate an absence of echolocation ability or of facial asymmetry. For example, *Pontoporia* and extant phocoenids show not only strong facial asymmetry but also are able to echolocate as in other extant odontocetes (e.g. Schenkkan, 1973; Mead, 1975; Huggenberger *et al.*, 2010), although cranial asymmetry is weak or absent in these taxa (e.g. Ness, 1967; Yurick and Gaskin, 1988; Figures 6, 7). All extinct odontocetes can be interpreted to possess echolocation ability on the basis of the premaxillary sac fossa, which indicates the presence of a developed nasal plug system (physeteroids are thought to have lost the premaxillary sac fossa). In addition, inner ear structures in a squalodontid fossil from the late Oligocene indicate that they already possessed high-frequency hearing for echolocation (Luo and Eastman, 1995). These facts suggest that extinct odontocetes (at least clade A, Figure 6) possessed echolocation ability. Furthermore, crania in several odontocetes developed cranial symmetry after to obtain sufficient facial asymmetry for echolocation ability.

Role of cranial symmetry in Odontoceti.—If the degree of cranial asymmetry plays an important role in echolocation, then morphological differences may reflect differences of acoustic reflective ability. Extant phocoenids and *Pontoporia* show similar soft anatomical features related to cranial symmetry (Cranford *et al.*, 1996), such as symmetrical dorsal bursae, which are fatty soft tissues associated with phonic lips and related echolocation clicks: on the other hand, in other extant odontocetes (except physeteroids) the dorsal bursae are asymmetrical. The extant delphinid *Cephalorhynchus* has a weakly asymmetrical skull with respect to the degree of leftward skewness (Ness, 1967), as well as symmetrical dorsal bursae (Cranford, 1992). However, its skull shows asymmetry with respect to the widths of the premaxillae around the external nares. Most of these small odontocetes, which are less than 2 m in body length, do not form large pods, and they share certain behavioral characteristics such as the production of narrow-band high-frequency clicks and rejection of whistling (Morisaka and Connor, 2007), unlike most other extant odontocetes (e.g. Au, 1993; von Fersen *et al.*, 2000; Melcón *et al.*, 2012). Narrow-band high-frequency clicks and the absence of whistling in these species have been thought to represent an adaptation to avoid acoustic detection by their predator, *Orcinus orca* (e.g. Anderson and Amundin, 1976; Madsen *et al.*, 2005; Morisaka and Connor, 2007), as *O. orca* cannot detect such high-frequency clicks. The extant physeteroid *Kogia breviceps* produces narrow-band high-frequency clicks and does not whistle, as in the taxa mentioned above. It has also been considered as an adaptation to avoid acoustic detection by *O. orca* (e.g. Madsen *et al.*, 2005; Morisaka and Connor, 2007). However, the skull in *K. breviceps* shows distinct asymmetry, unlike the skull of other narrow-band high-frequency clicking species. *Orcinus orca* and *Berardius bairdii* possess relatively weakly asymmetrical skulls, and neither possesses symmetrical dorsal bursae or narrow-band high-frequency clicks. Thus, even though some exceptions exist, cranial symmetry or weak asymmetry in extant odontocetes seems related to the presence of the symmetrical dorsal bursae and narrow-band high-frequency clicks, which are adaptations to avoid predation that evolved in four independent lineages. If these patterns can be extrapolated to fossil taxa, some basal delphinoids that had symmetrical crania might have produced narrow-band high-frequency clicks to avoid their predators, as is the case in some modern species. It is no wonder that several extinct delphinoids independently obtained cranial symmetry for producing narrow-band high-frequency clicks for this reason, as many predators such as squalodontids and killer sperm whales that might have been capable of passive listening were present in the Miocene oceans. The hypothesis reasonably explains the patterns observed in the fossil record that several basal delphinoids show cranial symmetry and others show cranial asymmetry like the present specimen. Consequently, we hypothesize that some extinct odontocetes possessing symmetrical crania produced narrow-band high-frequency clicks to avoid predators with sensitive passive listening capacities. This hypothesis could be tested by examining the differences of the zone of audibility between taxa with symmetrical skulls and their potential predators: i.e., estimating the zone of audibility from the inner ear structures by using micro CT scanning (e.g. Luo and Eastman, 1995; Luo and Marsh, 1996).

