

## A PLIOCENE GRAY WHALE (*ESCHRICHTIUS* SP.) FROM THE EASTERN NORTH ATLANTIC

CHENG-HSIU TSAI<sup>1</sup>, ALBERTO COLLARETA<sup>2,3,\*</sup> & MARK BOSSELAERS<sup>4,5</sup>

<sup>1</sup>Department of Life Science and Institute of Ecology and Evolutionary Biology, National Taiwan University, No. 1, Sec. 4, Roosevelt Rd., Taipei, 1617, Taiwan. E-mail: whaletsai@ntu.edu.tw; craniata@gmail.com

<sup>2\*</sup>Corresponding author. Dipartimento di Scienze della Terra, Università di Pisa, via Santa Maria 53, 56126 Pisa, Italy. E-mail: alberto.collareta@unipi.it.

<sup>3</sup>Museo di Storia Naturale, Università di Pisa, via Roma 79, 56011 Calci, Italy.

<sup>4</sup>Koninklijk Belgisch Instituut voor Natuurwetenschappen, Operationele Directie Aarde en Geschiedenis van het Leven, Vautierstraat 29, Brussel, Belgium. E-mail: mark.bosselaers@telenet.be.

<sup>5</sup>Koninklijk Zeeuwsch Genootschap der Wetenschappen, Kousteensedijk 7, 4331 JE, P.O. Box 378, 4330 AJ Middelburg, The Netherlands.

To cite this article: Tsai C.-H., Collareta A. & Bosselaers M. (2020) - A Pliocene gray whale (*Eschrichtius* Sp.) from the Eastern North Atlantic *Riv. It. Paleontol. Strat.*, 126(1): 189-196.

**Keywords:** Cetacea; Mysticeti; Eschrichtiidae; evolution; paleobiogeography; Lillo Formation; Belgium; North Sea.

**Abstract.** The gray whale *Eschrichtius robustus*, the only living member of the eschrichtiid lineage, currently inhabits only the North Pacific. Interestingly, however, the holotypes of both *E. robustus* and the late Miocene *Archaeschrichtius ruggieroi* (the oldest known eschrichtiid species) come from the North Atlantic and the Mediterranean, respectively. Here we describe a partial mysticete mandible from the Pliocene (3.71–2.76 Ma) of Belgium (Eastern North Atlantic). This new fossil displays a combination of morphological features that makes it nearly identical to modern *E. robustus*. Nevertheless, given its incomplete nature, the studied specimen is here identified in open nomenclature as belonging to *Eschrichtius* sp. The recognition of such an early record of *Eschrichtius* in the North Atlantic suggests that this genus developed a circum-Northern Hemisphere distribution not later than in Pliocene times, thus complicating our understanding of its origin, evolutionary history, and palaeobiogeographic patterns.

## INTRODUCTION

Nowadays, the gray whale *Eschrichtius robustus* (Lilljeborg, 1861) (the only living representative of the mysticete family Eschrichtiidae) solely inhabits the North Pacific (e.g., Wilson & Mittermeier 2014; Swartz 2018). Until the 18<sup>th</sup> century, however, *E. robustus* used to occur in the North Atlantic as well (e.g., Post 2005; Aaris-Sørensen et al. 2010; Garrison et al. 2019, and references therein), its regional extinction likely having resulted from whaling activity (Mead & Mitchell 1984). The North Atlantic (hereinafter regarded as including the Mediterranean cul-de-sac) is not only home to the holotype of

extant *E. robustus*, but also the region where the geologically oldest eschrichtiid species, *Archaeschrichtius ruggieroi* Bisconti & Varola, 2006 from the late Miocene of Italy, was found. That said, the fossil record of *Eschrichtius* Gray, 1864b that demonstrates its origin and evolutionary history appears to have been mostly recovered from North Pacific sites (e.g., Barnes & McLeod 1984; Ichishima et al. 2006; Tsai et al. 2014; Tsai & Boessenecker 2015).

Here, we report on a partial mandible from the Pliocene of Belgium whose morphology is strongly reminiscent of that observed in extant juveniles of *Eschrichtius*. In spite of their fragmentary nature, incomplete and isolated fossil remains of baleen-bearing whales have often provided new valuable information on several aspects of the life history (Clementz et al. 2014), origin and extin-

