Brief report

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A Late Miocene potential neobalaenine mandible from Argentina sheds light on the origins of the living pygmy right whale

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The origins and evolutionary relationships of the pygmy right whale (*Caperea marginata*), the only living member of the Neobalaeninae, have been the subject of a long-standing debate. This phylogenetic uncertainty is compounded by a limited neobalaenine fossil record. Here, we report a Late Miocene mysticete mandible from Patagonia, Argentina, and provisionally refer it to Neobalaeninae, gen. et sp. indet. The new material represents only the third report of a fossil neobalaenine, and the first fossil occurrence of this lineage in the southwestern Atlantic. It is also the oldest specimen so far reported, thus corroborating the idea of an early divergence time for neobalaenines.

Introduction

The pygmy right whale (*Caperea marginata*) is the most enigmatic of the living baleen whales, and the only member of the Neobalaeninae. Owing to its oceanic habits and restriction to the Southern Hemisphere, little is known about its behaviour, ecology, or life history (Kemper 2009; Kemper et al. 2012). Its origins and phylogenetic position are controversial with some cladistic analyses hypothesising a relationship of *Caperea* with right whales (Balaenidae) (Bisconti 2005, 2012; Steeman 2007; Ekdale et al. 2011; Churchill et al. 2012), while others have placed the species closer to rorquals and grey whales (Balaenopteroidea) (Deméré et al. 2008; McGowen et al. 2009; Steeman et al. 2009; Geisler et al. 2011; Marx 2011) or the extinct cetotheres (Fordyce and Marx 2012; Marx et al. 2013). This phylogenetic uncertainty is compounded by a rather patchy fossil record, comprising just two records from Australia (Fitzgerald 2012) and Peru (Bisconti 2012), as well as undescribed neobalaenine material reported from Angola (Graf et al. 2011). Here, we describe a Late Miocene mysticete mandible from Patagonia, Argentina, and provisionally refer it to Neobalaeninae. The new material represents the oldest known record of this subfamily, and the first formally documented Late Miocene mysticete from Argentina.

Institutional abbreviations.—CNPMAMM, Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; HMN, Hiwa Museum of Natural History, Hiwa, Japan; MGB, Museo Geopalaeontologico G. Capellini Bologna, Italy; MLP, Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; MNHN, Muséum national d'Histoire Naturelle, Paris, France; MPCNyO, Museo Provincial de Ciencias Naturales y Oceanográfico, Puerto Madryn, Chubut, Argentina; MPEF, Museo Paleontológico "Egidio Feruglio", Trelew, Chubut, Argentina; MRSN, Museo Regionale di Scienze Naturali, Torino, Italy; MSM, Museum Sønderjylland, Department of Natural History and Paleontology, Gram, Denmark; MSNTUP, Museo di Storia Naturale e del Territorio, Università di Pisa, Italy; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; NMVP, Museum Victoria Palaeontology Collection, Melbourne, Australia; OM, Otago Museum, Dunedin, New Zealand; OU, Geology Museum, University of Otago, Dunedin, New Zealand; SMNH, Saitama Museum of Natural History, Saitama, Japan; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA;

Geological setting

The mandible described here was preserved lateral side up, and was collected from a fallen block of soft sedimentary rock adjacent to a cliff exposing the Puerto Madryn Formation at Punta Ninfas, southeast coast of Golfo Nuevo, Chubut Province, Argentina (42°58'7" S, 64°18'39.9" W). The Puerto Madryn Formation comprises mostly unconsolidated sands with abundant silt, and represents a transgressive-regressive cycle indicative of a shallow marine environment (Scasso and del Río 1987). Known in the literature as the "Entrerriense" or "Paranense" sea (del Río et al. 2001 and references therein), it flooded a large area of Argentina during Miocene times. A southern branch of this "Entrerriense" sea occupied what is now Península Valdés and the area surrounding the city of Puerto Madryn (Chubut Province) in northeastern Patagonia, where the resulting deposits are part of the Puerto Madryn Formation. Vertebrates are uncommon in the Puerto Madryn Formation, but are generally well preserved and include some relatively complete skeletons of penguins and pinnipeds (Cozzuol 1993, 1996, 2001; Riva Rossi et al. 2000; Acosta Hospitaleche et al. 2007).

