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Enigmatic humerus of an archaic Oligocene-Miocene neocete from Miyazaki Prefecture, Kyushu, Japan

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Running head: Neocete humerus from Miyazaki

Abstract

The Late Palaeogene represents a crucial time in cetacean evolution that witnessed the origin of modern baleen and toothed whales (Neoceti) from their “archaeocete” ancestors. So far, this fundamental transition has been discussed mainly in terms of cranial morphology, whereas descriptions of postcranial material remain rare. Here, we report a small cetacean humerus from the Nichinan Group (Early Oligocene to Early Miocene), Kushima City, Miyazaki Prefecture, southern Kyushu, Japan. Our specimen resembles archaeocete humeri in being proximodistally elongate and in retaining a distinct deltoid ridge, but shares with neocetes the defining feature of an immobilised elbow joint. It resembles most Oligocene odontocetes in its small size and in lacking a notch marking the position of the distal epiphysis, and is furthermore similar to the enigmatic *Microzeuglodon* in having a transversely compressed shaft. A morphometric analysis based on five liner measurements, however, fails to cluster our specimen with any other known group of cetaceans, indicating

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that it is not easily referable to either basal mysticetes or odontocetes. Therefore, we here classify it as Neoceti *incertae sedis*.

Keywords: Cetacea, Neoceti, Nichinan Group, Humerus, Cenozoic, Morphometric analysis

Introduction

The latest Eocene and Oligocene are of major interest to the study of cetacean evolution, as it is likely during this time that modern whales and dolphins (Neoceti) first arose from their archaeocete forebears (Fordyce and de Muizon, 2001). Research into the origin of Neoceti is frequently tied to cranial features reflecting the evolution of baleen and echolocation, which characterise extant baleen whales (Mysticeti) and toothed whales (Odontoceti), respectively. However, the archaeocete–neocete transition also resulted in marked shifts in postcranial morphology. Freed from the need to support their own weight on land, neocetes lost external hind limbs, and the forelimbs became largely inflexible and primarily used for steering. Osteologically, the use of the forelimb as a flipper is reflected in a variety of features, including (1) the immobilisation of the elbow joint; (2) the shortening of the humerus relative to the radius and ulna; (3) the widening of the distal epiphysis of the humerus relative to the shaft; (4) the reduction of certain muscle attachment sites; and (5), in some taxa, the loss of one digit and /or the appearance of hyperphalangy (e.g. Cooper *et al.*, 2007a; Cooper *et al.*, 2007b).

Exactly when and in what order these changes occurred remains unclear, as the record of early neocete limbs bones is still extremely patchy. Here, we report a new Late Oligocene to Early Miocene cetacean humerus from Miyazaki Prefecture, Kyushu, Japan (Figure 1). The new specimen stands out both for its archaic morphology and its diminutive size, which puts it among the smallest cetaceans so far described. In addition, depending on its exact age, it may represent the first record of Cetacea from the Palaeogene of southern Kyushu.

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Material and Methods

We describe and compare the new material (MGF3848) with other cetacean humeri, following the morphological terminology of Flower (1885). Additionally, to provide a comparative context, we quantified the shapes of both our specimen and a range of archaic and modern taxa (Table 1) via a series of five linear measurements (Figure 2) as defined by Uhen (2004), which we then subjected to Principal Components Analysis in PAST, ver. 3.11 (Harper and Ryan 2001). Except for MGF3848 and the humerus of *Morawanocetus yabukii* (AMP 01), measurements were based on photographs and published figures, estimating the length of missing or hidden parts where necessary and feasible. All of the measurements were chosen so that they could be taken based on the outline of the humerus only. For consistency, humeri were preferably measured in lateral view, unless the latter was unavailable (Table 1). For modern taxa lacking a deltoid ridge, deltoid ridge breadth (DRB) was substituted by mid-distal humeral shaft breadth. Prior to the performing the PCA, we factored out body size by expressing all of our measurement data as ratios relative to the sum of the five linear measurements. The results of the PCA therefore reflect variations in shape only.

Institutional abbreviations.–AMP, Ashoro Museum of Paleontology, Hokkaido, Japan; KMNH, Kitakyushu Museum of Natural History and Human History, Fukuoka, Japan; LACM, Natural History Museum of Los Angeles County, California, USA; MGF, Miyazaki Prefectural Museum of Nature and History, Kyushu, Japan; MNHN, Muséum national d'histoire naturelle, Paris, France.

Results

Systematic Palaeontology

Cetacea Brisson, 1762

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Neoceti Fordyce and de Muizon, 2001

familia *incertae sedis*

Figure 3

Material.–MGF3848, a left humerus.

