

Eocene Antarctica: a window into the earliest history of modern whales

Mónica R. BUONO^{1*}, R. Ewan FORDYCE^{2,3}, Felix G. MARX^{4,5,6,7}, Marta S. FERNÁNDEZ⁸ & Marcelo A. REGUERO^{9,10}

¹ Instituto Patagónico de Geología y Paleontología, CCT CONICET-CENPAT, Bvd. Brown 2915, U9120ACD, Puerto Madryn, Chubut, Argentina;

² Department of Geology, University of Otago, 360 Leith Walk, PO Box 56, Dunedin, Otago 9054, New Zealand;

³ Departments of Paleobiology and Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA;

⁴ Directorate of Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium;

⁵ Department of Geology, University of Liège, B18, Quartier Agora, 14 Allée du 6 Août, 4000 Liège, Belgium;

⁶ School of Biological Sciences, Monash University, Clayton, Australia;

⁷ Palaeontology, Museums Victoria, Melbourne, Australia;

⁸ CONICET–División Paleontología Vertebrados, Unidades de Investigación, Anexo Museo, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 60 y 122, B1900FWA, La Plata, Argentina;

⁹ CONICET–División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina;

¹⁰ Instituto Antártico Argentino (Dirección Nacional del Antártico), 25 de Mayo 1151, 1650, San Martín, Argentina

Received 20 February 2019; accepted 2 April 2019; published online 17 June 2019

Abstract The Eocene–Oligocene Southern Ocean is thought to have played a major role in cetacean evolution. Yet, fossils from its heart—Antarctica—are rare, and come almost exclusively from the Eocene La Meseta and Submeseta formations of Marambio (Seymour) Island. Here, we provide a summary and update of this crucial fossil assemblage, and discuss its relevance in the broader context of cetacean evolution. To date, Eocene specimens from Antarctica include basilosaurids, a group of archaic stem cetaceans that had already fully adapted to life in water; and the archaic toothed mysticete *Llanocetus*, the second oldest crown cetacean on record (ca. 34 Ma). This Eocene co-occurrence of stem and crown cetaceans is highly unusual, and otherwise only observed in Peru. Though related, at least some of the Antarctic species appear to be different from, and notably larger than their Peruvian counterparts, suggesting an early differentiation of the high latitude cetacean fauna.

Keywords Marambio (Seymour) Island, Basilosauridae, Mysticeti, evolution

Citation: Buono M R, Fordyce R E, Marx F G, et al. Eocene Antarctica: a window into the earliest history of modern whales. *Adv Polar Sci*, 2019, 30(3): 293-302, doi: 10.13679/j.advps.2019.0005

1 Introduction

The polar oceans with their major upwelling systems and abundant seasonal food supply are crucial to understanding

modern cetacean diversity and distribution. Mysticetes, in particular, migrate to higher latitudes during the summer to feed, and the physiological demands of this behaviour, coupled with patchy prey distributions, may explain their signature gigantism (Marx and Fordyce, 2015; Slater et al., 2017). While this pattern is likely to be relatively

* Corresponding author, E-mail: buono@cenpat-conicet.gob.ar

modern—perhaps no older than the Pliocene (Slater et al., 2017)—the polar regions are nonetheless thought to have played a crucial role in cetacean evolution. Thus, much of the nutrient supply throughout the modern ocean is dependent on the deep-mixing effects of the Antarctic Circumpolar Current (Sarmiento et al., 2004), whose onset around the Eocene/Oligocene boundary may have facilitated the radiation of modern whales and dolphins (Fordyce, 1977, 1980; Berger, 2007).

There are few fossil sites that document the transition from archaic stem cetaceans ('archaeocetes') to early members of the crown group (neocetes). Although Eocene units abound across North Africa, North America, and even New Zealand, they appear to be devoid of neocetes (Köhler and Fordyce, 1997; Uhen, 2013; Gingerich and Zouhri, 2015). By contrast, Oligocene units across the globe have yielded only neocetes, with the notable exception of the late-surviving kekenodontids (Clementz et al., 2014; Hernández Cisneros and Tsai, 2016). To date, there are just two places where Eocene archaeocetes and neocetes have been shown to overlap: the Ica Desert of Peru, which has produced the oldest known baleen whale (Mysticeti) alongside a variety of basilosaurids (Uhen et al., 2011; Lambert et al., 2017; Martínez Cáceres et al., 2017); and Marambio (Seymour) Island, off the Antarctic Peninsula (Mitchell, 1989; Buono et al., 2016; Fordyce and Marx, 2018; Marx et al., 2019).