^{87}Sr/^{86}Sr dates based on pectinid shells collected from eight correlated coquinas at Península Valdés (Puerto Pirámides, Eje Tentativo and El Doradillo) indicate a Late Miocene age (10 ± 0.3 Ma; early Tortonian) for the Puerto Madryn Formation (Scasso et al. 2001). This estimate corroborates an earlier ^{40}K/^{39}Ar age of 9.41 Ma from volcanic tuff for the uppermost beds of this unit exposed at Bahía Cracker, on the southern coast of the Golfo Nuevo

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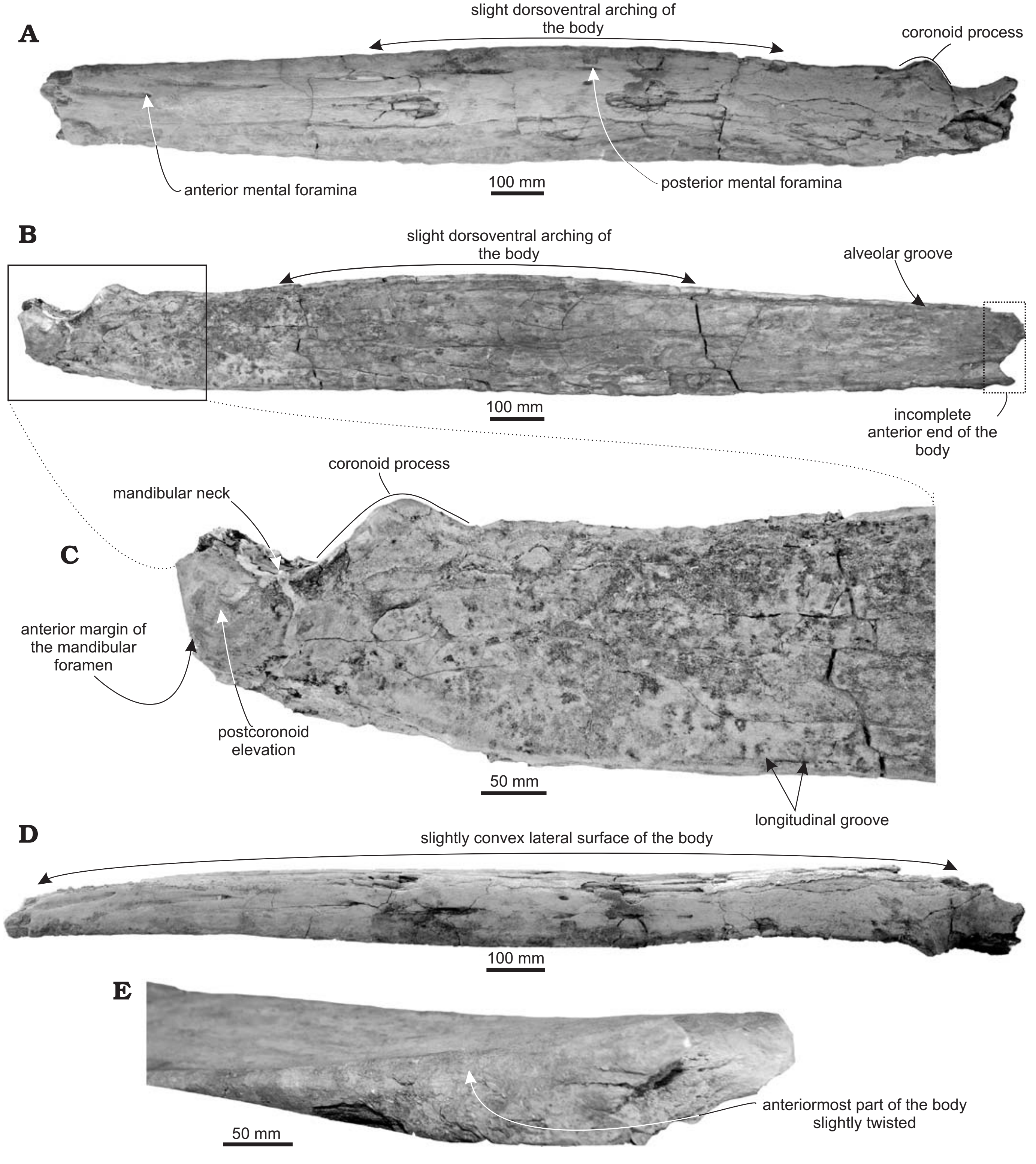