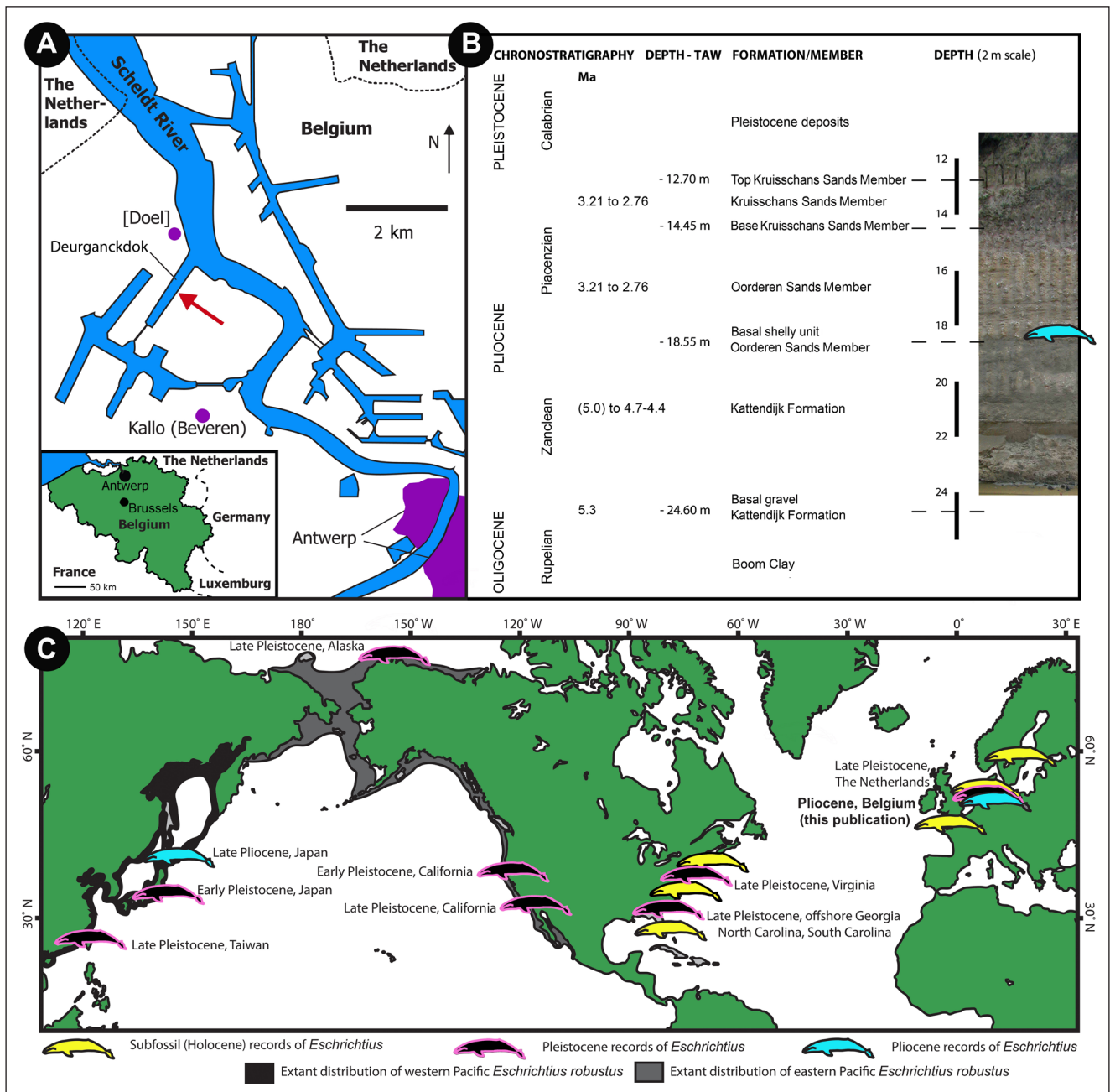


Fig. 1 - The geographic setting (A) and geological horizon (B) of the finding site of IRSNB M 2316, partially preserved right mandible of *Eschrichtius* sp. from the Pliocene of Belgium, and its collocation in the broader framework of the global distribution of living and fossil *Eschrichtius* (C). The red arrow in panel A indicates the finding site (Deurganckdok). The whale silhouette in panel B indicates the stratigraphic position of IRSNB M 2316, in the upper portion of the basal shelly unit of the Oorderen Sands Member of the Lillo Formation, about 22 m below the main level of the sea at Ostend at low tide (TAW: Tweede Algemene Waterpassing; see text for explanation). Repartition of the Deurganckdok deposits in formations and members as shown in panel B follows Louwe et al. (2004). The absolute ages of deposition of the Kattendijk Formation, Oorderen Sands member, and Kruisschans Sands member presented in panel B are reported from De Schepper et al. (2009). The labels in panel C refer to the pre-Holocene occurrences of *Eschrichtius* (data sources: Tsai & Boessenecker 2015; Kimura et al. 2018; this work). Panels A and B adapted and modified from Bisconti & Bosselaers (2016); panel C adapted and modified from Tsai & Boessenecker (2015).

ction (Tsai & Boessenecker 2017), regional diversity (Boessenecker 2013), breeding sites (Tsai 2017), anatomical features (Fitzgerald 2012), and survival of clades (Boessenecker & Fordyce 2017) in past mysticete communities and lineages. Similarly, the

new eschrichtiid specimen described herein from the Pliocene of Belgium (Fig. 1) represents a noteworthy fossil whose geological age is comparable to that of the previously oldest known occurrence of *Eschrichtius* from the North Pacific (Ichishima et

al. 2006); as such, it suggests that *eschrichtiids* developed a circum-Northern Hemisphere distribution before the Pleistocene, thus evoking a complex history for the emergence and evolution of *Eschrichtius*.

**Institutional abbreviations:** ECOMARE: Vonk collection at Museum Ecomare, De Koog, Texel, The Netherlands; IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NMR: Natuurhistorisch Museum Rotterdam, Rotterdam, The Netherlands.

## SYSTEMATIC PALEONTOLOGY

**CETACEA** Brisson, 1762

**MYSTICETI** Gray, 1864a

*Eschrichtiidae* Ellerman & Morrison-Scott, 1951

*Eschrichtius* Gray, 1864b

*Eschrichtius* sp.