Locality and horizon.–MGF3848 was collected at Takamatsu Beach (31° 27′ 21.5″ N, 131° 11′ 23.6″ E, WGS84), located in Kushima City, Miyazaki Prefecture, Japan (Figure 1). The layer that yielded the specimen forms part of the Nichinan Group (Figure 1), a large-scale olistostrome originally deposited during Early Oligocene to Early Miocene (Sakai *et al.*, 1987). The fossiliferous horizon belongs to the coherent unit of the Nichinan Group and appears to be located within the Honjo Olistolith of Sakai et al. (1987). Earlier work referred the deposits in the Takamatsu area to the Kushima Formation and dated them to the Middle Eocene–Early Oligocene (Kato, 1985). However, this subdivision of the sequence appears to include portions of the chaotic unit of the Nichinan Group, which is in turn derived from the older Hyuga Group (Sakai *et al.*, 1987) and thus likely to provide unreliable dates.

We failed in our attempts to obtain any microfossils, calcareous or otherwise, from the matrix surrounding the specimen, but note that the lithology (alternating beds of sandstone and siltstone), invertebrate fauna and paucity of microfossils at the locality strongly resemble marine sand bar, lagoon and tidal flat deposits exposed in the Toi-Misaki area, about 15 km to the south east (Sakai, 1988). At Toi-Misaki, those strata have yielded foraminifera indicative of planktonic foraminiferal zone P21, which at 29.2–26.9 Ma straddles the Early/Late Oligocene boundary (Anthonissen and Ogg, 2012; Vandenberghe *et al.*, 2012). This estimate may be corroborated by the occurrence of foraminifera correlating with zones P20 and P21 in a portion of the Honjo Olistolith exposed closer to the fossil locality, near the mouth of the Honjo river (Sakai *et al.*, 1987: fig. 3). Nevertheless, given the

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chaotic nature of the Nichinan Group and the absence of direct dating evidence, the actual age of MGF3848 remains open to question.

Description.– MGF3848 is small (132 mm long), gracile and proximodistally elongate, with fused proximal and distal epiphyses (Table 2; Figure 3). In lateral view, the humeral head is relatively small, oriented roughly dorsally and does not overhang the posterior margin of the shaft. The small tuberosity is well developed and nearly as large as the head itself. The great tuberosity is broken. Immediately distal to the humeral head, the shaft is transversely compressed and bears a moderately developed deltoid ridge along roughly three quarters of its anterior margin. The posterior margin of the shaft is weakly concave and, as in extant cetaceans, confluent with the articular facet of the ulna. By contrast, basilosaurids and a variety of basal neocetes have a distal epiphysis that is offset from the posterior border of a shaft by a distinct notch (Figure 4). The distalmost portion of the shaft is about as wide anteroposteriorly as the distal epiphysis. The radial and ulnar articular facets are relatively flat and separated by a distinct angle, thus rendering the elbow joint inflexible.

Morphometric analysis.–The first two principal components (PCs) explain 96% of the total variance (Figure 5). PC 1 defines a gradient separating basilosaurid archaeocetes (lower scores) from mysticetes and odontocetes. PC 2 is less well defined, but reasonably separates archaic mysticetes and odontocetes from their modern relatives (*Pelocetus, Balaenoptera,* and *Physeter*). The morphospaces occupied by archaic mysticetes (lower PC 1 and higher PC 2 scores) and odontocetes (higher PC 1 and lower PC 2 scores) are close, but do not overlap. Somewhat unexpectedly, MGF3848 is well separated from other archaic neocetes and instead plots between archaeocetes and modern neocetes, roughly in line with *Fucaia*, *Yamatocetus* and *Mirocetus* according to PC 1, primarily because of its considerable length (HL) and

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narrow shaft (DRB and HPD). Nevertheless, MGF3848 does plot within the 95% confidence ellipse of Odontoceti, but outside that of Mysticeti.

Discussion

Our morphometric analysis separates archaeocetes from neocetes, with the extant *Balaenoptera* and *Physeter* forming a distinct cluster with the relatively modern-looking *Pelocetus*. This grouping is driven by a widening of the distal epiphysis and the reduction or loss of the deltoid ridge, and reflects a certain degree of convergent evolution of modern mysticete and odontocete humeri. Archaic Mysticeti and Odontoceti are marginally separated, with *Mirocetus riabinini* and *Phoberodon arctirostris* plotting closer to archaeocetes and modern neocetes, respectively, than other Oligocene odontocetes. This patterns may be indicative of a morphological transition: whereas *M. riabinini*, a basal odontocete, retains a well-defined deltoid ridge and archaic-looking distal epiphysis (Sanders and Geisler, 2015), *Phoberodon*, a Miocene squalodontid, has a deltoid ridge that is more reduced than in other Oligocene neocetes (Cabrera, 1926). It should be noted, however, that our data on *Phoberodon* are limited to a relatively old drawing (Cabrera, 1926: fig.16), and that some apparent damage to the anterior surface of its humerus may have led us to underestimate HPD.