The first cetacean fossils from Antarctica were collected by the Swedish South Polar Expedition of 1903 (Wiman, 1905), and identified as "*Zeuglodon*" sp. (Kellogg, 1936). Subsequent Argentine-US (1974–1975), US (1982), Polish (1985) and Argentine-Polish (1993–1994) Antarctic expeditions yielded further presumed basilosaurids (Woodburne and Zinsmeister, 1984; Borsuk-Bialynicka, 1988; Fostowicz-Frelik, 2003; Table 1 here), and fragments of the holotype of the archaic toothed mysticete *Llanocetus denticrenatus* (Elliot et al., 1975; Mitchell, 1989). The remainder of the type specimen was collected in 1986–1987, during an US expedition including R. E. Fordyce and others (Fordyce and Marx, 2018). Since then, ongoing fieldwork by the Dirección Nacional del Antártico–Instituto Antártico Argentino (IAA) and the Museo de La Plata (MLP), Argentina, has recovered a series of further specimens referable to both *Llanocetus* and basilosaurids (Buono et al., 2016; Marx et al., 2019). Here, we review and synthesise the Eocene fossil record of cetaceans from Antarctica, and discuss its significance in the broader context of cetacean evolution and paleobiogeography.

2 Geological context

The La Meseta Formation comprises sandstones and mudstones, with intercalated shell-rich conglomerates, exposed on Marambio (Seymour) Island, northern Antarctic Peninsula (Figure 1) (Elliot and Trautman, 1982). The unit was originally