Fig. 2A–F, H, J

**Material:** IRSNB M 2316, a partially preserved right mandible. It includes the middle part of the horizontal ramus of the mandible, with the dorsal and ventral margins preserved, as well as mental and gingival foramina. Bioerosion scars (*Anellusichnus* Santos, Mayoral & Muñiz, 2005) due to the attachment of sessile acorn barnacles are common all over the cortical surface of the bone, evoking the permanence of the IRSNB M 2316 on a relatively shallow seafloor prior to burial [see e.g. Coletti et al. (2018) for a general interpretation of barnacle-rich Neogene deposits]. Measurements of IRSNB M 2316 are as follows: maximum preserved length, 284 mm; maximum preserved width, 52 mm; maximum preserved height, 110 mm.

### Geographical and geological setting.

IRSNB M 2316 was found along the southwestern border of the Deurganckdok tidal dock (geographic coordinates of the discovery site: N 51°17'23", E 4°15'48"), during harbor expansion at the port of Antwerp (Flanders, Belgium; Fig. 1A), at a depth of about 18.5 m below the Tweede Algemene Waterpassing (TAW). TAW stands for the standardized (rectified) second general water level (main level of the sea at Ostend at low tide). The stratigraphic horizon of the finding is located in the upper portion of the basal shelly unit (*sensu* Louwe et al. 2004) of the Oorderen Sands Member of the Lillo Formation, which marks the contact with the underlying Kattendijk Formation (Fig. 1B). The deposition of this horizon has been referred to the 3.21–2.76 Ma time span (i.e., early to mid Piacenzian, Late Pliocene) via the integration of dinoflagellate cyst biostratigraphy and sequence stratigraphy

(De Schepper et al. 2009). However, a large fraction of the siliciclastic and bioclastic material that comprises the basal shelly unit of the Oorderen Sands Member seemingly originates from reworking of the Luchtbal Sands Member, a geologically older unit that has not been detected at the finding site, the deposition of which appears to have occurred between 3.71 Ma and 3.21 Ma (De Schepper et al. 2009). Considering the fragmentary nature of IRSNB M 2316, as well as its aforementioned bioeroded appearance, reworking of this specimen from the Luchtbal Sands Member cannot be ruled out. Therefore, we conservatively propose a geological age of 3.71–2.76 Ma (i.e., late Zanclean to mid-Piacenzian, mid-Pliocene) for the cetacean fossil studied herein.

Detailed information on the deposits exposed at the finding locality has been provided by Louwe et al. (2004), Lambert & Gigase (2007), De Schepper et al. (2009), Colpaert et al. (2015), Bisconti & Bosselaers (2016), and Bisconti et al. (2017).

### Taxonomic identification and descriptive remarks.

IRSNB M 2316 displays a combination of morphological characters that makes this specimen nearly identical to *Eschrichtius robustus* (Fig. 2G, I), namely: 1) the laterodorsal surface of the preserved portion of the mandible is flattened to gently concave; 2) the preserved portion of the mandible is weakly bowed dorsally (i.e., it forms a slight dorsoventral arc); 3) the maximum value of transverse width of the dentary is observed in the lower half of the bone; 4) the mental foramina are elongated and sharply pointed posteriorly; 5) the orientation of the mental foramina changes along the mandible, with the posterior ones being more anterodorsally oriented than the anterior ones; 6) a weak mylohyoidal depression, instead of either a deep mylohyoidal sulcus (as in Balaenidae) or no cavity at all (as in Balaenopteridae), is present along the medioventral margin of the dentary; and 7) the disposition of the mental foramina depicts an arched line in lateral view, with the middle ones being slightly more dorsal than the peripheral ones (Fig. 2A–F). In particular, the combination of slight lateral and dorsoventral arcs with a weak mylohyoidal depression compares favorably with extant gray whale dentaries and is not observed in members of either balaenids, balaenopterids and neobalaenids.