MGF3848 is clearly a neocete, based on the immobilisation of the elbow – a feature that is typical of both mysticetes and odontocetes, but absent in archaeocetes (Uhen, 2004). Corroboration for this assessment comes from the lack of a notch separating the distal epiphysis from the posterior margin of the shaft, as seen in crown mysticetes and all but the most archaic odontocetes (Figure 4). The morphometric analysis also seems to provide some, albeit weak, support for this assessment, with MGF3848 being slightly closer to the archaic neocetes *Yamatocetus* and *Mirocetus* than to archaeocetes in terms of its PC 1 score (Fig. 5).

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On the other hand, MGF3848 also preserves a range of primitive, archaeocete-like features, including (1) its proximodistal elongation, (2) a well-developed deltoid ridge (relative to modern Neoceti) and (3) a distal epiphysis that is no wider anteroposteriorly than the humeral shaft. This preponderance of primitive traits again becomes apparent in the morphometric analysis, which places MGF3848 between archaeocetes and modern neocetes.

In some respects, MGF3848 is more similar to archaic odontocetes and the enigmatic *Microzeuglodon* – here regarded as a neocete owing to the angular arrangement of the radial and ulnar facets (see Lydekker, 1892) – than to archaic mysticetes: first, because it lacks the notch separating the distal epiphysis from the shaft, with the latter being present in aetiocetids and eomysticetids, but absent in *Microzeuglodon* and all described odontocetes save *Mirocetus* (Figure 4); secondly, because it specifically resembles *Microzeuglodon* in having a transversely compressed shaft; and, finally, because of its relatively small size. Thus, the humeral lengths of both *M. caucasicum* (ca 110 mm) and at least some Oligocene odontocetes (e.g. *Sulakocetus dagestanicus*, ca 130 cm) are comparable to that of MGF3848 (Lydekker, 1892; Mchedlidze, 1984).

By contrast, mysticetes are generally larger: all sufficiently known eomysticetids, including *Eomysticetus whitmorei*, *Tokarahia kauaeroa* and *Yamatocetus canaliculatus* have humeri that are twice as long or longer than MGF3848 (Boessenecker and Fordyce, 2015; Okazaki, 2012; Sanders and Barnes, 2002). Aetiocetids, such as *Fucaia goedertorum* (216 mm) and *Morawanocetus yabukii* (158 mm, T. Ando 2015, pers. comm.), are closer to MGF3848 in terms of their size but still consistently larger, with their known humeral lengths exceeding that of MGF3848 by 18% (in case of *M. yabukii*) or more. No limb material has yet been described for mammalodontids, which are also relatively small-bodied. However, mammalodontids have so far only been found in Australasia and, possibly, the Mediterranean (Bianucci *et al.*, 2011; Fitzgerald, 2010). Judging from the size of their skulls, they are

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probably also larger than MGF3848 and more comparable to medium-sized aetiocetids (Pyenson and Sponberg, 2011; Tsai and Ando, 2015), although it is important to note that there are currently no data on the relationship between skull and humerus/limb size in early neocetes.

In line with the above comparisons, the results of the morphometric analysis place MGF3848 outside the 95% confidence ellipse of Mysticeti, and inside – albeit barely – that of Odontoceti (Fig. 5). Nevertheless, the analysis also shows that MGF3848 is considerably more slender (i.e. proximodistally longer with a less developed deltoid ridge) than any other Oligocene neocete. In addition, MGF3848 specifically differs from *Mirocetus riabinini* and *Sulakocetus dagestanicus* in having a humeral head that is aligned with the posterior border of the shaft in lateral view, from *Otekaikea huata* and *Phoberodon arctirostris* in being more compressed transversely, and from *F. kelloggi*, *O. huata*, *Prosqualodon davidis* and *Phoberodon arctirostris* in having a better developed (compared to *Phoberodon* and *Prosqualodon*) or proximodistally longer deltoid ridge (compared to *Ferecetotherium* and *Otekaikea*). MGF3848 furthermore differs from *F. kelloggi*, *P. davidis* and, to a lesser degree, *O. huata* in lacking an anteroposteriorly expanded distal epiphysis, and from *O. huata* in lacking a well-defined fossa for the origins of the infraspinatus muscle (Cabrera, 1926; Flynn, 1948; Tanaka and Fordyce, 2015). Finally, MG3848 differs from *Microzeuglodon caucasicum* in that its small tuberosity that does not rise above the level of the head in anterior view. Overall, it therefore appears that, at least for the moment, MGF3848 is not clearly referable to any known neocete taxon.

