A new skull of the fossil porpoise *Numataphocoena yamashitai* (Cetacea: Phocoenidae) from the upper part of the Horokaoshirarika Formation (lower Pliocene), Numata Town, Hokkaido, Japan, and its phylogenetic position

Yoshihiro Tanaka and Hiroto Ichishima

**ABSTRACT**

An early Pliocene porpoise, *Numataphocoena yamashitai* from Hokkaido, Japan, is known from the holotype, a fairly well-preserved skeleton with an incomplete skull and a referred earbone. A new skull referred to *Numataphocoena yamashitai* found from almost the same locality as the holotype is interesting because it expands knowledge of skull morphology and improves the diagnosis of this taxon. *Numataphocoena yamashitai* differs from other phocoenids in having the characteristic feature in the maxilla associated with the posterior dorsal infraorbital foramen, narrower and sharper anterior part of the internal acoustic meatus, and a robust anterior process of the peri-otic. A new cladistic analysis places *Numataphocoena yamashitai* adjacent to *Haborophocoena toyoshimai* and *Haborophocoena minutus*, among a clade of early branching phocoenids, all of which are chronologically and geographically close to each other. The new skull is probably a younger individual because it is about 80% the size of that of the holotype and it shows closed but unfused sutures. Our description of this specimen helps to understand the intraspecies variation of the extinct species *Numataphocoena yamashitai*.

Yoshihiro Tanaka. Numata Fossil Museum, 2-7-49, Minami 1, Numata Town, Hokkaido, 078-2225 Japan, yoshihiro.tanaka@otago.ac.nz and Hokkaido University Museum, Kita 10, Nishi 8, Kita-ku, Sapporo, Hokkaido 060-0810 Japan

Hiroto Ichishima. Fukui Prefectural Dinosaur Museum, Terao 51-11, Muroko, Katsuyama, Fukui 911-8601, Japan, hiroto.ichishima@dinosaur.pref.fukui.jp

Key words: skull; Phocoenidae; phylogeny; maxillary terrace; ontogeny; intraspecies variation

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INTRODUCTION

Since 2000, fossil phocoenid study has been progressed dramatically (Ichishima and Kimura, 2000, 2005, 2009, 2013; Fajardo-Mellor et al., 2006; Lambert, 2008; Murakami et al., 2012a, 2012b, 2015; Racicot et al., 2014; Colpaert et al., 2015). Fossil phocoenids have long been known only from the eastern and southern Pacific since the study of Salumiphocaena stocktoni (Barnes, 1985a) from the late Miocene of California by Wilson (1973), a series of Piscolithax spp reported from Peru and Mexico (de Muizon, 1983; Barnes, 1984a), and an isolated periotic described from the late Miocene of New Zealand (Fordyce, 1989). Recently, a phocoenid with a unique feeding apparatus was reported from California (Boessenecker, 2013; Racicot et al., 2014). Now, a few specimens have been known from the Atlantic (Lambert, 2008; Colpaert et al., 2015).


Numataphocaena yamashitai from the early Pliocene of Numata Town, Hokkaido, Japan (Ichishima and Kimura, 2000) is a fairly well-preserved specimen represented by the partial skull, ear bones and postcrania. But it was too premature to perform the phylogenetic analysis for the holotype of Numataphocaena yamashitai at the time of description because of the incompleteness of the skull, which hampered a direct comparison with most other fossil phocoenids represented by the skull but lacking postcrania. A new skull, along with a referred periotic collected from the same locality (Tanaka, 2016), of Numataphocaena yamashitai allows us to determine the phylogenetic placement of the species.

Abbreviation. NFL – Numata Fossil Museum, Hokkaido, Japan.

MATERIAL AND METHODS

Numata Fossil Museum specimen NFL 2074, a skull; the premaxillae, left posterior maxilla, left frontal, left lacrimojugal, left palatine and left parietal. The specimen was originally prepared by Mr. Shigeru Yamashita using formic acid. Additional preparation was done by the first author under microscope with a fine air chisel.

NFL 2074 was collected from the riverbed of the Horonitchibetsu River, early Pliocene, upper part of the Horokaoshirarika Formation, at 4th Ebishima district, Numata Town, Hokkaido, Japan by Dr. Rei Nakashima in 1995. The site is about 3 km northwest of the Ishikari-Numata Station of the Japan Railroad (Figure 1).

Geological setting. In Numata Town, Hokkaido, the Miocene-Pliocene sediments, the upper and lower parts of the Horokaoshirarika Formation are about 200 m and 500 m in thickness, respectively (Watanabe and Yoshida, 1995) (Figure 1). A thin tuff, so-called Ops, separates the Horokaoshirarika Formation into the upper and lower parts (Kobayashi et al., 1969). This tuff layer is dated as 4.5 ± 0.7 Ma, based on fission track method (Wada et al., 1986). In the lower stream of the Horonitachibetsu River, the Ichinosawa and Bibaushi Formations overlie the Horokaoshirarika Formation. The Horoshin Formation is exposed about 2 km upstream from this locality. NFL 2074 was collected from the upper part of the Horokaoshirarika Formation. The upper part of the Horokaoshirarika Formation yielded other marine vertebrate remains: the holotype (NFL 7) and an isolated periotic (NFL 2617) of Numataphocaena yamashitai, a tusk of Odobenini (NFL 12) and a pinniped skeleton (NFL 10) have been reported (Yamashita and Kimura, 1990; Kohno et al., 1995; Ichishima and Kimura, 2000; Tanaka, 2016). Lithology of the upper part of the Horokaoshirarika Formation is muddy to sandy sediments, with shell clusters and bioturbation (Nakashima and Majima, 2000).

Paleoenvironment of the upper part of the Horokaoshirarika Formation is inner shelf (Nakashima and Majima, 2000). As it is mentioned above, Wada et al. (1986) reported the tuff age as 4.5 ± 0.7 Ma based on the fission track dating. Based on diatom biostratigraphy, the age of the upper part of the Horokaoshirarika Formation is about 4.5 to 3.5 Ma, corresponding to the Thalassiosira oestrupii zone (Nakashima and Watanabe, 2000). The age of the upper part of the Horokaoshirarika Formation is about 4.5 to 3.5 Ma, the early Pliocene.

SYSTEMATIC PALEONTOLOGY

Order CETACEA Brisson, 1762
Unranked taxon NEOCETI Fordyce and de Muizon, 2001
Suborder ODONTOCETI Flower, 1867
Superfamily DELPHINOIDEA (Gray, 1821) Flower, 1867
Family PHOCOENIDAE Gray, 1825, sensu Burmeister, 1885
Emended diagnosis. *Numataphocoena yamashitai* differs from other phocoenids in having a raised area along an extended sulcus from the medial border of the posterior dorsal infraorbital foramen on the dorsal surface of the maxilla, the maxillary terrace (new term, see Discussion); narrower and sharper anterior part of the internal acoustic meatus; and a robust anterior process of the periotic.

*Numataphocoena yamashitai* differs from later branching phocoenids (such as *Lomacetus*, *Piscolithax* spp, extant species) in absence of the maxillary crest (Character 28), and wide premaxillae against the maxillae at the level of the postorbital process (Character 35).

Description

Morphological terminology for the skull follows Mead and Fordyce (2009).

Ontogenetic age. The skull sutures are mostly closed but distinct in NFL 2074. Compared with the holotype of *Numataphocoena yamashitai* (NFL 7), which is a physically and sexually matured individual (Ichishima and Kimura, 2000), NFL 2074 is around 20% smaller in size, based on the length of the maxilla (the distance between the anterior tip of the antorbital process of the maxilla to the posterior end of the ascending process. NFL 2074: 145 mm; NFL 7: 188 mm) (Table 1). Ichishima and Kimura (2013) reported the referred specimen of *Haborophocoena toyoshimai* as a young individual on the basis of the incompletely fused supra/exoccipital suture, which is around 16% smaller skull size than the physically matured holotype of *Haborophocoena toyoshimai*. NFL 2074 is, therefore, most likely younger than the holotype.

