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Abstract. Two mandibles of fossil mysticetes from the early Pliocene, upper part of the Horokaoshirarika Formation at Numata Town, Hokkaido, Japan, belong to the archaic, extinct cetotheriid baleen whale, Herpetocetinae, gen. et sp. indet. by having an elongated angular process projecting posteriorly beyond the mandibular condyle. The new materials of the Herpetocetinae represent the northernmost occurrence in the North Pacific.
Key words: baleen whale, fossil, geographic range, Herpetocetinae, systematics

Introduction

The baleen whale family Cetotheriidae has varied in both its context and its content. Early accounts, for example, by Kellogg (1928) and Simpson (1945) included numerous species within this family that are now considered to belong to other mysticete clades. Today, Cetotheriidae are more strictly defined as the monophyletic clade including *Cetotherium rathkii* Brandt, 1843, as first recovered in the phylogenetic analysis of Bouetel and de Muizon (2006).

Steeman (2007) recognized the subfamily Herpetocetinae, which was subsequently defined by Whitmore and Barnes (2008) to include *Herpetocetus* and *Nannocetus* based on their distinctive cranio-mandibular articulation. Recently, Bisconti (2014) described a new mysticete, *Herentalia nigra*, referred to Herpetocetinae. However, *H. nigra* has a much larger skull than the known herpetocetines, and it forms a clade with *Herpetocetus* sp. (NMNS-PV 19540). The later analysis of Marx and Fordyce (2016) put *Herentalia* in the Cetotheriidae, but not in the Herpetocetinae. Thus, here, Herpetocetinae includes only *Herpetocetus* and *Nannocetus*.

There is an abundant record of herpetocetine material from Japan (Oishi and Hasegawa, 1995), but little has been formally described. Inside Japan, herpetocetines are known mostly from eastern Honshu. By contrast, records from northernmost Japan, specifically, the island of Hokkaido are rare. A single tympanic bulla was previously reported as having similarities with *Herpetocetus* sp. from Chiba and Sendai, but only diagnosed to "Cetotheriidae, genus and species indeterminate" (Shinohara and Tanaka, 2007). Here, we report two mandibles from exposures along...
the Uryu and Horonitachibetsu Rivers at Numata Town (Figure 1), Hokkaido, which are well known for their Pliocene marine fossils, including mysticetes (e.g. Ichishima, 2005; Kimura *et al*., 1987; Tanaka, 2016a). The two mandibles are referable to Herpetocetinae, and represent the northernmost record of the subfamily in the North Pacific.

*Institutional abbreviations.*—AMP = Ashoro Museum of Paleontology, Ashoro Town, Hokkaido, Japan; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHN = Muséum National d’Histoire Naturelle, Paris, France; NFL = Numata Fossil Museum, Numata Town, Hokkaido, Japan; NMNH-P = Academian V. A. Topachevsky Paleontological Museum of the National Museum of Natural History of the National Academy of Sciences of The Ukraine; NMNS = National Museum of Nature and Science, Tsukuba, Japan; SDNHM = San Diego Natural History Museum, San Diego, California, USA; UCMP = University of California Museum of Paleontology, Berkeley, California, USA; VMW = Sierra College Natural History Museum, Rocklin, California, USA.

**Systematic paleontology**

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Unranked taxon Neoceti Fordyce and de Muizon, 2001

Suborder Mysticeti Gray, 1864

Family Cetotheriidae Brandt, 1872

Subfamily Herpetocetinae Steeman, 2007

Herpetocetinae, gen. et sp. indet.
Remarks.—The two mandibles reported herein, NFL 14 and 1025 belong to the subfamily Herpetocetinae because of their far posteriorly projected angular process, which exceeds that of all other cetotheriids in length (see Whitmore and Barnes, 2008). This mandibular morphology is consistent with that of species that have previously been referred to *Herpetocetus*. However the specimens from Numata have angular processes that differ from those of any other previously named species.

Geologic age and stratigraphy.—The two mandibles (NFL 14 and NFL 1025) were collected from the upper part of the marine Horokaoshirarika Formation (Furusawa *et al.*, 1993) at Numata, Hokkaido, which is early Pliocene in age (Figure 1).