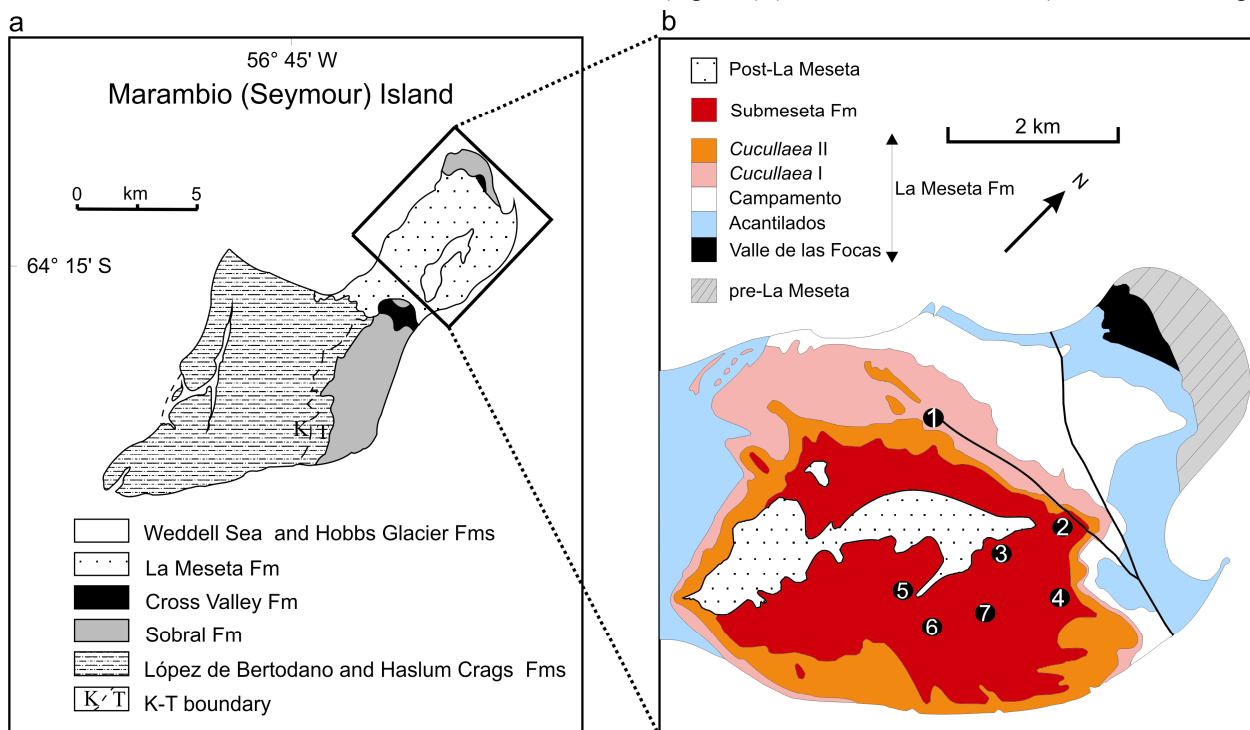


Figure 1 a, Geological map of Marambio (Seymour) Island (Antarctic Peninsula); b, Detailed geographical extent of the La Meseta allomembers, relative to the main cetacean fossil localities. 1, Basilosauridae indet. (MLP 11-II-21-3); 2, Basilosauridae indet. (MLP 13-I-25-10), ?Basilosauridae indet. (MLP 13-I-25-11); 3, *Llanocetus* sp. (IAA-PV-731); 4, *Llanocetus* sp. (MLP 12-XI-1-10 a, b); 5, *Llanocetus denticrenatus* (USNM 183022); 6, Mysticeti indet. (MLP 84-II-1-568), Cetacea indet. (MLP 82-IV-23-69); 7, ?Basilosauridae (MLP 83-V-20-386), Cetacea indet. (MLP 83-V-20-80). Modified from Buono et al. (2016).

subdivided into seven lithofacies (TELMs; Sadler, 1988), but then reorganised into six allomembers, named—in ascending order—Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I, *Cucullaea* II, and Submeseta (Marenssi et al., 1998).

Recently, the Submeseta allomember was raised to formation level (Montes et al., 2013), and itself subdivided

into three allomembers: Submeseta I, corresponding to TELMs 6 and 7 *in partem*; Submeseta II, corresponding to TELM 7 *in partem*; and Submeseta III, corresponding to upper TELM 7 (Figure 2). Overall, the Submeseta Formation is characterised by a uniformly sandy lithology, representing a storm-influenced tidal shelf.