Premaxilla. The distance between the tip of the premaxilla as preserved and the base of the rostrum at the level of the antorbital notch is 106 mm. Each premaxilla is flat anterior to the level of the antorbital notch, and posteriorly it rises dorsally as the premaxillary eminence, which projects dorsolaterally with a weak depression on the dorsal face (the premaxillary sac fossa). In dorsal view, the posterior end of the premaxillae is widest (27.0 mm on the left) at the level of the nares. A rounded end of the nasal process stops at the level of the posterior margin of the bony nares. Ventrally, the anterior
part shows sutures with the lost maxilla laterally, and with the vomer medially.

**Maxilla.** The preserved cranial part of the left maxilla is dorsoventrally thin and rises gradually posterodorsally at the level of the bony nares. The base of the rostrum is wide and has a distinct antorbital notch. On the ventral face, the maxilla forms a part of the palate, which is flat anteriorly and has a weak palatal crest posteriorly. Two shallow palatine sulci run anteroposteriorly on the right maxilla. A rounded antorbital process projects anteriorly and forms a sharp and deep antorbital notch medially. Medial to the antorbital process, there is an anterior dorsal infraorbital foramen.

In dorsal view, the maxilla covers most of the frontal. The posteromedial surface of the maxilla is steep at the level of the bony nares. The posterior dorsal infraorbital foramen opens into a groove, which continues posterolaterally to an area, the maxillary terrace (new term, see Discussion), whose posterior margin reaches the lateral edge of the skull roofing over the temporal fossa. The maxillary intrusion (*sensu* Arnold and Heinsohn, 1996), a dorsal exposure of the maxilla medial to the premaxilla and anterior to the bony nares is uncertain. An incipient fossa for the inferior vestibule (Mead, 1975) is just posterior to the nasal process of the premaxilla and lateral to the bony nares. The fossa for the inferior vestibule is circular and much shallower than that of modern phocoenids, which have a small expansion medially.

**FIGURE 2.** The skull, NFL 2074, referred specimen of *Numataphocoena yamashitai* in dorsal view. 1, photo, 2, line art.
In ventral view, just posteromedial to the lacrimo-jugal is the antorbital fossa, which includes the ventral infraorbital foramen anteriorly and the spheno-palatine foramen posteriorly.  

**Palatine.** Ventrally, the left palatine shows a smooth anterior wall of the pterygoid sinus fossa, which is a dorsoventrally long elliptical fossa.  

**Pterygoid.** The left anterior fragment of the pterygoid might be on the skull, just posterior to the palatine, but the suture is not clear.  

**Ethmoid.** The ethmoid is used in the sense of Mead and Fordyce (2009), but note that Ichishima (2011) suggested that the mesethmoid is probably absent in Odontoceti. The structure of the preserved left ethmoid is unclear in the specimen because of erosion and damage. A thin imperforated cribriform plate forms the posterior wall of the nasal passage. The cribriform plate rises to the fossa for nasals on the frontal. The dorsal end shows a partially damaged osseous nasal septum.  

**Vomer.** An anterior broken section of the vomer can be seen in the mesorostral groove, which is V-shaped in anterior view. The most posterior part of the vomer has been worn away.  

**Sphenoid.** Posteromedial to the orbital rim, there is a shallow and mediolaterally long groove, which might be the frontal groove of the sphenoid. In general, the frontal groove runs from a combined large foramen of the orbital fissure and optic canal, but the medial part of the frontal groove is broken away on NFL 2074.  

**Frontal.** The frontal contributes to the ventral surface of the orbit and the frontal boss at the vertex. The frontal boss is smooth and was originally

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**FIGURE 3.** The skull, NFL 2074, referred specimen of *Numataphocoena yamashitai* in ventral view. 1, photo, 2, line art.
bounded by the nasals and maxillae. The frontal forms the anterodorsal wall of the braincase and ventrally exposes around a half of the shallow and long orbit. Posterior to the frontal groove, there is a shallow fossa for the postorbital lobe of the pterygoid sinus, just anterior to the temporal fossa. The nasals are not preserved, and their articular surfaces on the frontal are shallow. The fossa for the nasal is anteroposteriorly longer than wide (around 2.0 cm long, 1.5 cm wide). The posteromedial corner of the nasal might be positioned more anterior than the posterolateral corner.

**Lacrimojugal.** The lacrimojugal is squared in ventral view and thin in lateral view. Its ventral surface

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**FIGURE 4.** The skull, NFL 2074, referred specimen of *Numataphocoena yamashitai* in lateral view. 1, photo, 2, line art.

**FIGURE 5.** The skull, NFL 2074, referred specimen of *Numataphocoena yamashitai* in anterior view. 1, photo, 2, line art.
is eroded. Anteromedially, there is a broken base of the lacrimojugal (8 mm diameter). The anterior border of the lacrimojugal forms the most anterior part of the antorbital process. The tubular posteromedial process is located posterolaterally. The medial process locates medial and just a bit anterior to the posteromedial process, and is covered by the maxilla medially.

Parietal. The preserved parietal is exposed as an anteroposteriorly narrow band dorsally, just posterior to the frontal. The parietal forms the dorsal part of the temporal fossa. The parietal/frontal suture is unclear at the posterolateral part of the skull. The nuchal crest of NFL 2074 is formed by the parietal dorsolaterally and might be formed by the frontal medially. The supraoccipital is lost in NFL 2074, which might also form the nuchal crest.

### TABLE 1

Measurements in mm of NFL 2074, referred specimen of *Numataphocoena yamashitai*: skull. Dimensions follow Fordyce et al. (2002). Measurements are rounded to the nearest 0.5 mm. For skull and mandible, distances are either horizontal or vertical. * shows a measurement, which is only of the left side (the measurement points to the median line).

<table>
<thead>
<tr>
<th></th>
<th>NFL 2074</th>
<th>NFL 7</th>
</tr>
</thead>
<tbody>
<tr>
<td>total length, from the most anterior point to posterior of occipital condyles</td>
<td>260.0+</td>
<td>199.0+</td>
</tr>
<tr>
<td>length of rostrum</td>
<td>111.5+</td>
<td>-</td>
</tr>
<tr>
<td>width of rostrum at the base</td>
<td>43.5*</td>
<td>-</td>
</tr>
<tr>
<td>cranial length</td>
<td>142.5+</td>
<td>199.0+</td>
</tr>
<tr>
<td>width of premaxillae at a line across posterior limits of antorbital notches</td>
<td>44.0*</td>
<td>-</td>
</tr>
<tr>
<td>maximum width of premaxillae about the level with mid-orbit</td>
<td>25.0*</td>
<td>56.0+</td>
</tr>
<tr>
<td>postorbital width, across apices of postorbital processes</td>
<td>85.5*</td>
<td>-</td>
</tr>
<tr>
<td>maximum width across narial aperture</td>
<td>19.5*</td>
<td>-</td>
</tr>
</tbody>
</table>
RESULTS

Phylogenetic Analysis

The phylogenetic position of Numataphocoena yamashitai is analyzed using a new data matrix, which is modified from Tanaka and Fordyce (2015), for understanding relationships of the Phocoenidae (see Appendices 1, 2, 3, 4, 5). In the matrix, three specimens of Numataphocoena yamashitai (NFL 7, the holotype; NFL 2074, the skull of our study; and NFL 2617, a periotic) are combined. There are no contradictory codings among these specimens. Semirostrum ceruttii (Racicot et al., 2014) and Borabocetus gigaseorum (Colpaert et al., 2015) are added in the matrix. Some changes of character coding and deletions of characters from the original matrix are listed in Appendix 4.


Character data and tree data were managed using Mesquite 2.75 (Maddison and Maddison, 2011). An analysis was performed with TNT 1.1 (Goloboff et al., 2008). All characters were treated as unweighted and unordered. The analysis used New Technology Search with the setting: recover minimum length trees = 1000 times.