At the localities, a sedimentary sequence is exposed, comprising approximately 200 m of the upper part and 500 m of the lower part of the Horokaoshirarika Formation (Watanabe and Yoshida, 1995). The boundary between the two is indicated by a thin tuff layer (Kobayashi *et al.*, 1969).

The marine Ichinosawa Formation and Bibaushi Formation both overlie the Horokaoshirarika Formation, and are exposed along the lower parts of the Horonitachibetsu River (Kobayashi *et al.*, 1969), but not along the bed of the Uryu River. The older, Miocene, marine Horoshin Formation underlies the Horokaoshirarika Formation, and is exposed 2 km upstream from the locality of NFL 1025, and 3 km upstream from the locality of NFL 14.

The tuff separating the lower and upper parts of the Horokaoshirarika Formation has been dated to approximately 4.5 Ma±0.7 Ma (Wada *et al.*, 1986). The diatom biostratigraphy suggests the age of the upper part of the Horokaoshirarika Formation to be approximately 4.5 Ma to 3.9 or 3.5 Ma, and corresponds to the *Thalassiosira*
oestrupii Zone (Nakashima and Watanabe, 2000). Therefore, the age of the upper part of the Horokaoshirarika Formation corresponds to approximately 4.5 Ma to 3.5 Ma, or the early Pliocene.

In addition to the fossil mysticetes described here, the upper part of the Horokaoshirarika Formation has also produced other marine vertebrates, including the phocoenid Numataphocoena yamashitai Ichishima and Kimura, 2000 (same locality as NFL 1025; see also Tanaka, 2016b; Tanaka and Ichishima, 2016) and fossil pinnipeds (Yamashita and Kimura, 1990; Kohno et al., 1995).

*Referred specimen NFL 14.*—An incomplete right mandible (Figures 2, 3, 6C, Table 1), collected by Toshitsugu Maeda on 17 August 1988, and prepared by Shigeru Yamashita. The locality is in the bed of the Uryu River, in the 2nd Takaho District of Numata Town (Figure 1).

Only the posterior portion of NFL 14 is preserved. The remaining part of the body is slightly curved laterally and dorsally, and contains five anteriorly-opening mental foramina, which are 3–4 mm in diameter. Anteriorly, the cross section of the body becomes both higher and thinner. At the point of fracture, the mandibular canal is round in cross section and has a diameter of 8.5 mm.

The ramus consists of the broken base of what appears to have been a relatively low coronoid process. The mandibular foramen is deeply excavated, with a robust lower border and a rounded anterior rim; it measures 33.0 mm in height and 22.5 mm in length. The articular surface of the mandibular condyle faces posterodorsally. The posterior end of the angular process extends far posterior to the articular surface of the mandibular condyle. Where the angular process is broken off, it is nearly rectangular in cross section (26.0+ mm wide, 20.0 mm high).
Referred specimen NFL 1025.—A nearly complete right mandible (Figures 4, 5, 6D, Table 2), found by Shigeru Yamashita on 15 June 1994, and collected by Shigeru Yamashita, Takaoki Harada and Hitoshi Furusawa. The locality is in the bed of the Horonitachibetsu River, in the 3rd Hokuryu District of Numata Town (Figure 1).

The posterior portion of the body of NFL 1025 is more clearly bowed laterally than NFL 14. In lateral view, the body is somewhat arched dorsally and markedly expands in height anteriorly. There are at least three anteriorly opening mental foramina, each of which is approximately 2.5 mm in diameter. The anterior end of the body is somewhat triangular in cross section, with the ventral border being relatively thin. The symphyseal groove is relatively shallow.

The mandibular foramen (Figures 4 and 5E, H) is deeply excavated, but otherwise poorly preserved. The articular surface of the mandibular condyle is elongate and oriented posterodorsally. As in NFL 14, the subcondylar furrow is broad and poorly defined. The angular process is nearly complete, elongate, and extends for approximately 58.0 mm posterior to the articular surface of the mandibular condyle. Dorsally, the robust apex of the angular process is connected to the mandibular condyle by a relatively narrow subcondylar furrow. Medially, the angular process is flat in the likely area of insertion of the medial pterygoid muscle.