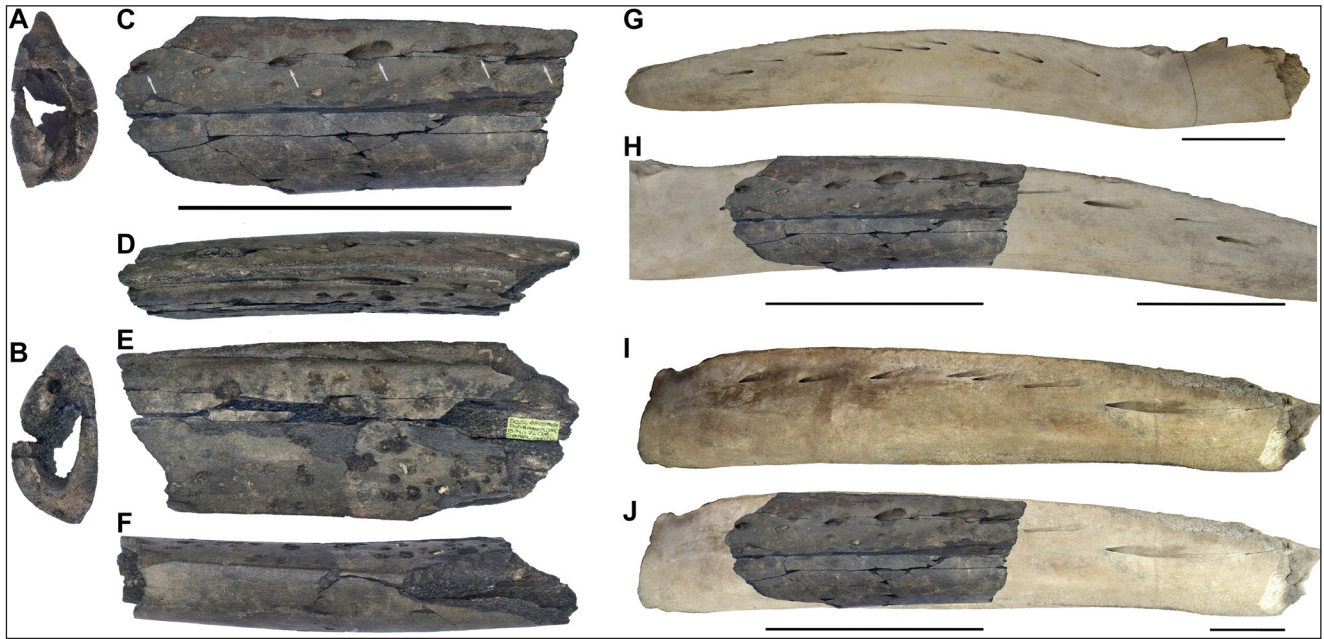


Fig. 2 - IRSNB M 2316, partially preserved right mandible of *Eschrichtius* sp. from the Pliocene of Belgium (panels A–F, H, J), and mandibles of juvenile and adult individuals of the extant species *Eschrichtius robustus* (panels G–J). A) posterior view of IRSNB M 2316; B) anterior view of IRSNB M 2316; C) lateral view of IRSNB M 2316, with superimposed arrows for highlighting the mental foramina; D) dorsal view of IRSNB M 2316; E) medial view of IRSNB M 2316; F) ventral view of IRSNB M 2316; G) lateral view of NMR 9991-1783, left mandible of a juvenile extant individual of *E. robustus*; H) close-up on a mirrored image of panel G, with a superimposed enlarged lateral view of IRSNB M 2316; I) lateral view of ECOMARE B2 492, subfossil right mandible of an adult individual of *E. robustus* from the Southern Bight (southern North Sea); J) the same as panel I, with a superimposed enlarged lateral view of IRSNB M 2316. The scale bar on the left side of the figure refers to panels A to F; the scale bars at the right margin of the figure refer to the modern mandibles depicted in panels G to J; the scale bars on the left part of panels G and I refer to the enlarged lateral views of IRSNB M 2316 superimposed therein. All the scale bars equal 20 cm.

Of note, a mylohyoidal depression or faint sulcus variably occurs in fossil and extant eschrichtiids (Bisconti & Varola 2006; Bisconti 2008; Garrison et al. 2012) and appears to be to some extent comparable to that of Balaenidae (e.g., Bisconti & Varola 2006; Marx & Fordyce 2015). Morphological similarities are particularly strong between IRSNB M 2316 and NMR 9991-1783, a juvenile individual of *Eschrichtius robustus* (Fig. 2G, H). Furthermore, IRSNB M 2316 also exhibits some features that seemingly distinguish it from the adult specimens of extant *Eschrichtius* (Fig. 2I, J), namely: 1) the overall small size of the bone; 2) the medial surface of the dentary being only gently concave; 3) the cross-section of the horizontal ramus being sub-oval rather than roughly D-shaped; and 4) the weaker dorsoventral bending of the bone. As IRSNB M 2316 is nearly identical to NMR 9991-1783 (Fig. 2H), the above differences between the former and the adults of the only living species of *Eschrichtius* (Figs. 2J; 3) might reasonably be interpreted as due to a juvenile ontogenetic stage of the Deurganckdok specimen. Besides, IRSNB M 2316 is most likely not a newborn, as the bone does

not show any sign of sponginess or incompletely ossified surfaces. Based on these considerations, and taking into account the incomplete nature of the Pliocene fossil described herein, we conservatively identify IRSNB M 2316 in open nomenclature as belonging to *Eschrichtius* sp.

## DISCUSSION AND CONCLUDING REMARKS

The fossil mysticete mandible IRSNB M 2316 from the Pliocene of Belgium closely matches the extant *Eschrichtius* in morphology, thus evoking the presence of phenetically modern eschrichtiids in the North Atlantic realm as early as *c.* 3.71–2.76 Ma. Prior to this find, the oldest record of *Eschrichtius* came from the Late Pliocene of Hokkaido, Japan, along the Northwestern Pacific margin (Ichishima et al. 2006) (Fig. 1C). The geological age of our specimen is therefore comparable to that of the Hokkaido fossil, strongly suggesting a circum-Northern Hemisphere distribution for *Eschrichtius* prior to the Pleistocene. Fossil eschrichtiid genera