The unweighted and unordered phylogenetic analysis shows 20 shortest trees of 238 steps. A tree file is provided as Appendix 5. The 50% majority rule consensus tree (Figure 7) shows similar topology as for the result of the analysis 2 in Tanaka and Fordyce (2015) such that Pterophocaena nishinoi is placed as the earliest diverging phocoenid, all phocoenids from Hokkaido, Japan are placed as a clade, Lomacetus and Australithax are monophyletic, and extant species are monophyletic. Differences from Tanaka and Fordyce (2015) included Archaeophocaena and Miophocaena monophyly (sister taxon relationship), hav-
ing an unresolved polytomy of Septemtoriocetus + Brabocetus + Semirostrum + Piscolithax longirostris + Piscolithax tedfordi + (Lomacetus + Australithax) + an extant clade, but having resolved extant clades.

The result of the phylogenetic analysis in our study is compared with previous studies (e.g., Fajardo-Mellor et al., 2006; Lambert, 2008; Murakami et al., 2012a, 2012b, 2014, 2015; Racicot et al., 2014; Colpaert et al., 2015). The topology is similar in pattern with those of Murakami et al., 2012a, 2012b, 2014, 2015; Racicot et al., 2006; Lambert, 2008; Colpaert et al. (2015) reconstructed Pterophocaena nishinoi as basal to all phocoenids as similar to this study, but among an unresolved polytomy with Delphinodon dividum and Kentriodon pernix. Both in our study and the Murakami studies, just crownward from Pterophocaena nishinoi, a clade of Archaeophocaena teshioensis and Miophocaena nishinoi are recovered. Colpaert et al. (2015) placed A. teshioensis and Miophocaena nishinoi with Semirostrum ceruttii as an unresolved polytomy. This study shows an unresolved polytomy, which includes Salumiphocaena + P. tedfordi + P. longirostris + (Septemtoriocetus + Brabocetus + Semirostrum) + an extant clade. Salumiphocaena stocktoni was reported from the early late Miocene (12.6 to 9.0 Ma) Valmonte Diatomite Member in California (Wilson, 1973; Barnes, 1985a), which is possibly the oldest known record of the Phocoenidae (Uhen et al., 2008). Semirostrum ceruttii is placed as one of the most crownward extant species in our study and also Racicot et al. (2014). Just basal from the extant clade, our study has a clade of Septemtoriocetus + Brabocetus + Semirostrum. In Colpaert et al. (2015), Brabocetus was placed just basal to the Septemtoriocetus. The three species of Piscolithax do not form a clade in this study and the previous studies, except Fajardo-Mellor et al. (2006).

**DISCUSSION**

**Comparison Between the Skulls of Numataphocoena yamashitai Holotype and NFL 2074**

Numataphocoena yamashitai can be diagnosed by having the maxillary terrace (new term). The maxillary terrace is a raised area along a sulcus from the medial border of the posterior dorsal infraorbital foramen. Modern phocoenids also have the raised area and sulci from the posterior dorsal infraorbital foramen, but they are much shorter sulci and weaker raised area than in Numataphocoena yamashitai.

The maxillary terrace is a natural structure, not a taphonomic artifact because the internal wall of the braincase does not show any deformations (holotype; NFL 7 and referred specimen; NFL 2074).

Comparison of the maxillary terrace in the holotype NFL 7 and the referred skull NFL 2074 reveals that the relationships of the maxillary terrace and the dorsal infraorbital foramen are different (Figure 8). On NFL 2074, the maxillary terrace is restricted by a sulcus extending from the medial border of the posterior dorsal infraorbital foramen, and its length is about 46 mm. On the other hand, the holotype NFL 7 shows an extra-extended sulcus, which continues anterior to the posterior dorsal infraorbital foramen. The anterior part of the maxillary terrace is broken in NFL 7, and the length of the sulcus is 55+ mm. The anterior part of the sulcus is seen only on the holotype. Additional skulls are required to consider the maxillary terrace variation.

In addition to the maxillary terrace, some morphological differences exist between NFL 7 and NFL 2074. The nuchal crest is different in the degree of development. In NFL 7 the nuchal crest is well-developed and rises dorsally, and its anterior margin is weakly bowed down anteriorly, continuing to the lateral margin of the frontal boss. On the other hand, NFL 2074 has an incipient crest on the preserved lateral part of the frontal. These differences may be due to ontogenetic variation as NFL 2074 is discussed as younger individual based on the skull size and fusions of the skull sutures. However, in an ontogenetic study of Stenella coeruleoalba, Ito and Miyazaki (1990) reported sexual dimorphism of the skull. Females over three years of age have a developed nuchal crest, compared to males, in which the nuchal crest is not developed at any growth stage. Thus, if Numataphocoena yamashitai had sexual variation on the nuchal crest like Stenella coeruleoalba, and if NFL 2074 was a different sex to NFL 7, NFL 2074 might not have developed a conspicuous nuchal crest even at attainment of physical maturity.

**A Clade of Fossil Phocoenids from Hokkaido**

The phylogenetic results show a clade of fossil phocoenids, which includes Archaeophocaena,
Miophocaena, and Haborophocoena spp. and Numataphocoena from the late Miocene to early Pliocene of Hokkaido, Japan. As an exception, Pterophocaena nishinoi, one of the phocoenids from Hokkaido is not included in the clade of fossil phocoenids from Hokkaido, and is reconstructed as just crown to the outgroup Kentriodon in our analysis. The clade of Hokkaido phocoenids has never been discussed before although the clade appeared in the appendix in an implied analysis (down weighting homoplastic characters) of Tanaka and Fordyce (2015), which is the original matrix of this study. A similar clade is seen in the results of Colpaert et al. (2015), which included four Hokkaido phocoenids (Haborophocoena spp., Miophocaena and Archaeophocaena).

The clade of Hokkaido phocoenids in this study is supported by three synapomorphies; the premaxillary foramen medial to the center of the premaxilla (Character 22), wide premaxillae compared to the rostrum at antorbital notch (Character 34), and the anterior-most dorsal infraorbital foramen lies posterior to the level of the antorbital notch (Character 114). A fossil phocoenid from Hokkaido, Pterophocaena nishinoi has the premaxillary foramen at the midpoint of the premaxilla (Character 22), and the anterior-most dorsal infraorbital foramen is located anterior to the antorbital notch (Character 114). Having a low premaxillary eminence is one of the diagnostic features of the clade of Hokkaido phocoenids. Pterophocaena does not have the premaxillary eminence. The low premaxillary eminence is also seen in the Atlantic species, Brabocetus and Septemtriocetus.

Our analysis recognizes two subclades, rather than having a pectinate topology of the stem taxa in which the clade of Hokkaido phocoenids (Numataphocoena and Haborophocoena) and another clade (Lomacetus, Piscolothax, Semirostrum and other species + extant species). The clade of Hokkaido phocoenids is branching immediately with a clade of the extant + Eastern Pacific + Atlantic clades. It means that the Phocoenidae was separated into Eastern and Western Pacific clades in the Late Miocene to Early Pliocene, early in the history of phocoenids (Figure 9).

Phocoenids from Hokkaido phocoenids includes two subclades, the Archaeophocaena + Miophocaena clade and the Haborophocoena toyoshimai + (Numataphocoena yamashitai + Haborophocoena minutus) clade.

FIGURE 8. The maxillary terrace from the posterior dorsal infraorbital foramen on the maxilla. 1 and 2, NFL 7, the type of Numataphocoena yamashitai. 3 and 4, NFL 2074, the referred specimen.
The branching pattern of fossil phocoenids from Hokkaido in previous works required the unnecessarily long ghost lineages in each branch (Murakami et al., 2012a, 2012b, 2014). Now, the phocoenids from Hokkaido as a clade makes the branching hypothesis of phocoenids highly valid based on parsimonious recognition because of minimizing a geological range of ghost lineages of each branch (Figure 9). Although the phocoenids from Hokkaido are geologically younger in age, early Pliocene, than those from the Northeastern Pacific and the Atlantic such as the early late Miocene Lomacetus, Australithax and Salumiphoencaena, and Piscolithax spp. from the latest Miocene, the former species have been recognized as being earlier diverging. The new branching pattern in this study shows that the common ancestor of the two subgroups appeared before the early late Miocene, based on the topology and the oldest known records of each subgroup. Moreover, our analyses revealed that the fossil phocoenids from Hokkaido was unrelated to the extant clade.