Conclusions

We described an asymmetrical basal delphinoid skull from the upper lower Miocene Yamato Formation of Hokkaido, northern Japan. The skull clearly shows cranial asymmetry; the nasal process of the left premaxilla is longer than that of the right premaxilla, the mesethmoid and frontals are left skewed 2.9°, and the right nasal is larger than the left. Evaluation of the deformation of the fossil based on the carbonate content of the matrix confirmed that the concretion that yielded the skull was formed in an early stage of diagenesis and that the present specimen was not affected by compaction during diagenesis. This new specimen supports the hypothesis that basal delphinoids with asymmetrical skulls are more common than previously thought. On the other hand, trait analyses suggest that the common ancestor of Delphinoidea had a symmetrical skull. The new specimen shows that cranial asymmetry of Delphinoidea extends back to the late early Miocene in the fossil record. We hypothesize that some extinct odontocetes with symmetrical crania produced narrow-band high-frequency clicks as in extant symmetrical cranial species, to avoid predators that possessed sensitive passive listening.

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Appendix 1. Character state scoring of a basal delphinoid NMV-72, for the matrix of Murakami *et al.* (2012b).

NMV-72
?????????? ?????????? ?????????? ?????????? ?????????? ?????0??10 ?????1001?
00??10?0?1 0??10??3?2 ??13??10?? ?????????? ????????1? 10???????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ????????1? ??

Appendix 2. Revised character status from Murakami *et al.* (2012b).

Character 55

Odobenocetops peruvianus: changed from ? to 1. *Archaeophocaena teshioensis*, *Australithax intermedia*, *Haborophocoena toyoshimai*, *Haborophocoena minutus*, *Lomacetus ginsburgi*, *Piscolithax longirostris*, *Piscolithax boreios*, *Piscolithax tedfordi*, *Salumiphocaena stocktoni*, *Septemtriocetus bosselaersi*: changed from 1 to 2. *Phocoena sinus*, *Phocoena spinipinnis*, *Phocoena dioptrica*, *Phocoena phocoena*, *Phocoenoides dalli*, *Neophocaena phocaenoides*, *Miophocaena nishinoi*: changed from 2 to 3.

Character 68

“*Stenella*” *kabatensis*: 0 to ?

Character 69

Delphinapterus leucas, *Monodon monoceros*, *Odobenocetops peruvianus*: changed from 1 to 2

Character 73

Odobenocetops peruvianus: changed from - to 0. *Lipotes vexillifer*, *Atocetus iquensis*: changed from 0 to 1. *Parapontoporia sternbergi*: changed from ? to 1. *Hemisyntrachelus cortesii*: changed from 1 to g = 1 or 2.

Character 94

Atocetus iquensis: changed from 2 to 3

Character 97

Kentriodon pernix: changed from 1 to 0. *Kogia breviceps*: changed from 0 to 1.

Character 121

Prosqualodon davidis, *Zarhachis flagellator*, *Squaloziphius emlongi*: changed from 1 to 0.

Character 123

Pliopontos littoralis: changed from 0 to 1.

Character 160

Neophocaena phocaenoides: changed from ? to 0.

Character 166

Hemisyntrachelus cortesii: changed from ? to 0.

Character 167

Hemisyntrachelus cortesii: changed from ? to 0.

Character 169

Hemisyntrachelus cortesii: changed from ? to 1.

Character 173

Hemisyntrachelus cortesii: changed from ? to 1.

Character 174

Salumiphocaena stocktoni: changed from ? to 0. *Hemisyntrachelus cortesii*: changed from ? to 1.

Character 176

Hemisyntrachelus cortesii: changed from 2 to g = (1 or 2).

Character 177

Hemisyntrachelus cortesii: changed from ? to 1.

Character 178

Salumiphocaena stocktoni, *Hemisyntrachelus cortesii*: changed from ? to 0.

Character 179

Salumiphocaena stocktoni, *Hemisyntrachelus cortesii*: changed from ? to 0.

Character 189

Salumiphocaena stocktoni: changed from ? to 0. *Hemisyntrachelus cortesii*: changed from ? to 1. *Lagenorhynchus acutus*, *Lagenodelphis hosei*, *Stenella attenuata*, *Steno bredanensis*, *Sotalia fluviatilis*: changed from 0 to 1.

Character 199

Hemisyntrachelus cortesii: changed from ? to 0.

Character 279

Lipotes vexillifer from - to 0.