Overall, the two mandibles are similar in size, as indicated by mandibular condyle widths of 30.0 mm (NFL 14) and 33.0 mm (NFL 1025), respectively. However, NFL 1025 differs in having a more elongate mandibular condyle, a more robust angular process and a thicker dorsal connecting ridge between the two (15.0 mm vs 8.0 mm). Such differences may reflect specific, ontogenetic, sexual, or individual variation, but other, more complete, specimens are required to elucidate this.
Discussion

Comparisons with other herpetocetines

Of all described cetotheriids, the mandibles from Numata most closely resemble herpetocetines. The only other possible contender, *Piscobalaena nana*, differs from the present material in having a shorter angular process, a less depressed posterior portion of the mandibular condyle, and a wider body with a blunter ventral and a sharper dorsal margin (e.g. MNHN SAS 1618; Bouetel and de Muizon, 2006).

The relatively large size of the mandibles from Numata suggests that they likely represent *Herpetocetus*, rather than the comparatively small *Nannocetus*. However, *Nannocetus* is currently only known from fragmentary juvenile cranium lacking the mandible, which makes comparisons with this taxon difficult. Better preserved material of an ontogenetically more mature individual is needed to clarify the morphology and relationships of *Nannocetus*, as well as its putative status as a genus separate from *Herpetocetus*.

Within *Herpetocetus*, the mandibles from Numata differ from *H. scaldiensis* (IRSNB 14; see also Whitmore and Barnes, 2008; Figure. 1) in having a shorter but also higher angular process. They resemble *H. bramblei* in having a dorsally arched body, but also differ from this species in being more elongated, more slender, and in having a somewhat more convex (dorsoventrally) medial border.

Finally, the specimens from Numata are both larger and more robust than the holotype of *H. morrowi* (UCMP 129450), which furthermore might also be 2–3 million years younger (El Adli *et al.* 2014). A paratype of *H. morrowi*, SDNHM 35294, preserves only the anterior part, and its size and shape is very similar to NFL 1025. Another paratype, SDNHM 32138, shows a broken angular process, but the
preserved base is more slender than that of NFL 1025.

**Overview of cetotheriid records from Hokkaido**

There are three previous reports of “cetotheriid” fossils from Hokkaido (Egashira and Kimura, 1998; Amano and Little, 2005; Shinohara and S. Tanaka, 2007); however, not all of these may be members of the Cetotheriidae as presently defined.

Egashira and Kimura (1998) reported “the first Cetotheriidae from Hokkaido”, AMP 35 (Taiki specimen 1 in the study) from a middle Miocene deposit. This specimen, which was also briefly mentioned by Kimura and Ozawa (2002), includes the posterior portion of the skull, the right mandible, the right tympanic bulla (not illustrated in the publication), and the atlas. The mandible has a relatively short angular process, that terminates anterior to the articular surface of the mandibular condyle, unlike in cetotheriids. Regarding the taxonomic history of the family Cetotheriidae, the early accounts by Kellogg (1928) and Simpson (1945) included numerous species within the family, which are now considered to belong to other mysticete clades. AMP 35 is one of the case, and is not demonstrably a member of the family Cetotheriidae *sensu stricto*.

In our opinion, AMP 35 is similar to the late early Miocene holotype of *Isanacetus laticephalus* Kimura and Ozawa, 2002, from Mie Prefecture, Japan. The two specimens share transversely narrow and anteroposteriorly elongated nasal bones, as well as a deeply concave orbital margin of the supraorbital process of the frontal. *Isanacetus* has been interpreted as a stem mysticete (Deméré *et al.*, 2005), a stem balaenopterid (Kimura and Ozawa, 2002), or a member of the clade Balaenopteridae + Cetotheriidae (Bisconti, 2008; Bisconti *et al.*, 2013; Gol’din *et al.*, 2014; Marx, 2015).

The second putative record of cetotheriids from Hokkaido consists of a skull
fragment of a mysticete (NMNS-PV 20913) from the lower middle Miocene Chikubetsu Formation exposed near Shosanbetsu Village. It was reported in association with mollusk fossils and identified as belonging to the "cetothere group" based on a personal communication with N. Kohno at NMNS (Amano and Little, 2005). More recently, open-access database at NMNS (http://db.kahaku.go.jp/webmuseum_en/collect/search_rule.do;jsessionid=9177FE1F1A1F696D4E8EFF8C4D2A8D7A?class_name=col_c2_02) has re-identified the specimen as a balaenomorph, instead of non-monophyletic “cetothere group.” The skull fragment does not show clear Cetotheriidae features; thus we follow the database identification.