Fig. 1. Left mandible of a fossil neobalaenine baleen whale, gen. et sp. indet. (MPEF-PV2572) from Punta Ninfas Chubut Province, Argentina; Puerto Madryn Formation (Late Miocene). **A**. Lateral view. **B**. Medial view. **C**. Medial view of the posterior region of the mandible showing the morphology of the coronoid process. **D**. Dorsal view of the mandible showing the lateral curvature of the body. **E**. Anteromedial view of the mandible showing the medial torsion of the anteriormost portion of the body.

(Zinsmeister et al. 1981). This locality, near Punta Ninfas, is 40 km to the south and correlates with the uppermost beds of the section at Puerto Pirámides (Scasso and del Río 1987). Finally, the Late Miocene age of Puerto Madryn Formation is further supported by the presence of an "Entrerriense" malacofauna (Martínez and del Río 2002; del Río 2004; on the Tortonian correlation, see Cione et al. 2011: Fig. 2) and palynological data (Palazzesi and Barreda 2004; Barreda and Palazzesi 2007).

Systematic palaeontology

Cetacea Brisson, 1762
Neoceti Fordyce and Muizon, 2001
Mysticeti Gray, 1864
Cetotheriidae Brandt, 1872
?Neobalaeninae Gray, 1873
Gen. et sp. indet.

Figs. 1, 2.

Material.—MPEF-PV2572, left mandible; Punta Ninfas, Chubut Province, Argentina; Puerto Madryn Formation (Late Miocene).

Description.—MPEF-PV2572 (Fig. 1) is a nearly complete left mandible lacking the anterior end of the body, the angular process, and the mandibular condyle. Most of the mandibular condyle was originally preserved in the field (Fig. 2), but later broke and was lost during excavation and preparation. The preserved anteroposterior length of the mandible (measured in a straight line) is +1800 mm.

In cross section, the lateral surface is slightly convex, while the medial surface is nearly flat. In dorsal view, the anteriormost part of the body is slightly twisted in a medial direction, with the ventral border of the body pointing medially. As preserved, the body is almost straight, although burial-related flattening and a break ca. 500 mm anterior to the condyle reduce the original extent of lateral curvature. In lateral view, the body is slightly arched, with the dorsoventral height increasing from 230 mm along the posterior third of the body to 260 mm near its midpoint, before falling to 170 mm towards the anterior end of the mandible. Anterior to the coronoid process, there are five anteriorly opening mental foramina aligned along the dorsolateral surface of the body; of these, the posterior ones are smaller and located more dorsally than the anterior ones (Fig. 1A). One of the most conspicuous characters of the mandible is the small, but distinct, coronoid process. The latter is bluntly triangular, longer anteroposteriorly (110 mm) than high dorsoventrally (40 mm), and located near the dorsal crest of the mandible. The transversely thick (ca. 43 mm) anterior margin of the coronoid process (length = 47 mm) rises gradually and is oriented laterally, while the thin posterior margin (length = 71 mm) descends more abruptly and is oriented medially. Posterodorsally, the dorsal border of the mandibular neck between the posterior margin of the coronoid process and the anteriormost point of the mandibular condyle measures 180 mm and is strongly concave both laterally and dorsally. Based on observations of the specimen in the field, the condyle was directed posterodorsally, with its dorsal edge dorsoventrally elevated above the level of the dorsal edge of the coronoid process. The dorsal edge of the mandibular neck running up to the condyle forms an obtuse angle with the longitudinal axis of the body of the mandible (Fig. 2). This position of the condyle does not seem to be the result of distortion related to burial.