This study uses larger numbers of taxa and characters than Colpaert et al. (2015). The results of Colpaert et al. (2015) and our study show a similar pattern in terms of recognizing two subclades, rather than having a pectinate topology. In the Colpaert et al. (2015), the fossil phocoenids from Hokkaido were in a clade with Semirostrum. But, in our result, Semirostrum is placed among the unresolved polytomy, which is outside of the clade of fossil phocoenids from Hokkaido.

**Phylogenetic Relationships and Morphologies of Numataphocoena yamashitai and Haborophocoena spp**

Numataphocoena yamashitai and Haborophocoena minutus are located in the clade of phocoenids from Hokkaido, which is supported by two synapomorphies, that is, the relatively large exposure of the lacrimojugal in ventral view (between
2015). Colpaert et al. (2015) found two species of *Haborophocoena* among the early branching phocoenids, all of which are chronologically and geographically close to each other, being all from Hokkaido. The new referred skull (NFL 2074) of *Numataphocoena yamashitai* from the upper part of the Horokao-shirarika Formation (early Pliocene), Numata, Hokkaido, Japan, adds diagnostic characters of the species, recognizes variations among the species and reveals the phylogenetic position among the Phocoenidae. Our cladistic analysis places *Numataphocoena yamashitai* adjacent to *Haborophocoena toyoshimai* and *Haborophocoena minutus*, among a clade of early branching phocoenids, all of which are chronologically and geographically close to each other, being all from Hokkaido. *Numataphocoena yamashitai* differs from other phocoenids in having a maxillary ter-

2012a, 2012b, 2014, 2015; Tanaka and Fordyce, the extant phocoenids (Murakami et al., 2015) is sister to the clade containing *Numataphocoena yamashitai* + *Haborophocoena minutus*. The three species is supported by one synapomorphy: flat (not bent) posterior process of the periotic in lateral view (Character 84).

The genus *Haborophocoena* is paraphyletic in the result of this study and also previous studies, which included the two species of *Haborophocoena*. Some studies found *Haborophocoena minutus* into a clade with later branching phocoenids and the extant phocoenids (Murakami et al., 2012a, 2012b, 2014, 2015; Tanaka and Fordyce, 2015). Colpaert et al. (2015) found *Haborophocoena minutus* in a clade with *Archaeophocoena* + *Miophocaena* + *Semiurostrum* clade.

The character state shared only between the two species of *Haborophocoena* but not with *Numataphocoena* is having narrow mandibular fossae of the squamosals (Character 112). *Numataphocoena yamashitai* shows a wider mandibular fossa of the squamosal, which receives the mandibular condyle. This character is changed in the two lineages independently in this analysis, and might be related with mandibular movement and/or feeding styles. The preserved posterior left mandible of *Haborophocoena toyoshimai* shows a wider and more tilted clockwise mandibular condyle, compared to *Phocoena phocoena*, which has a narrower mandibular condyle. *Numataphocoena yamashitai* does not preserve the mandibular condyle. In short, these mandibular variations among the three species suggest that they might have different feeding ecology.

**CONCLUSION**

The new referred skull (NFL 2074) of *Numataphocoena yamashitai* from the upper part of the Horokao-shirarika Formation (early Pliocene), Numata, Hokkaido, Japan, adds diagnostic characters of the species, recognizes variations among the species and reveals the phylogenetic position among the Phocoenidae. Our cladistic analysis places *Numataphocoena yamashitai* adjacent to *Haborophocoena toyoshimai* and *Haborophocoena minutus*, among a clade of early branching phocoenids, all of which are chronologically and geographically close to each other, being all from Hokkaido. *Numataphocoena yamashitai* differs from other phocoenids in having a maxillary ter-

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APPENDIX 1.

Cladistic matrix of Tanaka and Ichishima (2016) in nexus format.
Available in zipped format with Appendix 2 and Appendix 5 online at palaeo-electronica.org/content/2016/1663-a-new-skull-of-numataphocoena

APPENDIX 2.

Cladistic matrix of Tanaka and Ichishima (2016) in TNT format.
Available in zipped format with Appendix 1 and Appendix 5 online at palaeo-electronica.org/content/2016/1663-a-new-skull-of-numataphocoena
APPENDIX 3.

Morphological characters used in the phylogenetic analysis.
Terminology generally follows that of the cladistic papers cited, which in a few cases does not agree with the recommended uses of Mead and Fordyce (2009). For each character, references are given for the main past uses, with the relevant published character number given with a hatch # thus:

Murakami et al. (2012a) #1.

Rostrum, Dental, and Mandibular

1) Length of rostrum as percent skull length: moderately long, 50–55% (0); long, 55–60% (1); very long, >60% (2); medium, 50–40% (3); very short, 40–35% (4). (Murakami et al. (2012a, 2012b) #1; modified from Arnold and Heinsohn (1996) #8; Bianucci (2005) #1; Lambert (2008) #1; Tanaka and Fordyce (2014, 2015) #1).

2) Premaxillae transverse proportion: transversely inflated almost entire length of rostrum (0); flat almost entire length of the rostrum (1). (Murakami et al. (2012a, 2012b) #2; Tanaka and Fordyce (2014, 2015) #2).

3) Premaxillae mediolateral proportion: not compressed mediolaterally (0); compressed mediolaterally at anterior of rostrum (1). (Murakami et al. (2012a, 2012b) #3; Tanaka and Fordyce (2014, 2015) #3).

4) Premaxillae at apex of rostrum: with lateral margins parallel or diverging (0); narrowing (1). (Murakami et al. (2012a, 2012b) #4; modified from Bianucci (2005) #2; Tanaka and Fordyce (2014, 2015) #4).

5) Mesorostral groove constricted posteriorly, anterior to the nares and behind the level of the antorbital notch, then rapidly diverging anteriorly: absent (0); present (1). (modified from Murakami et al. (2012b) #279; Tanaka and Fordyce (2014, 2015) #7).

6) Lateral margin of rostrum anterior to maxillary flange: concave (0); straight (1); convex (2); absent (3) (Murakami et al. (2012a, 2012b) #7; modified from Bianucci (2005) #3; Tanaka and Fordyce (2014, 2015) #8).

7) Antorbital notch: absent or weakly developed (0); well developed (1). (Messenger and McGuire (1998) #1426; Fajardo-Mellor et al. (2006) #6; Murakami et al. (2012a, 2012b) #9; Tanaka and Fordyce (2014, 2015) #10).

8) Width of premaxillae at mid-rostrum as percent greatest width of maxillae at level of postorbital processes: wide, >25% (0); medium, 25–15% (1); narrow, <15% (2). (Murakami et al. (2012a, 2012b) #10; modified from Aguirre-Fernandez et al. (2009) #4; Tanaka and Fordyce (2014, 2015) #11)

9) Width of rostrum at mid-length as percent greatest width of maxillae at level of postorbital processes: wide, >35% (0); medium, 35–30% (1); narrow, <30% (2). (Murakami et al. (2012a, 2012b) #11; modified from Aguirre-Fernandez et al. (2009) #6; Tanaka and Fordyce (2014, 2015) #12).


Teeth


12) Upper anterior "teeth": about same size as upper posterior teeth (0); clearly smaller than upper posterior teeth or absent (1). (Murakami et al. (2012a, 2012b) #22; modified from Tanaka and Fordyce (2014, 2015) #22).