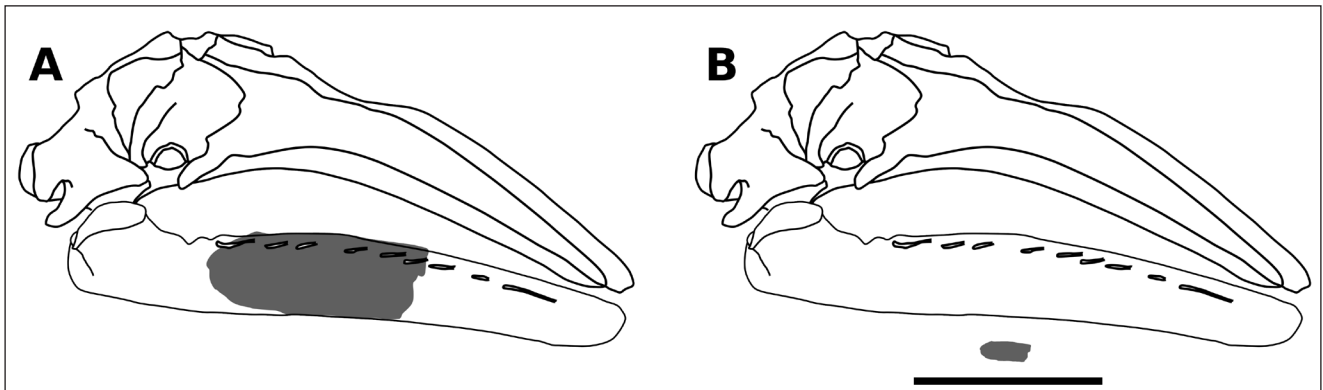


Fig. 3 - A) Line drawing of a cranium and mandible of *Eschrichtius* in right lateral view (the gray-shaded area represents the bone portions preserved in the Pliocene Belgian specimen IRSNB M 2316); B) size comparison between the cranium and mandible of an average full-grown extant individual of *Eschrichtius robustus* (line drawing) and the partially preserved fossil right mandible IRSNB M 2316. The scale bar for panel B equals 1 m.

also include the early late Miocene (i.e., Tortonian) *Archaeschrichtius* Bisconti & Varola, 2006 from the Mediterranean, the Early Pliocene *Eschrichtioides* Bisconti, 2008 from the Mediterranean, and the Early Pliocene *Gricetoides* Whitmore and Kaltenbach, 2008 from the western North Atlantic. Although various analyses have attempted to assess the phylogenetic relationships between the above genera and extant *Eschrichtius* (e.g., Boessenecker & Fordyce 2015; Marx & Fordyce 2015; Bisconti & Bosselaers 2016), the origin and evolutionary history of *Eschrichtius* remain only partly deciphered so far. Indeed, the overall paucity and poor preservation state of fossil *Eschrichtius* specimens worldwide still preclude a comprehensive understanding of which species is the precursor of extant gray whales (see e.g. Tsai & Fordyce 2015 for the proposal of an ontogenetic clade to recognize the ancestry of modern baleen whales) or how *Eschrichtius* survived as the sole relict species of the eschrichtiid lineage (see Pyenson & Lindberg 2011 for a discussion on feeding mode shifts as a tool for Pleistocene survival). With the three extinct genera of eschrichtiids (*Archaeschrichtius*, *Eschrichtioides*, and *Gricetoides*) all being found in the North Atlantic, the occurrence of a Pliocene fossil of *Eschrichtius* (represented by IRSNB M 2316) in Belgium evokes a North Atlantic setting for the origin of *Eschrichtius*.

The discovery of IRSNB M 2316 also stimulates further conjectures about the evolutionary history of *Eschrichtius*. Until very recent times, *Eschrichtius* was regarded as a monotypic genus, only including the extant species *Eschrichtius robustus*. Kimura et al. (2018) recently described *Eschrichtius*

*akishimaensis* Kimura, Hasegawa & Kohno, 2018 from the Early Pleistocene of Japan (Fig. 1C), thus hinting to a more complex evolutionary path following the origin of *Eschrichtius*. If *Eschrichtius* really originated in the North Atlantic, then a currently undescribed species of *Eschrichtius* might have dispersed through the Arctic Ocean into the Pacific, eventually giving rise to the extant *E. robustus* and the extinct *E. akishimaensis*. This interpretation might be supported by the presence of *Eschrichtius* in the Pleistocene of Alaska (Repenning 1983), but more finds of well-preserved material are needed to confirm or disprove our hypothesis. In addition, the presence of *Eschrichtius* in the Pliocene of Belgium also raises the issue of species longevity. The exact time span of species is scarcely discussed for mysticetes and, more in general, for all cetaceans, and the same can be said for the longevity of higher taxonomic ranks such as genera. This issue involves evolutionary rates, which might range within an extremely broad spectrum. For example, diversity and growth patterns suggest that the balaenopterids (i.e., *Balaenoptera* Lacépède, 1804 and *Megaptera* Gray, 1846) are characterized by a fast evolutionary rate, whereas it is much slower in the neobalaenid *Caperea* Gray, 1864a (a possible relict cetotheriid; Fordyce & Marx 2012; Marx & Fordyce 2016) (Tsai & Fordyce 2014). Although eschrichtiids have not been tested so far, their phylogenetic affinity (e.g., Árnason et al. 2018; Marx & Fordyce 2015) with the quickly evolving balaenopterids (Tsai & Fordyce 2014) but low diversity (similar to the slowly evolving neobalaenids) might suggest an intermediate (i.e., moderate) rate in evolution.