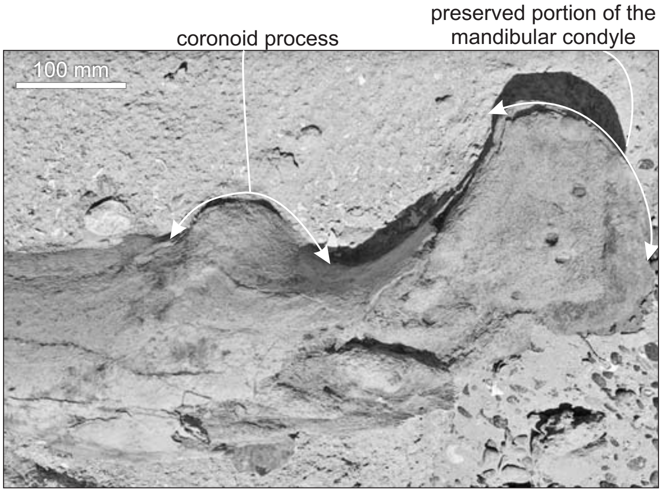

Fig. 2. Left mandible of a fossil neobalaenine baleen whale, gen. et. sp. indet. (MPEF-PV2572) from Punta Ninfas, Chubut Province, Argentina; Puerto Madryn Formation (Late Miocene), showing the mandibular condyle as preserved in the field prior to excavation.

In medial view, a small portion of the alveolar groove is evident along the anterodorsal margin of the mandible. The symphyseal surface is not preserved. On the posteromedial surface of the body, near the ventral margin, there is a short (length = 105 mm), well-defined longitudinal groove, which comes to an abrupt end anteriorly (Fig. 1C). Posterior to the coronoid process, and close to the dorsal margin of the ramus, there is a rounded, inward elevation (postcoronoid elevation sensu Kimura 2002) (Fig. 1C). The medial surface of the ramus at the level of the coronoid process is slightly dorsoventrally concave. The mandibular foramen (height = 86 mm; transverse width = +75 mm) lies entirely posterior to the coronoid process, and is separated from the latter by a horizontal distance of 160 mm. Judging from observations made in the field, the anterior margin of the mandibular foramen was located close to the mandibular condyle. The anterior margin of the mandibular foramen is poorly preserved, but seems to have been roughly semicircular in medial view.

Comparisons.—MPEF-PV2572 differs from all described living and fossil mysticetes except *Caperea* and some eschrichtiids (see below) in its dorsoventrally arched body and low, bluntly triangular coronoid morphology. In adults of living balaenids, such as *Eubalaena* spp. (MLP 1508, USNM 504886,), the coronoid process is greatly reduced and evident only as a low, albeit robust, crest. By contrast, *E. australis* juveniles (CNPMAMM 747, 748) an undescribed fossil balaenid mandible from Argentina (MLP 5-21), originally identified as *Morenocetus parvus* by Cabrera (1926), do preserve a more distinct coronoid process (SOM: fig. S1 in Supplementary Online Material available at http://app.pan.pl/SOM/app59-Buono_etal_SOM.pdf); however, the latter is low, broad-based and plate-like, and thus clearly different from the triangular structure of MPEF-PV2572 (Marx et al. 2013). The coronoid process is high and steep-sided or finger-like in *Mauicetus parki* (OU 22545), balaenopterids (e.g., *Balaenoptera* spp., MSNTUP M250, M260, CNPMAMM 750; "*Megaptera*" *hubachi*, MB Ma28570; *Megaptera novaeangliae* NMNS M33734) and some Miocene "cetotheres" of uncertain affinity (e.g., *Aglaocetus moreni*, MLP 5-14; *Diorocetus*