Orbit

14) Antorbital process shape in dorsal view: squared (0); rounded (1); tapered (2), reduced (3). (Bianucci (2005) #4; Murakami et al. (2012a, 2012b) #34; modified from Tanaka and Fordyce (2014, 2015) #34).

15) Combined anteroposterior length of the lacrimal and jugal exposure that is posterior to antorbital notch: with skull in ventral view, exposure is small and combined length forms <5% of that distance (0); medium, 5–3% (1); small, <3% (1) (Murakami et al. (2012a, 2012b) #25; Aguirre-Fernandez et al. (2009) #15; modified from Tanaka and Fordyce (2014, 2015) #25).
(16) Dorsolateral edge of internal opening of infraorbital foramen: formed by maxilla (0); formed by maxilla and lacrimal and/or jugal (l); formed by lacrimal and/or jugal (2); formed by frontal (3). (Geisler and Sanders (2003) #57; Geisler et al. (2011) (2012) #57; Murakami et al. (2012a, 2012b) #43; derived from Miller (1923); Tanaka and Fordyce (2014, 2015) #43).

(17) Ventromedial edge of internal opening of infraorbital foramen: formed by maxilla (0); formed by maxilla and palatine and/or pterygoid (1); formed by pala-
tine and/or pterygoid (2). (Geisler and Sanders (2003) #58; Geisler et al. (2012, 2011) #58; Murakami et al. (2012a, 2012b) #44; derived from Miller (1923); Tanaka and Fordyce (2014, 2015) #44).

(18) Direction of apex of postorbital process of frontal: projected postero-
laterally and slightly ventrally (0); directed ventrally (1); not clear because

(19) Shape of postorbital process of frontal: triangular, trapezoidal, or an an-
teroposteriorly widened falci-
form (0); dorsoventrally long falci-
form (1); robust, blunt descending posteriorly (2). (modified from

Facial Region

(20) Anterior dorsal infraorbital foramina: two (0); three or
more (1). (Murakami et al. (2012a, 2012b) #49; modified from Barnes (1984b); Geisler and Sanders (2003) #64; Geisler et al. (2011) #64 (2012) #64; Tanaka and Fordyce (2014, 2015) #64).

(21) Width of premaxillae at antorbital notches as per-
cent width of rostrum at antorbital notch: narrow, <49% (0); moderate, 50–64% (1); wide, >65% (2); antorbital notch absent (3). (Geisler and Sanders (2003) #66; Geisler et al. (2011)#66 (2012) #66; modified from Murakami et al. (2012a, 2012b) #51; Tanaka and Fordyce (2014, 2015) #51).

(22) Premaxillary foramen locating: medial (0); midpoint
to lateral (1) absent (2). (modified from Murakami et al. (Murakami et al., 2014); Murakami et al. (2012b) #280; Tanaka and Fordyce (2014, 2015) #55).

(23) Lateral margin of the right premaxilla posterior to
premaxillary foramen: wider posteriorly (0); straight (1). (Murakami et al. (2012b) #281; Tanaka and Fordyce (2014, 2015) #56).

(24) Postero-lateral sulcus: deep (0); shallow or absent

(25) Posterior projections of premaxillae: both premaxill-
lae extending posterior to anterior tip of nasals (0); neither premaxillae extending beyond external nares, and premaxillae displaced laterally by
medial projection of maxilla (1); neither premaxillae extending posterior to external nares, and narrow posterior end of premaxillae adjacent to external nares (2); only right maxilla extending beyond or in line with anterior-most portion of nasals (3). (Murakami et al. (2012a, 2012b) #76; modified from

(26) Maxilla on dorsal surface of skull: does not contact supraoccipital posteriorly, maxilla separated by

(27) Anterolateral corner of maxilla overlying supraorbital
process of frontal: thin and equal in thickness to
tails postero-medial (0); thickened with thinner

(28) Maxillary crest on supraorbital process of maxilla:
longitudinal ridges absent except at lateral edge of
anterorbit al process (0); presence of longitudinal ridge except at lateral edge of antorbital process (1); longitudinal ridge present and joined with
maxillary flange (2); presence of transversely compr

(29) Fossa for inferior vestibule on maxilla lateral to
external nares or lateral to premaxilla: absent (0);

(30) Maxillary intrusion, anterior to external nares and
encroaching the postero-medial or medial face of
each premaxilla: absent (0); maxilla visible within opened mesorostral canal as small exposure medi
ally (1); exposure of maxilla reaches dorsally to level of premaxilla and forms a square, rectangular
to triangular plate (2); exposure of maxilla reaches
dorsally and forms a small subcircular to polygonal
ossicle (3). (Muizon (1984) (1988); Arnold and
(31) Premaxillary crest or posterior maxillary crest adjacent to nasal: absent (0); present (1). (transverse premaxillary crest, sensu Lambert (2005) #6; Murakami et al. (2012a, 2012b) #70; Tanaka and Fordyce (2014, 2015) #72).

(32) Premaxilla: not overhanging itself or maxilla laterally (0); overhanging itself or maxilla laterally, from anterior to midpoint of external nares (1). (Murakami et al. (2012a, 2012b) #71; Tanaka and Fordyce (2014, 2015) #73).

(33) Premaxillary sac fossa: smooth (0); rugose (1). (Messenger and McGuire (1998) #1551; Murakami et al. (2012a, 2012b) #72; Tanaka and Fordyce (2014, 2015) #74).

(34) Ratio of width of right premaxilla to width of left premaxilla in line with midpoint of external nares: 0.90–1.19 (0); 1.20–1.50 (1); 1.50> (2). (Murakami et al. (2012a, 2012b) #73; Tanaka and Fordyce (2014, 2015) #75).

(35) Ratio of greatest width of premaxillae to greatest width of maxillae at level of postorbital processes: ≥0.50 (0); 0.49–0.38 (1); <0.38 (2). (Murakami et al. (2012a, 2012b) #74; Tanaka and Fordyce (2014, 2015) #76).

(36) Premaxillary eminence: absent (0); present but low (1); present and high (2). (Lambert (2008) #4; Murakami et al. (2012a, 2012b) #75; modified from Muizon (1984); Barnes (1985a); Heyning (1989) #36 (1997) #68; Arnold and Heinsohn (1996) #12; Messenger and McGuire (1998) #1410; Geisler and Sanders (2003) #68; Fajardo-Mellor et al. (2006) #2; Geisler et al. (2011) #68 (2012) #69; derived from Flower (1967); Noble and Fraser (1971); Tanaka and Fordyce (2014, 2015) #77).

(37) Mesethmoid: not expanded posterodorsally (0); extended posterodorsally but narrow (1); expanded posterodorsally and visible in lateral view (2). (Murakami et al. (2012a, 2012b) #81; modified from Muizon (1984, 1988); Messenger and McGuire (1998) #1454; Bianucci (2005) #9; Tanaka and Fordyce (2014, 2015) #82).

Vertex and Area Adjacent to the Nares

(38) Nasals: lower than frontals (0); nearly same height as frontals (1); clearly higher than frontals (2). (Muizon (1988); Messenger and McGuire (1998) #1434; Geisler and Sanders (2003); #124; Geisler et al. (2011) #124 (2012) #124; Murakami et al. (2012a) #86; Tanaka and Fordyce (2014, 2015) #87).


(40) Both nasals: straight anterior edges in one transverse plane (0); with point on midline and gap on each side between premaxilla and nasal (1); concave posteriorly on midline and gap on each side between premaxilla and nasal (2); concave posteriorly on midline (3). (Murakami et al. (2012a, 2012b) #88; modified from Geisler and Sanders (2003) #116; Geisler et al. (2011) #116 (2012) #116; derived from Moore (1968); Tanaka and Fordyce (2014, 2015) #89).

(41) Lateral edges of nasals: not overhanging or covering maxillae or premaxillae (0); overhanging or partly covering maxillae or premaxillae (1). (Murakami et al. (2012a, 2012b) #92; Tanaka and Fordyce (2014, 2015) #93).