Additionally, given its small size (Figs. 2H, J, 3), IRSNB M 2316 likely represents a rather young individual. Owing to the incompleteness of IRSNB M 2316, its ontogenetic stage cannot be ascertained. However, as its size is roughly comparable with that of the mandibles of very young individuals of extant gray whale (i.e., NMR 9991-1783; Fig. 2G, H), IRSNB M 2316 might represent a very young *Eschrichtius*, even though not a newborn, but more complete congeneric specimens need to be collected for confirming this hypothesis. Nevertheless, if our interpretation is correct, it might be possible to identify previously unknown breeding/calving sites of *Eschrichtius* in the North Atlantic via the finding of newborn specimens and the reconstruction of the landscapes and climates of the North Sea during the Pliocene (Funnell 1996; Louwye et al. 2004; De Schepper et al. 2009). In the present case, unfortunately, an unambiguous reconstruction of the palaeoenvironment where the *Eschrichtius* specimen described herein used to live is frustrated by uncertainties regarding the possible reworking of this fossil: indeed, the Luchtbal Sands Member and the Oorderen Sands Member bear different palaeoclimatic significances (while the former testifies to relatively cool waters, the latter reflects deposition in mostly warm-temperate conditions; De Schepper et al. 2009). More generally, recognition of past mysticete reproduction areas is often problematic, but with sound evidence and careful consideration, it can be demonstrated. For example, abundant specimens of the extinct baleen whale *Parietobalaena yamaokai* Otsuka & Ota, 2008 were recovered from a single middle Miocene horizon in Hiroshima, Japan; further detailed examination of this fossil scenario, including the occurrence of an unequivocal newborn of *Parietobalaena* Kellogg, 1924 and the restoration of paleocoastlines, provided convincing direct evidence for a long-lost breeding site (Tsai 2017). Similarly, indirect evidence, such as the collection of fossil whale barnacles (Cirripedia: Coronulidae) that live exclusively on the cetacean skin, can also suggest ancient mysticete migration routes or breeding/calving sites (e.g., Collareta et al. 2016, 2018a, b). As a matter of fact, coronulid shells identified as belonging to *Coronula barbara* Darwin, 1854 (a likely junior synonym of the extinct species *Coronula bifida* Bronn, 1831) are known from the Oorderen Sands Member of the Lillo Formation (Marquet et al. 2009), whereas at least one subfossil specimen of

*Cryptolepas rhachianecti* Dall, 1872 (a host-specific coronulid phoront of extant *Eschrichtius*; Pilsbry 1916) is known so far from the North Sea region (Bosselaers & Collareta 2016). Therefore, further finds will hopefully contribute to depict the lost nursery areas of *Eschrichtius* in the North Atlantic.

*Acknowledgements.* Our gratitude to Annelise Folie, Cécilia Cousin, and Alain Dreze (for curating the fossil specimen IRSNB M 2316), as well as to Bram Langeveld (for curating the extant specimen NMR 9991-1783). We are also grateful to Ir. Aerts for the excellent cooperation and technical assistance at the Deurganckdok construction site. Klaas Post and Felix Marx are thanked for positive, constructive discussions on several issues addressed in the present paper. Thanks are also due to the anonymous fisherman who trailed the subfossil mandible ECOMARE B2 492 and saved it for science, as well as to Adri and Ineke Vonk and Museum Ecomare, for allowing access to this specimen. Furthermore, we are indebted to Olivier Lambert for fruitful discussions and for making different mysticete mandibles available for comparison.

We also thank Olivier Lambert and an anonymous reviewer for constructive suggestions, and Giorgio Carnevale for helpful editorial guidance to shape this work into its present form.

*Funding.* CHT was partly supported by the Taiwan Ministry of Science and Technology (MOST 107-2621-B-002-005 and 108-2621-B-002-006-MY3 to CHT) and public donations to the Lab of Evolution and Diversity of Fossil Vertebrates, National Taiwan University.

## REFERENCES

- Aaris-Sørensen K., Rasmussen K.L., Linze C. & Petersen K.S. (2010) - Late Pleistocene and Holocene whale remains (Cetacea) from Denmark and adjacent countries: species, distribution, chronology, and trace element concentrations. *Marine Mammal Science*, 26: 253-281.
- Árnason Ú., Lammers F., Kumar V., Nilsson M.A. & Janke A. (2018) - Whole-genome sequencing of the blue whale and other rorquals finds signatures for introgressive gene flow. *Science Advances*, 4: article #eaap9873.
- Barnes L.G. & McLeod S.A. (1984) - The fossil record and phyletic relationships of gray whales. In: Jones M.L., Swartz S.L. & Leatherwood S. (Eds.) - *The Gray Whale*: 3-32. Academic Press, New York.
- Bisconti M. (2008) - Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the Early Pliocene of northern Italy. *Zoological Journal of the Linnean Society*, 153: 1-186.
- Bisconti M. & Bosselaers M. (2016) - *Fragilicetus velponi*: a new mysticete genus and species and its implications for the origin of Balaenopteridae (Mammalia, Cetacea, Mysticeti). *Zoological Journal of the Linnean Society*, 177: 450-474.
- Bisconti M., Lambert O. & Bosselaers M. (2017) - Revision of "*Balaena*" *belgica* reveals a new right whale species, the possible ancestry of the northern right whale, *Eubalaena glacialis*, and the ages of divergence for the living right