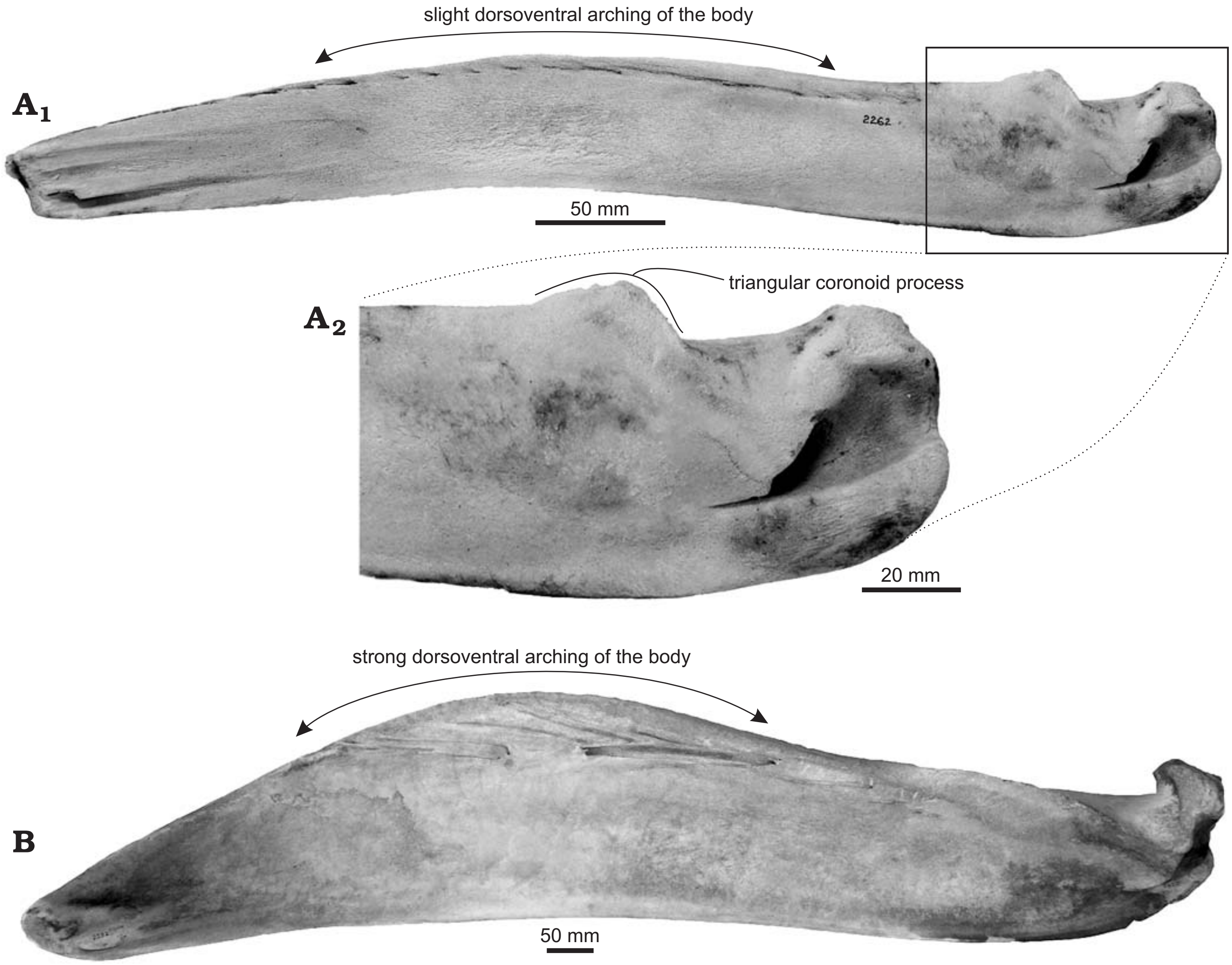

Fig. 3. Right mandible of the living pygmy right whale *Caperea marginata* Gray, 1846 from Northland, North Island, New Zealand. **A**. Medial views of a juvenile mandible (NMNZ MM002262) showing slight dorsoventral arching of the body (A_1) and details of the morphology of the coronoid process (A_2). **B**. Medial view of an adult mandible (NMNZ MM002232) showing strong dorsoventral arching of the body.

spp., SMNH VeF68, USNM 23494; *Parietobalaena* spp., HMN F00044, USNM 11535; *Pelocetus calvertensis*, USNM 11976; *Titanocetus*, MGB 1CMC1729073; *Uranocetus*, MSM p813) (SOM: fig. S1), unlike the relatively low and long coronoid of MPEF-PV2572. The coronoid process of Cetotheriidae (e.g., *Piscobalaena*, MNHN SAS1618; see Boessenecker [2011] for herpetocetines) resembles that of MPEF-PV2572, but is generally longer anteroposteriorly and marked by a laterally bent apex (SOM: fig. S1).