(42) Nasal-frontal suture: anterior wedge (nasial process) between frontal posterior ends of nasals (0); W or reversed U suture line (1). (Murakami et al. (2012a, 2012b) #93; modified from Muizon (1988); Geisler and Sanders (2003) #121; Geisler et al. (2011) #121 (2012) #121; Tanaka and Fordyce (2014, 2015) #94).

(43) Frontals posterior to nasals and between premaxillae: narrower than transverse width of nasals, maxillae expanded medially posterior to nasals (0); same as transverse width of nasals (1); wider than maximum transverse width across nasals (2). (Geisler and Sanders (2003) #125; Geisler et al. (2011) #125 (2012) #125; Murakami et al. (2012a, 2012b) #94; modified from Messenger and McGuire (1998) #1457; Tanaka and Fordyce (2014, 2015) #95).


(45) Nuchal crest: below frontals and/or nasals (0); at same level as frontals and/or nasals (1). (Murakami et al. (2012a, 2012b) #99; modified from Geisler and Sanders (2003) #128; derived from Moore (1968); Tanaka and Fordyce (2014, 2015) #100).

Temporal Fossae, Zygomatic Arch, and Occipitals

(46) Temporal fossa shape in lateral view: height lower than anteroposterior length (0); higher (1); lower and its posterior end is rounded (2). (Tanaka and Fordyce (2014, 2015) #281).


(48) Parietals in dorsal view: completely absent in skull roof (0); visible only as triangular areas, dorsolateral to supraoccipital, with non-overlapping supraoccipital separated from and contacting parietals...

(49) Interparietal: present (0); absent or fused and therefore not distinguishable from parietals and frontals (1). (Geisler and Sanders (2003) #135; Geisler et al. (2011) #135 (2012) #135; Murakami et al. (2012a) #105; Tanaka and Fordyce (2014, 2015) #106).

(50) Anterior zygomatic process end of squamosal in lateral view: tapered (0); squared (1). (Tanaka and Fordyce (2014, 2015) #110).

(51) Zygomatic process of squamosal: directed anterolaterally (0); directed anteriorly (1). (Sanders and Barnes, 2002; Geisler and Sanders (2003) #142; Geisler et al. (2011) #142 (2012) #142; Murakami et al. (2012a, 2012b) #108; Tanaka and Fordyce (2014, 2015) #109).

(52) Zygomatic process of squamosal in lateral view: part of dorsal face visible (0); entire dorsal surface of squamosal visible (1). (Murakami et al. (2012a, 2012b) #109; Tanaka and Fordyce (2014, 2015) #110).

(53) Emargination of posterior edge of zygomatic process by neck muscle fossa, skull in lateral view: deep emargination (0); shallow emargination (1). (Geisler and Sanders (2003) #144; Geisler et al. (2011) #144 (2012) #144; Murakami et al. (2012a, 2012b) #110; Tanaka and Fordyce (2014, 2015) #111).

(54) Ventral edge of zygomatic process of squamosal in lateral view: concave (0); almost straight (1); convex (2). (Geisler and Sanders (2003) #150; Geisler et al. (2011) #150 (2012) #150; Murakami et al. (2012a, 2012b) #112).

(55) Postglenoid process of squamosal: not reduced (0); greatly reduced (1). (Murakami et al. (2012a, 2012b) #113; Tanaka and Fordyce (2014, 2015) #114).

(56) Postglenoid process in lateral view: tapering ventrally (0); squared off ventrally (1); same as state 1 except very wide anteroposterior diameter of process (2). (Geisler and Sanders (2003) #151; Lambert (2005) #24; Geisler et al. (2011) #151 (2012) #151; Murakami et al. (2012a, 2012b) #114; derived from Muizon (1991); Tanaka and Fordyce (2014, 2015) #115).

(57) Relative ventral projections of postglenoid and post-tympanic processes of squamosal: postglenoid process more ventral or at same level as post-tympanic process (0); apex of postglenoid process dorsally higher than post-tympanic process (1). (Lambert (2005) #25; Murakami et al. (2012a, 2012b) #115; Tanaka and Fordyce (2014, 2015) #116).

(58) Dorsal condyloid fossa: present, situated anterodorsal to dorsal edge of condyle (0); present and forming deep pit (1). (Geisler and Sanders (2003) #156; Geisler et al. (2011) #156 (2012) #156; Murakami et al. (2012a, 2012b) #118; derived from Sanders and Barnes (2002); Tanaka and Fordyce (2014, 2015) #119).

## Anterior Basicranium

(59) Lateral lamina of palatine relationship with orbit: does not form bony bridge “over” (= ventral to) orbit (0); does form bony bridge “over” (= ventral to) orbit (1). (Muizon (1984); Messenger and McGuire (1998) #1444; Murakami et al. (2012a, 2012b) #123; Tanaka and Fordyce (2014, 2015) #124).

(60) Pterygoids in anteroventral view: separated from each other by posteroventrally elongated palatines and/or vomer (0); contacting entire length of hamular process (1); contacting each other partially (2). (Murakami et al. (2012a, 2012b) #124; modified from Arnold and Heinsohn (1996) #5; Messenger and McGuire (1998) #1445; Fajardo-Mellor et al. (2006) #9; derived from Flower (1884); Barnes (1985a); Marsh et al. (1989); Tanaka and Fordyce (2014, 2015) #125).

(61) Lateral lamina of pterygoid: present and articulated with alisphenoid (0); partial, restricted to region lateral to hamular process (1). (Murakami et al. (2012a) #126; modified from Arnold and Heinsohn (1996) #121; Messenger and McGuire (1998) #1446; Geisler and Sanders (2003) #164; Lambert (2005) #32; Geisler et al. (2011) #164 (2012) #164; derived from Miller (1923); Kellogg (1936); Fraser and Purves (1960); Tanaka and Fordyce (2014, 2015) #127).

(62) Subtemporal crest: present (0); present but reduced, or absent (1). (modified from Geisler and Sanders (2003) #165; Geisler et al. (2011) #165 (2012) #165; Murakami et al. (2012a, 2012b) #127; Tanaka and Fordyce (2014, 2015) #128).

(63) Superior lamina of pterygoid: absent from sphenoidal region but present in orbital region (0); present and covers most of ventral exposure of alisphenoid (1); partially absent from orbital region (2); completely absent from orbital region (3). (Murakami et al. (2012a, 2012b) #128; modified from Arnold and Heinsohn (1996) #16; Geisler and Sanders (2003) #167; Geisler et al. (2011) #167 (2012) #167; derived from Miller (1923); Fraser and Purves (1960)); Tanaka and Fordyce (2014, 2015) #129.

(64) Depth of pterygoid sinus fossa in basicranium: deep, and extended dorsally into orbit (0); deep, excavated dorsally to level of cranial foramen oval (1). (modified from Fordyce (1994) #6; Lambert (2005) #30; Murakami et al. (2012a, 2012b) #130; Tanaka and Fordyce (2014, 2015) #131).

(65) Anterior level of pterygoid sinus fossa: interrupted posterior to, or the level of, antorbital notch (0);
(66) Fossa for preorbital lobe of pterygoid sinus in orbit: absent (0); present (1). (Fraser and Purves (1960); Arnold and Heinsohn (1996) #18; Murakami et al. (2012a, 2012b) #131; Tanaka and Fordyce (2014, 2015) #132).


(68) Postorbital lobe of pterygoid sinus fossa: absent (0); present (1); large and deep (2). (Arnold and Heinsohn (1996) #18; Geisler and Sanders (2003) #170; Geisler et al. (2011) #170 (2012) #170; Murakami et al. (2012a, 2012b) #135; derived from Fraser and Purves (1960); Tanaka and Fordyce (2014, 2015) #136).

(69) Anteroposteriorly elongated pterygoid sinus fossa, at level of orbit, bordered by mediolaterally compressed subtemporal crest of frontal: absent (0); present (1). (Murakami et al. (2012a, 2012b) #136; Tanaka and Fordyce (2014, 2015) #137).