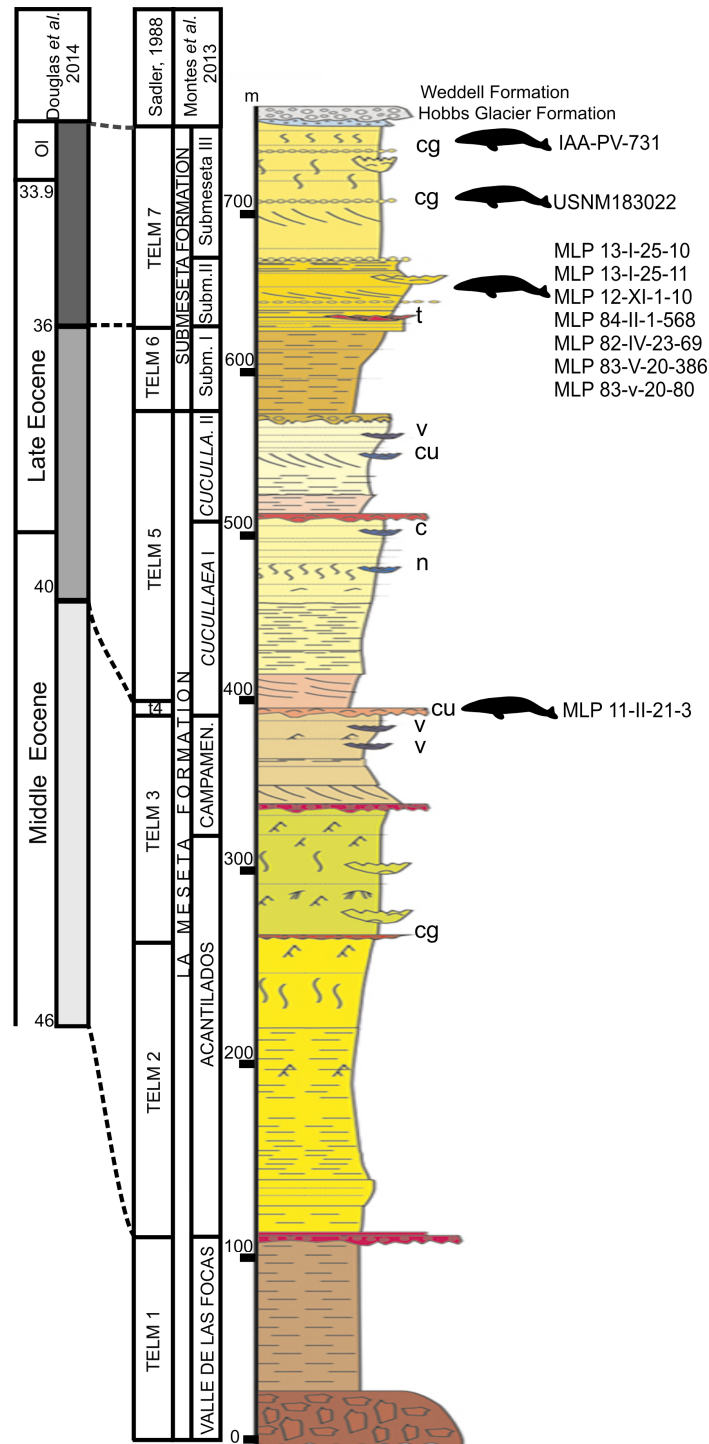


Figure 2 Stratigraphic column of the La Meseta and Submeseta formations, indicating the major cetacean fossil horizons. Modified from Buono et al. (2016). Abbreviations: cu, *Cucullaea*; cg, conglomerates and sandstones; n, naticids; v, veneroids; t, *Turritella*.

Together, the La Meseta and Submeseta formations span much of the Eocene, with dinoflagellate cysts indicating a range of 45–34 Ma (Wrenn and Hart, 1988; Douglas et al., 2014). This is consistent with an independently derived nannofossil date of 45–36 Ma for the Acanthilados to *Cucullaea* II interval (Concheyro et al., 2016), as well as a mollusc-derived $^{87}\text{Sr}/^{86}\text{Sr}$ date of 34.2 ± 0.87 Ma for the top of the Submeseta Formation (Dingle and Lavelle, 1998; Fordyce, 2003). The ages of individual horizons within the La Meseta Formation, however, remain poorly constrained.

3 Eocene whales from Antarctica

To date, cetacean fossils have primarily come from three horizons: the base of the *Cucullaea* I allomember of the La Meseta Formation (*Cucullaea* I shell bank, corresponding to TELM 4; Buono et al., 2016); and allomembers II (level 38) and III (level 39) of the Submeseta Formation (Table 1). Among the assemblage are representatives of two major lineages: basilosaurids, a family of fully aquatic stem cetaceans generally thought to form a clade with crown cetaceans (Pelagiceti; Uhen, 2008); and stem mysticetes belonging to the family Llanocetidae. The former are mostly represented by fragmentary and isolated specimens, whereas the

latter include a relatively complete skull.

3.1 Basilosauridae

Basilosaurids contribute about half of the identifiable material. The first specimens to be described were two isolated caudal vertebrae from the Submeseta Formation initially referred to *Zeuglodon* (= *Basilosaurus*) (Wiman, 1905), but later reclassified as ‘archaeocete’ indet. (Wiman, 1905; Kellogg, 1936). Further material tentatively identified as basilosaurid includes a lumbar vertebra (Borsuk-Białynicka, 1988) and an isolated tooth (Fostowicz-Frelik, 2003), both from the Submeseta Formation/TELM 7. Overall, none of these specimens are diagnostic, and they should thus be regarded as Cetacea indet. (Uhen, 2013).

More recent fieldwork has continued to reveal abundant postcranial material, but also some more diagnostic specimens that finally confirm the occurrence of basilosaurids in Middle–Late Eocene Antarctica (Buono et al., 2016). Among the latter is a nearly complete mandible preserving the p2 (MLP 11-II-21-3; Figure 3a) from the La Meseta Formation/TELM 4, and three isolated teeth (MLP 13-I-25-10, UCR* 21797/RV 8405), including two from the Submeseta Formation/TELM 7 (Figures 3b–3d). The mandible belongs to a mid-sized basilosaurid clearly different from its contemporaries, and may thus indicate the presence