MPEF-PV2572 further differs from all balaenids in having a relatively straight, rather than laterally bowed, mandibular body (even when post-depositional deformation is taken into account), and in lacking a clearly developed mylohyoidal sulcus developed along the length of the mandible. Although MPEF-PV2572 has a short sulcus in roughly the same position as the mylohyoidal sulcus of balaenids, in the latter the sulcus originates from the anteroventral border of the mandibular foramen and runs anteriorly along the inside of the body for at least half the length of the mandible or more.

MPEF-PV2572 differs from *Aglaocetus moreni*, *Diorocetus* spp., *Mauicetus parki*, *Parietobalaena* spp., *Pelocetus*, *Titanocetus*, *Uranocetus* and balaenopterids in having the articular surface of the mandibular condyle directed posterodorsally (SOM: fig. S1). In addition, MPEF-PV2572 differs from balaenopterids in its evenly-curved, rather than sigmoidal, dorsal outline of the mandible (on which, see Deméré et al. 2005), and from *Aglaocetus moreni*, *Diorocetus* spp., *Parietobalaena* spp., and *Uranocetus* in having the anterior border of the mandibular foramen located posterior to the level of the apex of the coronoid process.

MPEF-PV2572 shares a dorsoventrally arched body with both *Caperea marginata* (MPCNyO 817.2, NMNZ MM002232, MM002235) and *Eschrichtius robustus* (USNM 364975). It further shares a long and low, bluntly triangular coronoid process with the extinct eschrichtiid *Eschrichtioides gastaldii* (MRSN PU13802) and the extant *E. robustus*, although in the latter the coronoid is considerably lower and less well defined (SOM: fig. S1). However, MPEF-PV2572 differs from all de-

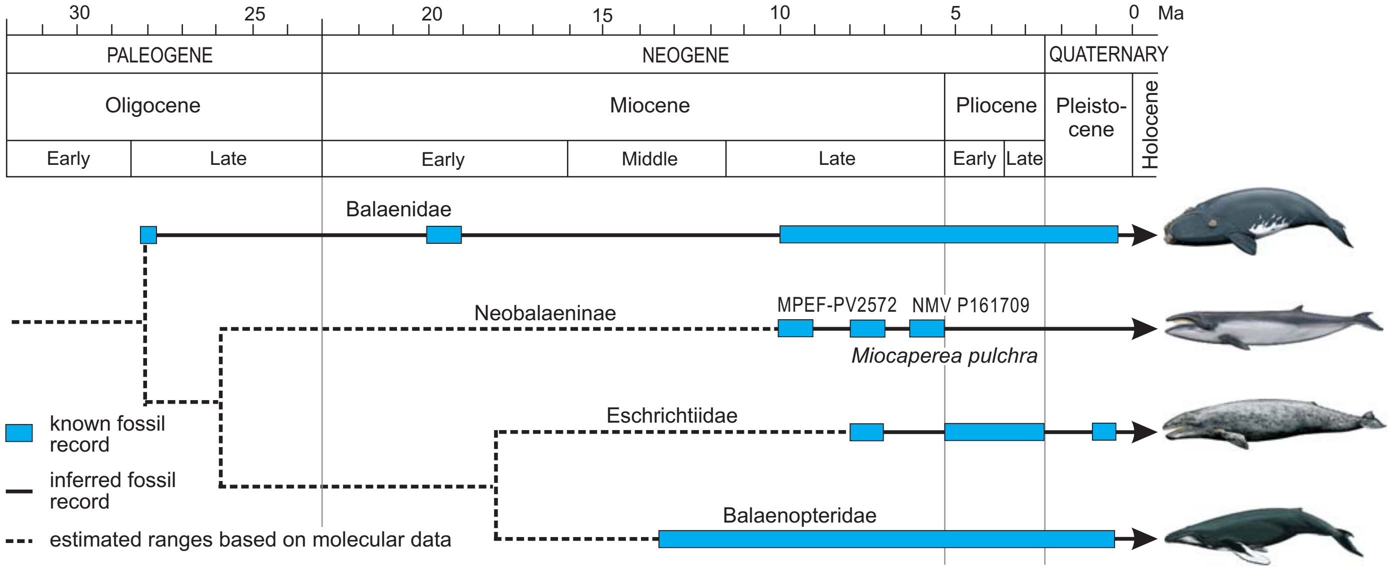

Fig. 4. Phylogeny, stratigraphic range, and divergence times of extant mysticete families (modified from Fitzgerald 2012). Illustrations of whales are by Carl Buell.

scribed eschrichtiids in having the anterior border of the mandibular foramen located close to the posterior border of the condyle, as well as in the lack of a satellite process (see Bisconti and Varola 2006).