Conclusion

MG3848 is a neocete characterised by a mix of primitive and derived features, including an inflexible elbow joint and the lack of a posterior notch on the distal epiphysis,

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but does not present an obvious match with any described early neocete limb material. We therefore refrain from assigning it to either mysticetes or odontocetes. Its small size is most consistent with MGF3848 representing an archaic odontocete or, possibly, a stem neocete, similar to *Microzeuglodon caucasicum*, but neither of these suggestions is unequivocally borne out by the results of our morphometric analysis. The apparent separation of MGF3848 from other neocetes may suggest that it represents a novel type of archaic neocete not clearly assignable to any established family. It is equally possible, however, that its relative isolation simply reflects a lack of comparative material, and will diminish or disappear with the publication of additional data on early neocete limb morphology. Future discoveries of additional archaic neocete limb bones, likely also from the Oligocene, will help to settle this question.

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Figure captions

Figure 1. Age of the Nichinan Group (A) and locality map of Kushima City, Kyushu, Japan (B). The star marks the exact locality of MGF3848 on Takamatsu Beach. Stratigraphy after Sakai et al. (1987), modified according to Vandenberghe et al. (2012).

Figure 2. Measurements used for the morphometric analysis. Abbreviations: HHD, humeral head diameter; HPD, humeral proximal diameter; HL, humeral length; DRB, deltoid ridge breadth; HDB, humeral distal breadth. In neocetes lacking a deltoid ridge, DRB was replaced with the diameter of the distal humeral shaft. Figure 2

Figure 3. Photographs of MGF3848. A, medial view; B, anterior view; C, lateral view.

Figure 4. Comparison of the distal epiphysis of the humerus of various archaic cetaceans. The dashed lines indicate the contour of the posterior border at the distal epiphysis. A, MGF3848; B, the basilosaurid archaeocete *Dorudon atrox*; C, the aetiocetid mysticete *Fucaia goedertorum*; D, the eomysticetid mysticete *Yamatocetus canaliculatus*; E, the enigmatic neocete *Microzeuglodon caucasicum*; F, waipatiid odontocete *Sulakocetus dagestanicus*; and G, the balaenopteroid mysticete *Pelocetus calvertensis*. Note the absence of a notch

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separating the distal epiphysis from the posterior border of the shaft in MGF3848, *Microzeuglodon*, *Sulakocetus* and *Pelocetus*.

Figure 5. Results of the morphometric analysis. Note the position of MGF3848 between archaeocetes and modern neocetes. The straight dashed lines represent the projections of the original variables. 95% confidence ellipses for Odontoceti and Mysticeti are also shown. For abbreviations, see Figure 2.

Table captions

Table 1. Humerus measurement ratios used for the morphometric analysis. See Fig. 2 for abbreviations. *: measurements taken in medial view; #: estimated measurements.

Table 2. Measurements of MGF3848 (in mm, with error of +/- 0.1 mm). See Fig. 2 for abbreviations; #estimated measurement.