The final report of a cetotheriid from Hokkaido is that of Shinohara and Tanaka (2007), who identified a bulla, NFL 2162 as belonging to a cetotheriid. Regarding the study, NFL 2162 is similar to *Herpetocetus* based on having an echelon, which was mentioned by Oishi and Hasegawa (1995) as a diagnosis of the *Herpetocetus*. Shinohara and Tanaka (2007) did not identify in genus level, because lack of comparison with other cetotheriids. Here, we follow the authors’ identification, and recognize that the specimen is the first cetotheriid *sensu stricto* record from Hokkaido, but cannot identify as a *Herpetocetus* because the feature is also seen on a species of the family Cetotheriidae, *Piscobalaena* sp. (see Fig. 33 of Bouetel and de Muizon, 2006), and probably be highly effected by ontogeny.

In the text of Shinohara and Tanaka (2007), the two mandibles (NFL 14 and 1025) were mentioned possibilities as *Herpetocetus* sp. and *Nannocetus* sp. with personal communication of H. Furusawa.

**Paleobiogeographic patterns**

Herpetocetinae appear to have been distributed throughout the temperate latitudes of the Northern Hemisphere with records from both the eastern and western North
Pacific, and the eastern and western North Atlantic. Together, these occurrences range in age from the late Miocene through the Pliocene, and at least one species may have persisted into the Pleistocene (Boessenecker, 2013b) (Figure 7, Table 2).

Whitmore and Barnes (2008) reviewed the typology and geologic provenance of *Herpetocetus scaldiensis* Van Beneden, 1872, and assigned to the species additional specimens, all of them from the same deposit in Belgium that yielded the lectotype and the other specimens that were originally described by Van Beneden (1872, 1882). The first report of the genus *Herpetocetus* in the fossil record of the western North Atlantic was the description of *Herpetocetus transatlanticus* Whitmore and Barnes, 2008 from the early Pliocene of North Carolina, U.S.A. In the eastern North Pacific basin, *Herpetocetus* occurs in the latest Miocene to earliest Pliocene parts of the Capistrano Formation in southern California and from the approximately contemporaneous Purisima Formation in central California (Barnes 1977; Boessenecker 2013a; Whitmore and Barnes, 2008). The geochronologically youngest named species is the late Pliocene *Herpetocetus morrowi* El Adli *et al.*, 2014, from the San Diego Formation at San Diego, California, U.S.A (El Adli *et al.*, 2014).

Records of *Herpetocetus* and of *Herpetocetus*-like mysticetes are not uncommon in Japan (Hatai *et al.*, 1963; Oishi and Hasegawa, 1995; Shinohara and S. Tanaka, 2007; the present study). The early Pliocene *Herpetocetus* bullae recorded from Choshi in Chiba Prefecture by Oishi and Hasegawa (1995) are the southern-most records of *Herpetocetus* in Japan. By contrast, the mandibles from Numata Town, Hokkaido, are the northern-most records of Herpetocetinae in the North Pacific Ocean.

**Conclusions**
Two mandibles from the early Pliocene Horokaoshirarika Formation at Numata, Hokkaido, Japan, represent the northernmost record of the fossil mysticete subfamily Herpetocetinae in the North Pacific. These mandibles cannot currently be assigned to this genus owing to the uncertainty surrounding the status of *Nannocetus*. The mandibles in particular appear to differ from all described species of *Herpetocetus*, and may indicate a further increase in herpetocetine taxonomic diversity.

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16–22. (in Japanese with English abstract)


List of figures and tables

**Figure 1.** Maps showing the localities of herpetocetine cetotheriid mysticetes from Numata Town, Hokkaido, Japan, reported in this study. **A**, locality of NFL 1025 on the bed of the Horokaoshirarika River; **B**, locality of NFL 14 on the bed of the Uryu River. **C**, stratigraphic column at the localities, which is modified from Tanaka and Ichishima (2016). The map of Japan and Numata Town are modified from Tanaka and Kohno (2015) and Tanaka and Ichishima (2016) respectively.