The coronoid morphology of MPEF-PV2572 differs from that of adult *C. marginata* (NMNZ MM002232), in which the coronoid is almost absent, but is virtually identical to that of *C. marginata* juveniles (NMNZ MM002262) (Fig. 3). In addition, MPEF-PV2572 resembles *C. marginata* in having the anterior border of the mandibular foramen located close to the mandibular condyle, and in the occasional presence of a sulcus (of uncertain function) near the posteroventral margin of the mandible (e.g., NMNZ MM002232). MPEF-PV2572 differs from *C. marginata* in its larger size and lesser degree of dorsoventral arching, although it should be noted that the arching of the body is only slightly developed in *C. marginata* juveniles (e.g., NMNZ MM002262) (Fig. 3A).

Based on the combination of a dorsoventrally arched body, the bluntly triangular coronoid process and the posterior location of the mandibular foramen, we provisionally refer MPEF-PV2572 to Neobalaeninae gen. et sp. indet. (Fig. 4), pending the future discovery of more complete specimens.

Concluding remarks

The similarity of the coronoid process of MPEF-PV2572 with that of juvenile *C. marginata* is striking, as are the clear differences between the coronoid morphology of the present specimen and juvenile balaenids. Based on the combination of this and the other features shared by MPEF-PV2572 and *C. marginata*, we suggest that the juvenile coronoid morphology of the living pygmy right whale genuinely reflects the ancestral condition of the lineage (see also Marx et al. 2013). However, the fragmentary nature and uncertain taxonomic assignment of MPEF-PV2572 means that any conclusions derived from its study must be tentative. Furthermore, the disparate morphology of living balaenids and *C. marginata*—the only extant neobalaenine—makes direct comparisons difficult.

At an age of 10 Ma (early Tortonian), MPEF-PV2572 predates other occurrences of fossil neobalaenines from the Late Miocene of Peru (Bisconti 2012) and Australia (Fitzgerald 2012) by at least 2 Myr, thus corroborating the idea of an early divergence time for neobalaenines (McGowen et al. 2009; Steeman et al. 2009) (Fig. 4). Furthermore, at a length of more than 1800 mm, MPEF-PV2572 is considerably larger than *C. marginata* (ca. 1150–1200 mm, based on MPCNyO 817.2 and OM VT227), as well as *Miocaperea pulchra*, which Bisconti (2012) reported as comparable to or slightly smaller than modern *C. marginata*. A similar discrepancy in size has been reported for a fragmentary Late Miocene neobalaenine periotic from Australia, which Fitzgerald (2012) reported to be about 30% larger than the equivalent structure in *C. marginata*. Together, these specimens indicate that archaic neobalaenines may have included species larger than the living pygmy right whale.

All neobalaenine fossils described to date are from the Southern Hemisphere, despite the fact that most of the Northern Hemisphere has been more intensively sampled (Uhen and Pyenson 2007; Uhen 2013). Including our own material, fossil neobalaenines have now been found to occur in both the southwestern and southeastern Pacific (Fitzgerald 2012; Bisconti 2012) and the southwestern and southeastern Atlantic (Graf et al. 2011; this study). With the exception of the Indian Ocean, for which fossil sampling is generally poor (Uhen 2013), this geographic distribution matches that of living *C. marginata* as summarised by Kemper (2009), indicating that neobalaenines have occupied Southern Hemisphere waters for as much as 10 Myr. This stratigraphic distribution, and the lack of reported neobalaenines from well-studied Northern Hemisphere sequences, is consistent with a possible austral origin of the *Caperea* lineage.

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