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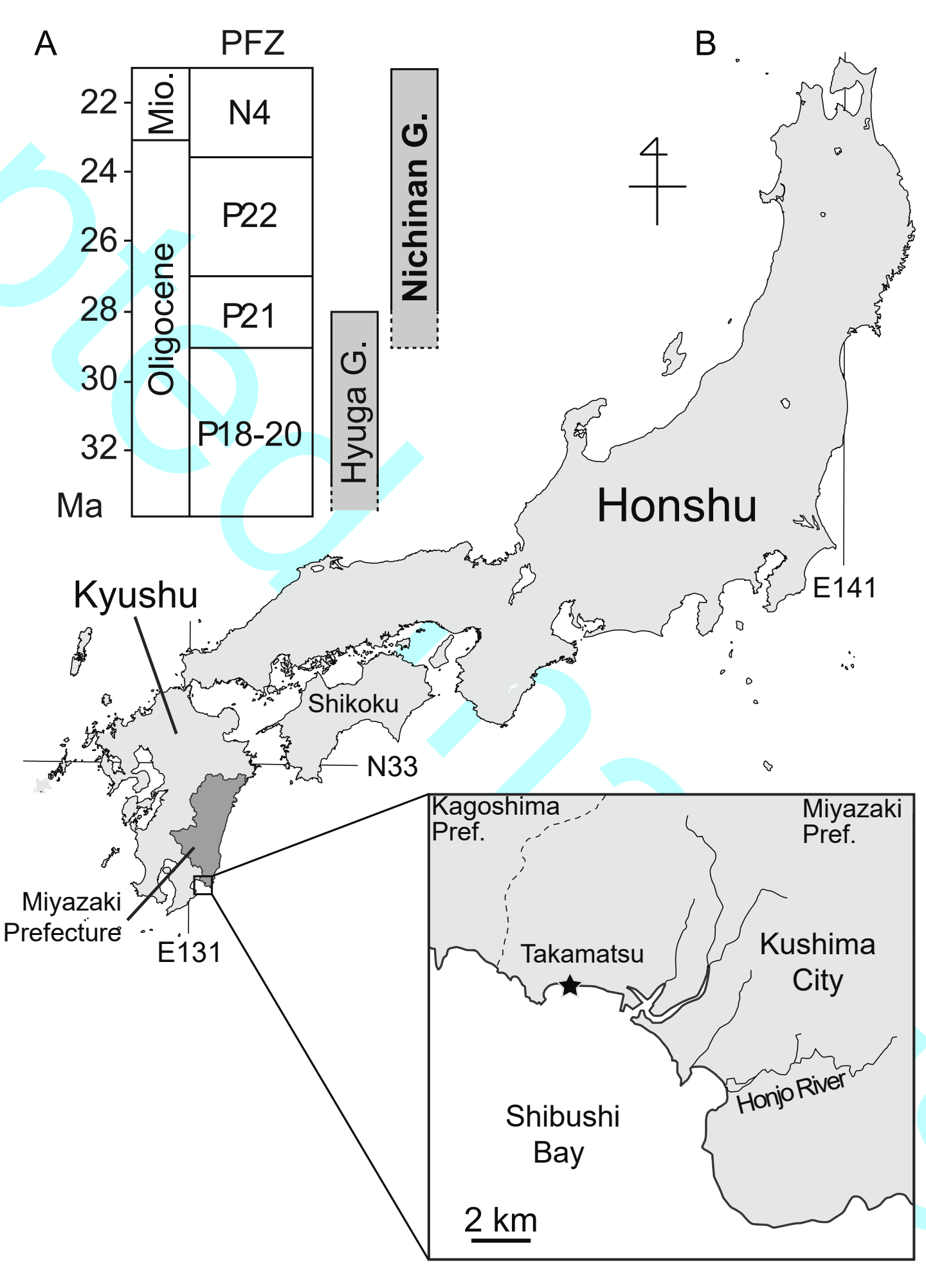
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