- whale species. *PeerJ*, 5: article #e3464.
- Bisconti M. & Varola A. (2006) - The oldest eschrichtiid mysticete and a new morphological diagnosis of Eschrichtiidae (gray whales). *Rivista Italiana di Paleontologia e Stratigrafia*, 112: 447-457.
- Boessenecker R.W. (2013) - A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California, part II: Pinnipeds and Cetaceans. *Geodiversitas*, 35: 815-941.
- Boessenecker R.W. & Fordyce R.E. (2015) - A new genus and species of eomysticetid (Cetacea: Mysticeti) and a reinterpretation of '*Manicetus*' *lophocephalus* Marples, 1956: transitional baleen whales from the upper Oligocene of New Zealand. *Zoological Journal of the Linnean Society*, 175: 607-660.
- Boessenecker R.W. & Fordyce R.E. (2017) - A new eomysticetid from the Oligocene Kokoamu Greensand of New Zealand and a review of the Eomysticetidae (Mammalia, Cetacea). *Journal of Systematic Palaeontology*, 15: 429-469.
- Bosselaers M. & Collareta A. (2016) - The whale barnacle *Cryptolepas rhachianecti* (Cirripedia: Coronulidae), a phoront of the grey whale *Eschrichtius robustus* (Cetacea: Eschrichtiidae), from a sandy beach in The Netherlands. *Zootaxa*, 4154: 331-338.
- Brisson A.D. (1762) - Regnum Animale in Classes IX distributum sive synopsis methodica. Editio altero auctior. Theodorum Haak, Leiden, 294 pp.
- Bronn H. (1831) - Italiens Tertiär-Gebilde und deren organische Einschlüsse. Gross, Heidelberg, 176 pp.
- Clement M.T., Fordyce R.E., Peek S.L. & Fox D.L. (2014) - Ancient marine isoscapes and isotopic evidence of bulk-feeding by Oligocene cetaceans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 400: 28-40.
- Coletti G., Bosio G., Collareta A., Buckeridge J., Consani S. & El Kateb A. (2018) - Palaeoenvironmental analysis of the Miocene barnacle facies: case studies from Europe and South America. *Geologica Carpathica*, 69: 573-592.
- Collareta A., Margiotta S., Varola A., Catanzariti R., Bosselaers M. & Bianucci G. (2016) - A new whale barnacle from the early Pleistocene of Italy suggests an ancient right whale breeding ground in the Mediterranean. *Comptes Rendus Palevol*, 15: 473-481.
- Collareta A., Insacco G., Reitano A., Catanzariti R., Bosselaers M., Montes M. & Bianucci G. (2018a) - Fossil whale barnacles from the lower Pleistocene of Sicily shed light on the coeval Mediterranean cetacean fauna. *Carnets de Géologie*, 18: 9-22.
- Collareta A., Regattieri E., Zanchetta G., Lambert O., Catanzariti R., Bosselaers M., Covelo P., Varola A. & Bianucci G. (2018) - New insights on ancient cetacean movement patterns from oxygen-isotope analyses of a Mediterranean Pleistocene whale barnacle. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 288: 143-159.
- Colpaert W., Bosselaers M. & Lambert O. (2015) - Out of the Pacific: a second fossil porpoise from the Pliocene of the North Sea Basin. *Acta Palaeontologica Polonica*, 60: 1-10.
- Dall W.H. (1872) - On the parasites of the cetaceans of the N.W. coast of America, with descriptions of new forms. *Proceedings of the California Academy of Sciences*, 4: 299-301.
- Darwin C. (1854) - A monograph on the subclass Cirripedia, with figures of all the species. The Balanidae, the Verucidae, etc. Ray Society, London, 684 pp.
- De Schepper S., Head M.J. & Louwe S. (2009) - Pliocene dinoflagellate cyst stratigraphy, palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium. *Geological Magazine*, 146: 92-112.
- Ellerman J.R. & Morrison-Scott, T.C.S. (1951) - Checklist of Palearctic and Indian Mammals 1758 to 1946. Trustees of the British Museum (Natural History), London, 810 pp.
- Fitzgerald E.M. (2012) - Archaeocete-like jaws in a baleen whale. *Biology Letters*, 8: 94-96.
- Fordyce R.E. & Marx F.G. (2012) - The pygmy right whale *Carperea marginata*: the last of the cetotheres. *Proceedings of the Royal Society B: Biological Sciences*, 280: article #20122645.
- Funnell B.M. (1996) - Plio-Pleistocene palaeogeography of the southern North Sea basin (3.75–0.60 Ma). *Quaternary Science Reviews*, 15: 391-405.
- Garrison E.G., McFall G., Cherkinsky A. & Noakes S.E. (2012) - Discovery of a Pleistocene mysticete whale, Georgia Bight (USA). *Palaeontologia Electronica*, 15: article #15.3.31A.
- Garrison E.G., Morgan G.S., McGrath K., Speller C. & Cherkinsky A. (2019) - Recent dating of extinct Atlantic gray whale fossils, (*Eschrichtius robustus*), Georgia Bight and Florida, western Atlantic Ocean. *PeerJ*, 7: article #e6381.
- Gray J.E. (1846) - On the British Cetacea. *Annals and Magazine of Natural History, Series 1*, 17: 82-8.
- Gray J.E. (1864a) - On the Cetacea which have been observed in the seas surrounding the British Islands. *Proceedings of the Zoological Society of London*, 1864: 195-248.
- Gray J.E. (1864b) - Notes on the whalebone-whales; with a synopsis of the species. *Annals and Magazine of Natural History, Series 3*, 14: 345-353.
- Ichishima H., Sato E.R.I., Sagayama T. & Kimura M. (2006) - The oldest record of Eschrichtiidae (Cetacea: Mysticeti) from the Late Pliocene, Hokkaido, Japan. *Journal of Paleontology*, 80: 367-379.
- Kellogg, R. (1924) - Description of a new genus and species of whalebone whale from the Calvert Cliffs, Maryland. *Proceedings of the United States National Museum*, 63: 1-14.
- Kimura T., Hasegawa Y. & Kohno N. (2018) - A new species of the genus *Eschrichtius* (Cetacea: Mysticeti) from the Early Pleistocene of Japan. *Paleontological Research*, 22: 1-20.
- Lacépède B.G. (1804) - Histoire naturelle des Cétacées. Chez Plassan Imprimeur-Libraire, Paris, 329 pp.
- Lambert O. & Gigase P. (2007) - A monodontid cetacean from the Early Pliocene of the North Sea. *Bulletin de l'Institut royal des Sciences naturelles de Belgique-Sciences de la Terre*, 77: 197-210.
- Lilljeborg W. (1861) - Hvalben funna i jorden på Gräsön i Roslagen i Sverige. *Föredrag vid Naturforskaremotet i Köpenhamn*, 1860: 599-616.
- Louwe S., Head M.J., De Schaepper S. (2004) - Dinoflagellate