(70) Orbitosphenoid: not contacting lacrimal or lacrimojugal (0); contacting lacrimal or lacrimojugal (1). (Murakami et al. (2012a, 2012b) #137; Tanaka and Fordyce (2014, 2015) #138).

(71) Ratio of length of hamular process of pterygoid to cranium length: <0.30 (0); 0.30–0.44 (1); 0.45–0.59 (2); >0.60 (3). The length of the hamular process of the pterygoid is measured from anterior edge of the pterygoid to posterior edge of the hamular process. The cranium length is measured from anterior edge of the antorbital process to posterior edge of occipital condyles. (Murakami et al. (2012a, 2012b) #138; modified from Heyning (1989) #18 (1997) #50; Muizon (1991); Messenger and McGuire (1998) #1447; Lambert (2005) #31; Tanaka and Fordyce (2014, 2015) #139).

(72) Keel affecting ventral surfaces of hamular processes: absent (0); present (1). (Muizon (1988); Messenger and McGuire (1998) #1449; Bianucci (2005) #14; Murakami et al. (2012a, 2012b) #139; modified from Fajardo-Mellor et al. (2006) #10; Tanaka and Fordyce (2014, 2015) #140).

(73) Exposure of medial lamina of pterygoid hamuli in lateral view: complete or broad exposure due to extreme reduction of lateral lamina of pterygoid hamuli (0); no exposure due to a posterior extension of lateral lamina extending posterior to medial lamina (1); medial lamina of pterygoid hamuli exposing lateral lamina through ovoid window in lateral view (2). (Muizon (1988); Fajardo-Mellor et al. (2006) #11; Murakami et al. (2012a, 2012b) #140; derived from Noble and Fraser (1971); Tanaka and Fordyce (2014, 2015) #141).

(74) Shape of restricted area between postorbital ridge of frontal and subtemporal crest from ventral view: anteroposteriorly long elliptical (0); wide fan-shape (1); narrow fan-shape (2), rhombus (3). (Tanaka and Fordyce (2014, 2015) #280)

**Posterior Basicranium**

(75) Tympanosquamosal recess: very large, forming large fossa bordering entire medial edge of glenoid fossa (0); present and enlarged, forming triangular fossa medial and anteromedial to postglenoid process (1). (Geisler and Sanders (2003) #178; Geisler et al. (2011) #178 (2012) #178; Murakami et al. (2012a, 2012b) #143; modified from Lambert (2005) #35; derived from Fraser and Purves (1960), and Fordyce (2002); Tanaka and Fordyce (2014, 2015) #144).

(76) Fossa for the basisphenoidal sinus: absent (0); present (1). (Fraser and Purves (1960); Mead and Fordyce (2009); Murakami et al. (2012a, 2012b) #145; Tanaka and Fordyce (2014, 2015) #146).

(77) Posterior portion of periotic fossa of squamosal: fossa absent (0); fossa present but shallow (1); posteromedial portion contains large deep fossa (2). (Geisler and Sanders (2003) #187; Geisler et al. (2011) #187 (2012) #187; Murakami et al. (2012a, 2012b) #149 and #151; Tanaka and Fordyce (2014, 2015) #151).

(78) Length of zygomatic process of squamosal as percent of greatest width of maxilla at postorbital process: >31% (0); ≤30% (1). (Murakami et al. (2012a, 2012b) #152; modified from Heyning (1989) #33, 35, 65, 67; Geisler and Sanders (2003) #188; Geisler et al. (2011) #188 (2012) #188; Tanaka and Fordyce (2014, 2015) #152).

(79) Fossa for posterior sinus in exoccipital: absent or slightly concave (0); moderately concave (1); forming deep sack-like structure (2). (Murakami et al. (2012a, 2012b) #161; modified from Muizon (1991); Lambert (2005) #38; Tanaka and Fordyce (2014, 2015) #161).

(80) Occipital condyles; on pedicle (0); lacking pedicle, unified with occipital (1). (Tanaka and Fordyce (2014, 2015) #284)

**Periotic**

(81) Relative position of dorsal depth of stapedial muscle fossa and fenestra rotunda: ventral to, or in line with, dorsal edge of fenestra rotunda (0); well dorsal to fenestra rotunda (1). (Geisler and Sanders (2003) #223; Geisler et al. (2011) #223 (2012) #223; Murakami et al. (2012a, 2012b) #177; Tanaka and Fordyce (2014, 2015) #176).
(82) Aperture for cochlear aqueduct: smaller than aperture for vestibular aqueduct (0); approximately same size as aperture for vestibular aqueduct (1); much larger than aperture for vestibular aqueduct, with narrow posterior edge (2). (Geisler and Sanders (2003) #227; Geisler et al. (2011) #227 (2012) #227; Murakami et al. (2012a, 2012b) #181; modified from Muizon (1987); Fordyce (1994); Lambert (2005) #52; Tanaka and Fordyce (2014, 2015) #180).


(84) Posterior process of periotic in lateral view: ventrally bent (0); in same plane as body of periotic (1). (Bianucci (2005) #19; Murakami et al. (2012a, 2012b) #189; modified from Arnold and Heinsohn (1996) #28; Lambert (2005) #54; Tanaka and Fordyce (2014, 2015) #189).

(85) Angle between posterior process of periotic and long axis of pars cochlearis from dorsal or ventral views: >135° (0); ≤135° (1). (Murakami et al. (2012a, 2012b) #190; modified from Geisler and Sanders (2003) #246; Lambert (2005) #54; Geisler et al. (2011) #246 (2012) #246; derived from Kasuya (1973); Barnes (1990); Luo and Marsh (1996); Tanaka and Fordyce (2014, 2015) #189).

(86) Length of posterior process of periotic as percent length of pars cochlearis: long, >85% (0); short, ≤84% (1). (Murakami et al. (2012a, 2012b) #193; modified from Barnes (1990); Luo and Marsh (1996) #24; Geisler and Sanders (2003) #245; Geisler et al. (2011) #245 (2012) #245; Tanaka and Fordyce (2014, 2015) #193).


(88) Width of tympanic bulla as percentage of its length along its long axis: wide, ≥65% (0); narrow and long, ≤64% (1). (Geisler and Sanders (2003) #251; Bianucci (2005) #23; Geisler et al. (2011) #251 (2012) #251; Murakami et al. (2012a, 2012b) #198; derived from Kasuya (1973); Tanaka and Fordyce (2014, 2015) #198).


(91) Elliptical foramen of tympanic bulla: present (0); absent or close (1). (Geisler and Sanders (2003) #261; Geisler et al. (2011) #261 (2012) #261; Murakami et al. (2012a, 2012b) #204; derived from Kasuya (1973); Tanaka and Fordyce (2014, 2015) #204).

(92) Surface of posterior process of tympanic bulla: spiny or irregular edges (0); rounded and pachyostotic (1). (Muizon (1991); Messenger and McGuire (1998) #1483; Murakami et al. (2012a, 2012b) #206; derived from Kasuya (1973); Tanaka and Fordyce (2014, 2015) #206).

(93) Posterior edge of medial prominence of involucrum: approximately in line with posterior edge of lateral prominence (0); distinctly anterior to posterior edge of lateral prominence (1). (Muizon (1987); Geisler and Sanders (2003) #269; Geisler et al. (2011) #269 (2012) #269; Murakami et al. (2012a, 2012b) #209; derived from Kasuya (1973); Tanaka and Fordyce (2014, 2015) #209).

(94) Posterior end of ventromedial keel: not protruding and directed medially (0); protruding and directed medially (1). (Geisler and Sanders (2003) #275; Geisler et al. (2011) #275 (2012) #275; Murakami et al. (2012a, 2012b) #214; Tanaka and Fordyce (2014, 2015) #213).

(95) Basihyal and thyrohyal shape: arched (0); angled (1). (Murakami et al. (2012a, 2012b) #216; modified from Bianucci (2005) #25; Tanaka and Fordyce (2014, 2015) #215).