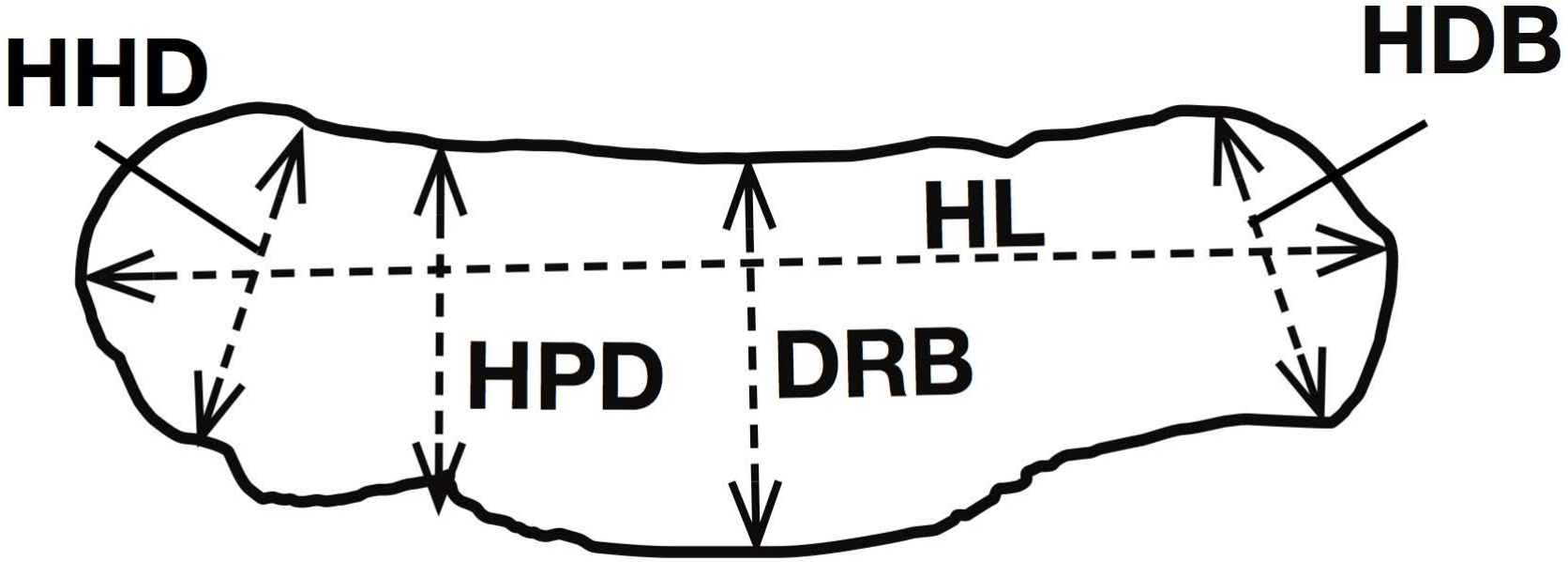
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