**Figure 2.** Herpetocetinae, gen. et sp. indet., incomplete right mandible, NFL 14. **A**, dorsal view; **B**, medial view; **C**, ventral view; **D**, lateral view; **E**, posterior view; **F**, anterior view. Dashed lines indicate missing parts based on published specimens of *Herpetocetus* and NFL 1025, described herein.

**Figure 3.** Herpetocetinae, gen. et sp. indet., incomplete right mandible with structures labeled, NFL 14. **A**, dorsal view; **B**, medial view; **C**, ventral view with cross section; **D**, lateral view; **E**, posterior view; **F**, anterior view showing cross section at transverse break. Dashed lines indicate missing parts based on published specimens of *Herpetocetus* and on NFL 1025, described herein.

**Figure 4.** Herpetocetinae, gen. et sp. indet., nearly complete right mandible, NFL 1025. **A**, dorsal view; **B**, medial view; **C**, lateral view; **D–H**, enlarged views of separated posterior part; **D**, lateral view; **E**, posterior view; **F**, dorsal view; **G**, ventral view; **H**, medial view.

**Figure 5.** Herpetocetinae, gen. et sp. indet., nearly complete right mandible with
structures labeled, NFL 1025. **A**, dorsal view; **B**, medial view; **C**, lateral view; **D–H**, enlarged views of separated posterior part; **D**, lateral view; **E**, posterior view; **F**, dorsal view; **G**, ventral view; **H**, medial view. Dashed lines indicate missing parts based on other published specimens of *Herpetocetus* and on NFL 14, described herein.

**Figure 6.** Cetotheriidae, posterior parts of mandibles of various species in lateral view. **A**, *Cetotherium riabinini* (holotype, NMNH-P 668/1) redrawn from Gol’din *et al.*, (2014); **B**, *Piscobalaena nana* (MNHN SAS 1618) redrawn from Bouetel and de Muizon (2006); **C**, Herpetocetinae gen. et sp. indet. NFL 14; **D**, Herpetocetinae gen. et sp. indet. NFL 1025; **E**, *Herpetocetus morrowi* (holotype, UCMP 129450) redrawn from El Adli *et al.*, (2014); **F**, *Herpetocetus scaldiensis* (lectotype, IRSNB 14) redrawn and reversed from Van Beneden (1882); **G**, *Herpetocetus bramblei* (UCMP 219079) redrawn and reversed from Boessenecker (2013a); **H**, *Herpetocetus* sp. (NMNS-PV 19540) redrawn and reversed from Bouetel and de Muizon (2006).

**Figure 7.** Paleogeographic distribution of the cetotheriid subfamily Herpetocetinae.

**Table 1.** Herpetocetinae, gen. et sp. indet., measurements in mm of mandibles, NFL 14 and NFL 1025, following the methods of Tsai and Fordyce (2015). Measurements are rounded to the nearest 0.5 mm. Parameters are measured in either the transverse or the dorso-ventral dimensions.

**Table 2.** List of reported Herpetocetinae.
<table>
<thead>
<tr>
<th></th>
<th>NFL 14</th>
<th>NFL 1025</th>
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<tr>
<td>Length of mandible, as preserved in straight line</td>
<td>490.0+</td>
<td>1250.0+</td>
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<td>Height of mandible, from coronoid process to ventral margin</td>
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<td>Maximum preserved height of mandible</td>
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<td>69.0</td>
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<tr>
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<tr>
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<td>-</td>
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<tr>
<td>Width of body at just anterior to coronoid process</td>
<td>32.0</td>
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<tr>
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<td>Falor Fm.</td>
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<td>San Diego Fm.</td>
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<td>Horokashirakawa Fm.</td>
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<td>Yushima Fm.</td>
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<tr>
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<td>Na-arai Fm.</td>
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<td><em>Herpetocetus bramblei</em> (Type)</td>
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<td>Purisima Fm.</td>
</tr>
<tr>
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<td>Yorktown Fm.</td>
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<td>Calvert Fm.</td>
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<tr>
<td>aff. <em>Herpetocetus</em> sp.</td>
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