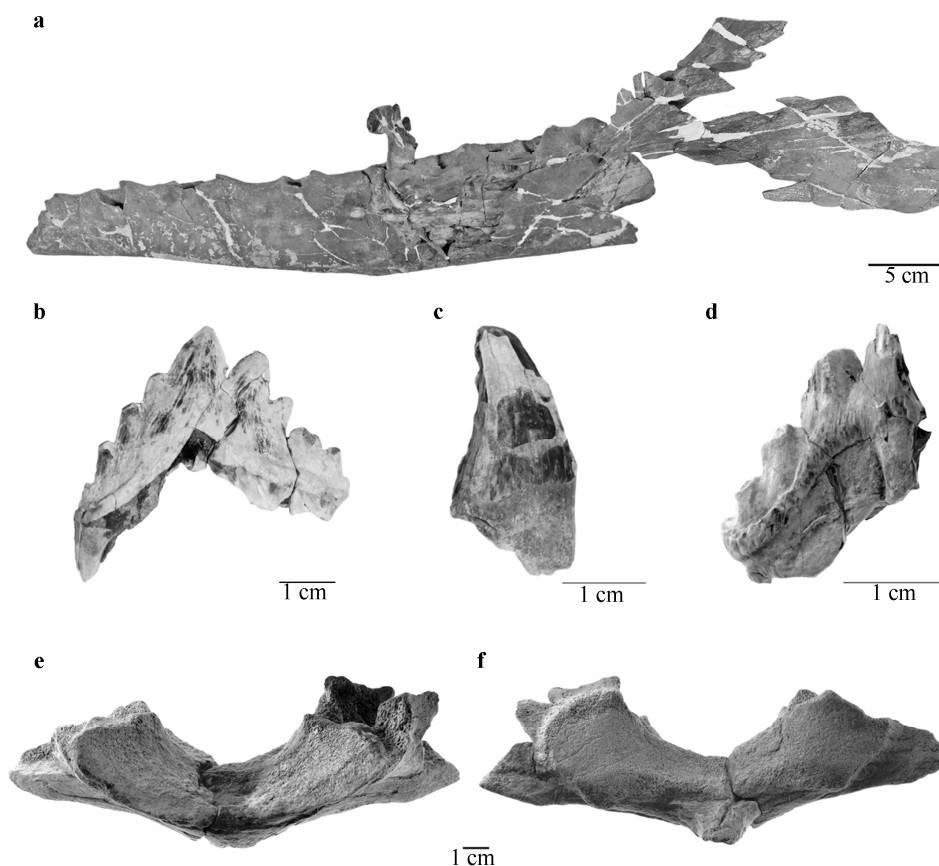


Figure 3 Basilosaurids from the La Meseta and Submeseta formations. **a**, Lateral view of the left mandible with p2 in situ (MLP 11-II-21-3); **b**, Labial view of isolated cheek tooth (MLP 13-I-25-10); **c**, Labial view of isolated incisor (MLP 13-I-25-10); **d**, Lingual view of isolated premolar (UCR 21797/RV 8405); Fragmentary atlas (UCR REF-43) in anterior (**e**), and posterior view (**f**).

of a new species. Notably, it appears to date to ca. 46–40 Ma, making it the oldest basilosaurid—and indeed pelagicete—worldwide (Buono et al., 2016; Concheyro et al., 2016). Other, more tentatively identified specimens include an incomplete mandible (MLP 13-I-25-11; Buono et al., 2016; Figure 6) and a partial atlas (UCR REF-43; Figures 3e–3f), both from the Submeseta II allomember.

3.2 Mysticeti

Toothed mysticetes are only known from the Submeseta Formation. The first remains were collected during fieldwork conducted by the IAA in 1974–1975 and

initially misidentified as *?Zeuglodon* (Elliot et al., 1975), before being re-described as the archaic toothed mysticete *Llanocetus denticrenatus* (Mitchell, 1989). The remains were found near the top of TELM 7 and have been strontium-dated to ca. 34 Ma, making *Llanocetus* the second-oldest neocete on record after *Mystacodon* (Lambert et al., 2017; Fordyce and Marx, 2018). The initially rather incomplete holotype (USNM* 183022), a mandible fragment and a cranial endocast, was complemented by the subsequent discovery of the almost complete skull by R. E. Fordyce in 1987 (Figures 4a–4b) (Fordyce and Marx, 2018).