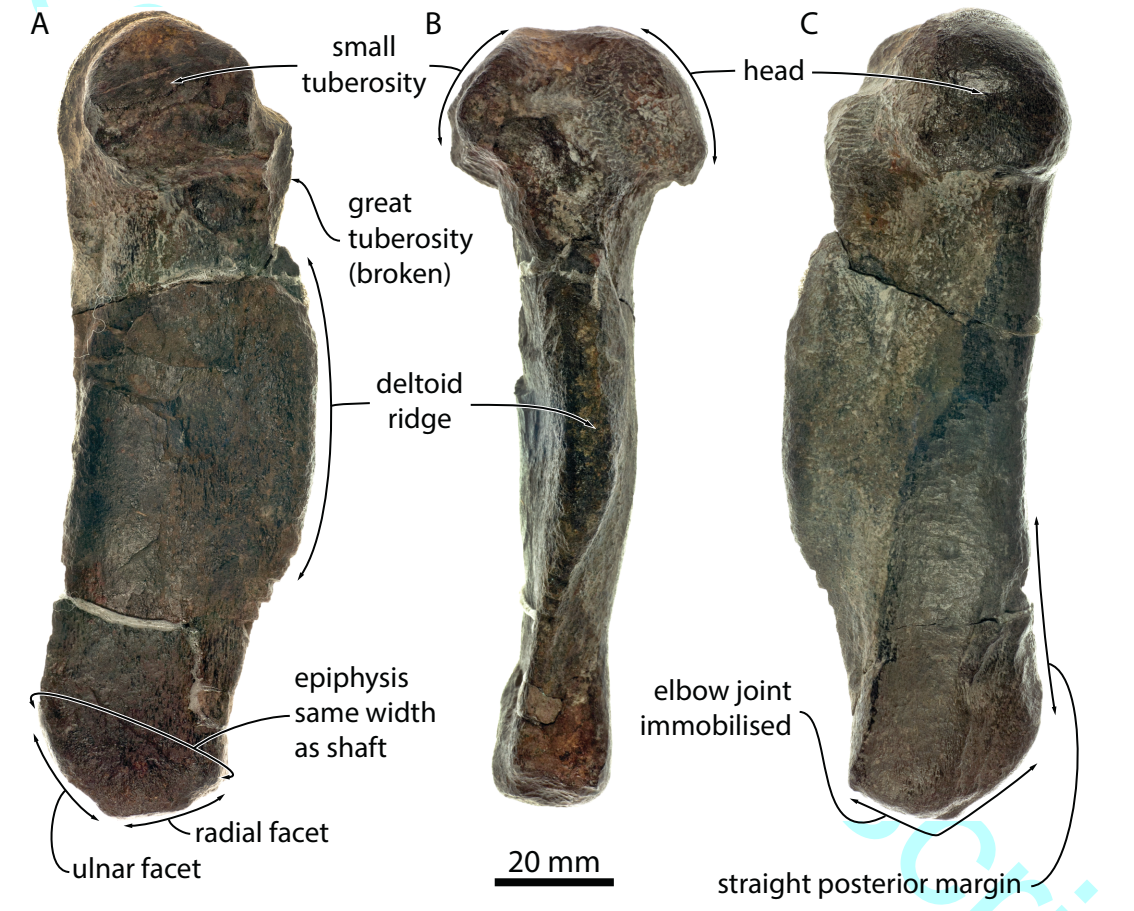
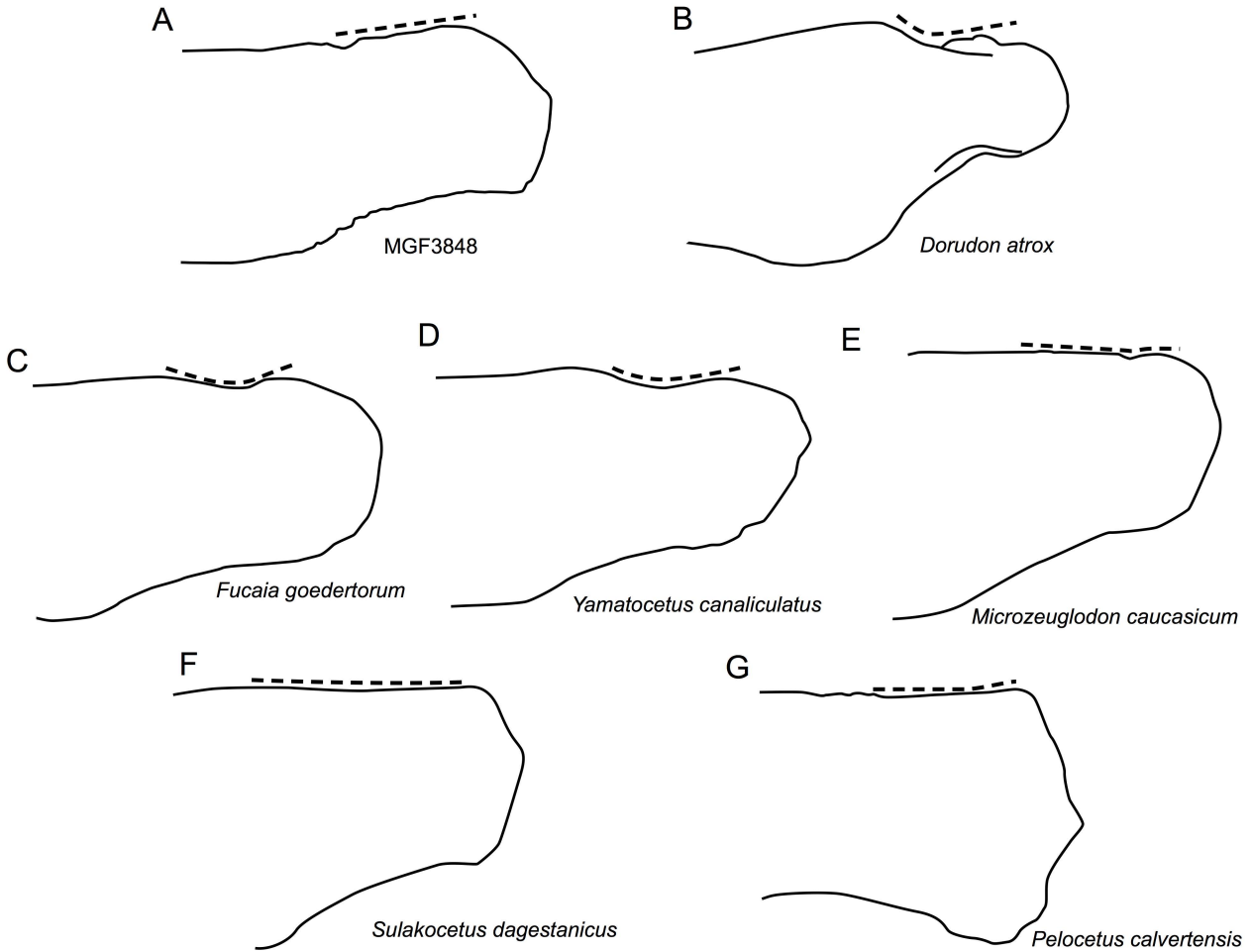
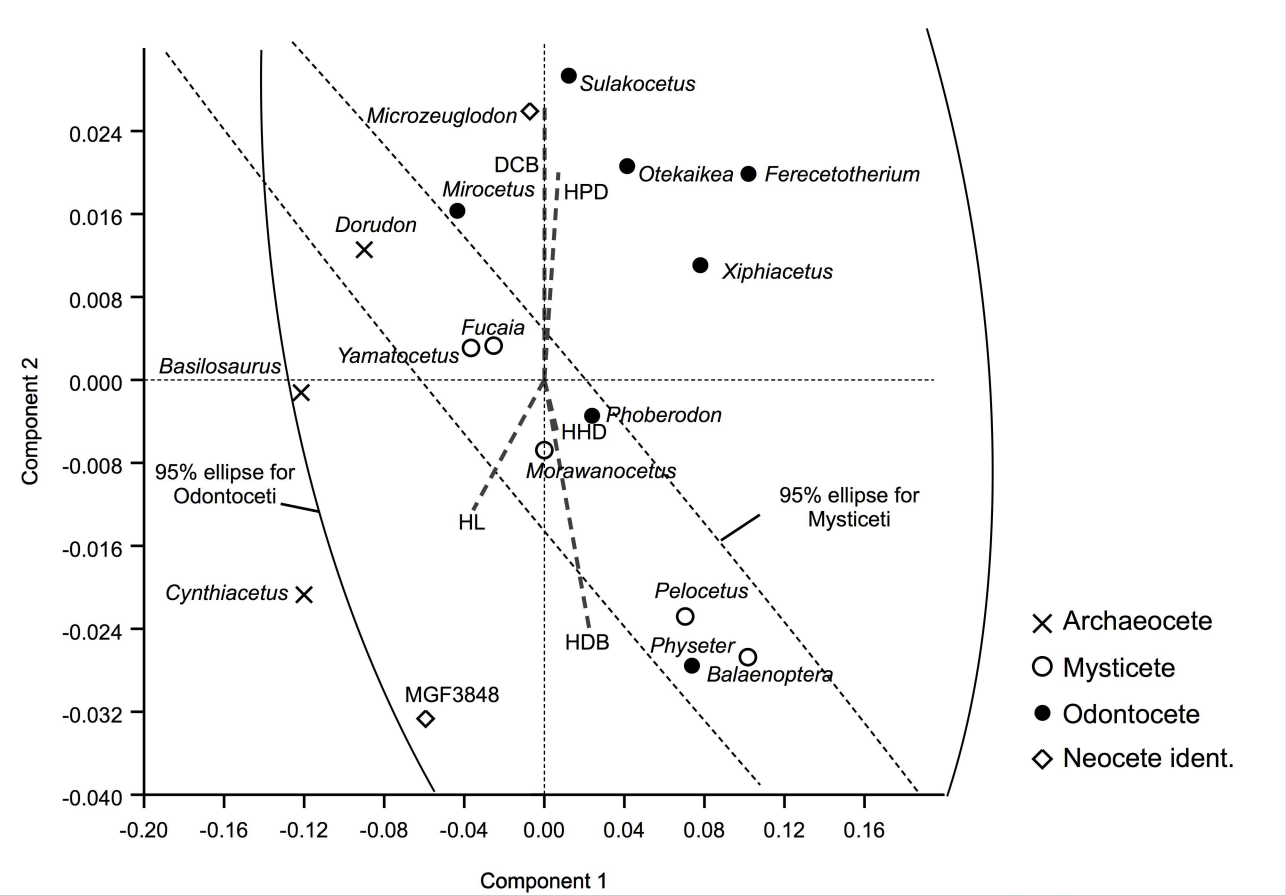