(96) Dorsal transverse process of atlas: developed dorso-laterally (0); absent or rudimentary obtuse angle (1). (Murakami et al. (2012a, 2012b) #217; modified from Muizon (1988); Barnes (1990); Tanaka and Fordyce (2014, 2015) #216).

(97) Roof of neural canal of atlas: arched (0); straight (1). (Murakami et al. (2012a, 2012b) #218; Tanaka and Fordyce (2014, 2015) #217).
(98) Postzygapophysis of axis in anterior view: appearing as crest, elongated dorsolaterally (0); appearing as rudimentary crest (1); not appearing (2). (Murakami et al. 2012a, 2012b) #219; Tanaka and Fordyce (2014, 2015) #218.

(99) Cervical vertebrae: unfused (0); atlas and axis fused (1); C1–C3 or C1–C4 fused (2); C1–C6 or C1–C7 fused (3); C2–C7 fused (4). (Murakami et al. 2012a, 2012b) #220; modified from Arnold and Heinsohn (1996) #9; Messenger and McGuire (1998) #1501; Geisler and Sanders (2003) #278, 279; Fajardo-Mellor et al. (2006) #18; Lambert (2008) #18; Geisler et al. (2011) #278, 279 (2012) #278, 279; derived from Allen (1923); Miller (1923); Fraser and Noble (1971); De Smet (1977); Rommel (1990); Tanaka and Fordyce (2014, 2015) #219.

(100) Length of cervicals (C1–C7) as percent of height of vertebral body plus neural canal of atlas: long, >150% (0); short, <150% (1). (Murakami et al. 2012a, 2012b) #221; Tanaka and Fordyce (2014, 2015) #220.


Scapula

(102) Anterdorsal part of scapula: rounded (0); almost rectilinear (1). (Murakami et al. 2012a, 2012b) #232; Tanaka and Fordyce (2014, 2015) #232.

(103) Ventral projection on anterior border of scapula: absent (0); present (1). (Fajardo-Mellor et al. 2006) #26; Murakami et al. (2012a, 2012b) #233; derived from Noble and Fraser (1971); Tanaka and Fordyce (2014, 2015) #233.

(104) Coracoid process of scapula: not expanded distally (0); expanded distally (1); notably reduced or absent (2). (Murakami et al. 2012a, 2012b) #237; modified from Muizon (1987, 1994); Messenger and McGuire (1998) #1504; Geisler and Sanders (2003) #292; Lambert (2005) #73; Bianucci (2005) #33; Geisler et al. (2011) #292; derived from True (1904); Tanaka and Fordyce (2014, 2015) #237.

(105) Coracoid process of scapula, with glenoid fossa: directed horizontally (0); directed anteroventrally (1). (modified from Murakami et al. 2012a, 2012b) #238; modified Barnes (1990); Tanaka and Fordyce (2014, 2015) #238.

(106) Acromion of scapula: narrow and not expanded distally (0); expanded distally (1). (Murakami et al. 2012a, 2012b) #239; modified from Bianucci (2005) #34; Tanaka and Fordyce (2014, 2015) #239.

(107) Acromion of scapula, when glenoid fossa direct ventrally: directed horizontally (0); directed antero- dorsally (1); directed anteroventrally (2). (Murakami et al. 2012a, 2012b) #240; modified from Barnes (1990); Tanaka and Fordyce (2014, 2015) #240.

Forelimb (except scapula)

(108) Ratio of length of humerus to length of radius: long, >1.1 (0); short, <0.8 (1). (Murakami et al. 2012a, 2012b) #242; modified from Sanders and Barnes (2002); Geisler and Sanders (2003) #297; Geisler et al. (2012; 2011) #297; Tanaka and Fordyce (2014, 2015) #242.

(109) Prominent deltoid crest on anterior edge of humerus: present, forms greatest anteroposterior diameter along shaft (0); forming a knob-like tuberosity (1); tuberosity or crest absent (2). (Geisler and Sanders (2003) #294; Geisler et al. (2011) #294 (2012) #294; Murakami et al. 2012a, 2012b) #244; derived from Sanders and Barnes (2002); Tanaka and Fordyce (2014, 2015) #244.

(110) Radial and ulnar facets of humerus in lateral view: facets forming a semicircular articulation surface (0); facets forming an obtuse angle (1). (Barnes, Barnes (1990); Geisler and Sanders (2003) #296; Geisler et al. (2011) #296 (2012) #296; Murakami et al. 2012a, 2012b) #245; Tanaka and Fordyce (2014, 2015) #245.

(111) Olecranon process: present as a distinct process (0); present as a slightly raised proximal posterior edge (1); absent (2). (Messenger and McGuire (1998) #1507; Geisler and Sanders (2003) #296; Geisler et al. (2011) #284 (2012) #284; Murakami et al. 2012a, 2012b) #246; derived from Muizon (1984); Barnes (1990); Arnold and Heinsohn (1996) #10; Fajardo-Mellor et al. (2006) #28; derived from Howell (1927); Bianucci (2005) #37; Tanaka and Fordyce (2014, 2015) #246.

Added characters to Tanaka and Fordyce (2015)

(112) Mandible fossa of squamosal: wider than squamosal recess (0); narrower than squamosal recess (1).

(113) Anterior end of zygomatic process in ventral view: rounded (0); tapered (1).

(114) Most anterior maxillary foramen: anterior to or in line with antorbital notch (0); posterior to antorbital notch (1). (Ichishima and Kimura (2005); Colpaert et al. (2015) #3)

(115) Longitudinal sulcus through premaxillary eminence: 0, absent; 1, present. This additional sulcus is thought to be present in Brabocetus, at least on right side. (de Muizon (1984); Colpaert et al. (2015) #6)

(116) Dorsal extension of pterygoid sinus fossa between frontal and maxilla: absent or poorly developed (0); deep (1). (Lambert (2008); Fajardo-Mellor et al. (2006); Colpaert et al. (2015) #13)

(117) Number of teeth in each upper tooth row: tooth counts >35 (0); tooth counts between 35 and 30


Heyning, J.E. 1989. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. *Contributions in Science, Natural History Museum of Los Angeles County*, 405:1-64.


Tanaka, Y., and Fordyce, R.E. 2014. Fossil dolphin *Otekaiea marplesi* (latest Oligocene, New Zealand) expands the morphological and taxonomic diversity

True, F.W. 1904. The whalebone whales of the western North Atlantic compared with those occurring in European waters with some observations on the species of the North Pacific. *Smithson Contribution to Knowledge*, 33:1-332.

APPENDIX 4.

List of modifications to the original codings and character descriptions of Tanaka and Fordyce (2015). The changed codings were originally coded by Murakami (2012b). The initial number refers to the character number in Appendix 3. Character numbers are identified in parentheses.

(26) Maxilla on dorsal surface of skull: does not contact supraoccipital posteriorly, maxilla separated by frontal and/or parietal (0); contact present (1).
   *Haborophocoena toyoshimai* ? to 0

(46) Temporal fossa shape in lateral view: height lower than anteroposterior length (0); higher (1); lower and its posterior end is rounded (2).
   *Haborophocoena minutus* ? to 0
   *Haborophocoena toyoshimai* 0 to 1

(56) Postglenoid process in lateral view: tapering ventrally (0); squared off ventrally (1); same as state 1 except very wide anteroposterior diameter of process (2).
   *Haborophocoena toyoshimai* 0 to 1

(84) Posterior process of periotic in lateral view: ventrally bent (0); in same plane as body of periotic (1).
   *Haborodelphis toyoshimai* 0 to 1
   *Miophocaena nishinoi* ? to 0
   *Semirostrum ceruttii* 1 to 0
APPENDIX 5.

Treefile of the analysis of Tanaka and Ichishima (2016). Available in zipped format with Appendix 1 and Appendix 2 online at palaeo-electronica.org/content/2016/1663-a-new-skull-of-numataphocoena