- cysts stratigraphy and palaeoecology of the Pliocene in northern Belgium, southern North Sea basin. *Geological Magazine*, 141: 353-378.
- Marx F.G. & Fordyce R.E. (2015) - Baleen boom and bust: a synthesis of mysticete phylogeny, diversity and disparity. *Royal Society Open Science*, 2: article #140434.
- Marx F.G. & Fordyce R.E. (2016) - A link no longer missing: new evidence for the cetotheriid affinities of *Caperea*. *PLOS ONE*, 11: article #e0164059.
- Marquet R., Collins J., Jagt J. & Van Bakel B. (2009) - The invertebrate fauna of the Pliocene in Belgium. Part I. Annelida, Anthozoa and Crustacea. *Palaeofocus*, 2: 41-61.
- Mead J.G. & Mitchell E.D. (1984) - Atlantic gray whales. In: Jones M.L., Swartz S.L. & Leatherwood S. (Eds.) - The Gray Whale, *Eschrichtius robustus*. 33-53. Academic Press, San Diego.
- Otsuka H. & Ota Y. (2008) - Cetotheres from the early Middle Miocene Bihoku Group in Shobara District, Hiroshima Prefecture, West Japan. *Miscellaneous Reports of the Hima Museum for Natural History*, 49: 1-66.
- Pilsbry H.A. (1916) - The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. *Bulletin of the United States National Museum*, 93: 1-366.
- Post K. (2005) - A Weichselian marine mammal assemblage from the southern North Sea. *Deinsea*, 11: 21-27.
- Pyenson N.D. & Lindberg D.R. (2011) - What happened to gray whales during the Pleistocene? The ecological impact of sea-level change on benthic feeding areas in the North Pacific Ocean. *PLOS ONE*, 6: article #e21295.
- Repenning C.A. (1983) - New evidence for the age of the Gubik Formation Alaskan North Slope. *Quaternary Research*, 19: 356-372.
- Santos A., Mayoral E. & Muñiz F. (2005) - Bioerosion scars of acorn barnacles from the southwestern Iberian Peninsula, upper Neogene. *Rivista Italiana di Paleontologia e Stratigrafia*, 111: 181-189.
- Swartz S.L. (2018) - Gray Whale: *Eschrichtius robustus*. In: Würsig B., Thewissen J.G.M. & Kovacs K. (Eds.), *Encyclopedia of Marine Mammals*, 3rd Edition: 422-428. Academic Press, San Diego.
- Tsai C.H. & Boessenecker R.W. (2015) - An Early Pleistocene gray whale (Cetacea: Eschrichtiidae) from the Rio Dell Formation of northern California. *Journal of Paleontology*, 89: 103-109.
- Tsai C.H. & Boessenecker R.W. (2017) - The earliest-known fin whale, *Balaenoptera physalus*, from the Early Pleistocene of northern California, USA. *Journal of Vertebrate Paleontology*, 37: article #e1306536.
- Tsai C.H. & Fordyce R.E. (2014) - Disparate heterochronic processes in baleen whale evolution. *Evolutionary Biology*, 41: 299-307.
- Tsai C.H. & Fordyce R.E. (2015) - Ancestor–descendant relationships in evolution: origin of the extant pygmy right whale, *Caperea marginata*. *Biology Letters*, 11: article #20140875.
- Tsai C.H. (2017) - A Miocene breeding ground of an extinct baleen whale (Cetacea: Mysticeti). *PeerJ*, 5: article #e3711.
- Tsai C.H., Fordyce R.E., Chang C.H. & Lin L.K. (2014) - Quaternary fossil gray whales from Taiwan. *Paleontological Research*, 18: 82-94.
- Whitmore Jr F.C. & Kaltenbach J.A. (2008) - Neogene Cetacea of the Lee Creek phosphate mine, North Carolina. *Virginia Museum of Natural History Special Publication*, 14: 181-269.
- Wilson D.E. & Mittermeier R.A. (2014) - Handbook of the mammals of the world, volume 4: sea mammals. Lynx Edicions, Barcelona.