A
B
C
small tuberosity
head
great tuberosity (broken)
deltoid ridge
epiphysis same width as shaft
elbow joint immobilised
radial facet
ulnar facet
20 mm
straight posterior margin


A
MGF3848
B
Dorudon atrox
C
Fucaia goedertorum
D
Yamatocetus canaliculatus
E
Microzeuglodon caucasicum
F
Sulakocetus dagestanicus
G
Pelocetus calvertensis


Sulakocetus
Microzeuglodon
DCB
HPD
Otekaikea
Ferecetotherium
Mirocetus
Dorudon
Xiphiacetus
Fucaia
Yamatocetus
Basilosaurus
Phoberodon
HHD
Morawanocetus
95% ellipse for Odontoceti
95% ellipse for Mysticeti
HL
Cynthiacetus
Pelocetus
HDB
Physeter
Balaenoptera
MGF3848
0.024
0.016
0.008
0.000
-0.008
-0.016
-0.024
-0.032
-0.040
-0.20
-0.16
-0.12
-0.08
-0.04
0.00
0.04
0.08
0.12
0.16
Component 2
Component 1
Archaeocete
Mysticete
Odontocete
Neocete ident.

Taxon	Source	HHD	HPD	HL	DRB	HDB
MGF 3848	direct measurement	0.12	0.13#	0.47	0.15	0.13
Archaeocetes						
Basilosaurus cetoides	Owen (1839)	0.12	0.12	0.52	0.14	0.07
Cynthiacetus peruvianus	Martínez Cáceres and de Muizon	0.13	0.12	0.52#	0.14	0.07
Dorudon atrox	Uhen (2004)	0.12	0.13	0.49	0.18	0.08
Neoceti indet.						
Microzeuglodon caucasicum	Pilleri (1986)	0.14	0.17	0.42	0.17	0.11
Mysticeti						
Balaenoptera brydei	photograph of KMNH VR110,101	0.18	0.14	0.40#	0.17	0.15
Fucaia goedertorum	photograph of LACM 131146	0.14	0.16	0.44	0.15	0.11
Morawanocetus yabukii	direct measurement of AMP 01	0.14	0.15	0.42	0.15	0.13
Pelocetus calvertensis	Kellogg (1965)	0.16	0.15	0.37	0.15	0.18
Yamatocetus canaliculatus	Okazaki (2012)	0.13	0.15	0.45	0.16	0.11
Odontoceti						
Ferecetotherium kelloggi	Mchedlidze (1984)	0.13	0.17	0.33	0.18	0.18
Mirocetus riabinini	Sanders and Geisler (2015)	0.13	0.14	0.45	0.18	0.1
Otekaikea huata	Tanaka and Fordyce (2015)	0.13	0.17#	0.38	0.17#	0.15
Physeter macrocephalus	photograph of KMNH VR110,102	0.16	0.13	0.41	0.13	0.17
Phoberodon arctirostris	Cabrera (1926)	0.13	0.14#	0.4	0.17	0.15
Sulakocetus dagestanicus	Mchedlidze (1984)	0.14	0.17	0.38	0.17	0.14
*Xiphiacetus bossi**	Kellogg (1925)	0.15	0.16	0.35	0.17	0.16

Manuscript

HHD	HPD	HL	DRB	HDB
35	36#	133	40	33

Accepted manuscript