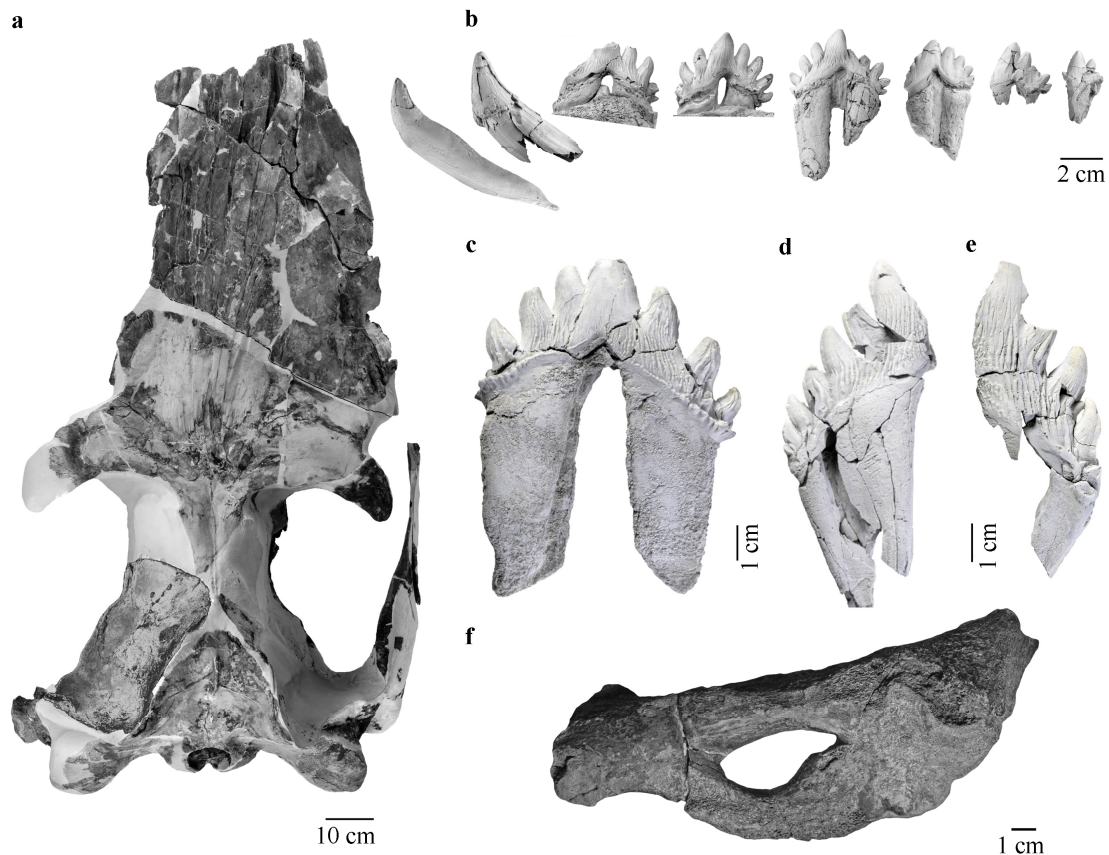


Figure 4 Toothed mysticete fossils from the La Meseta and Submeseta formations. *Llanocetus denticrenatus* (USNM 183022): **a**, Dorsal view of the skull; **b**, Labial view of the lower dentition. *Llanocetus* sp.: **c**, Labial view of left P3 (IAA 52-16); **d**, Labial view of right p4 (MLP 12-XI-1-10a); **e**, Labial view of left lower premolar (MLP 12-XI-1-10b). Mysticeti indet.: **f**, Lateral view of right pelvis (MLP 84-II-1-568).

Beyond *L. denticrenatus*, three morphologically similar but notably larger isolated teeth have recently been referred to *Llanocetus* sp. (Marx et al., 2019) (Figures 4c–4e). In addition, an isolated pelvis previously described as *?Basilosauridae* (MLP 84-II-1-568; Figure 4f) resembles that of the archaic baleen whale *Mystacodon*—and differs from that of basilosaurids—in having an elongate obturator foramen, a relatively short ischium, and a somewhat anterodorsally oriented ilium (Buono et al., 2016; Lambert et al., 2017). Accordingly, we here refer it to Mysticeti indet.

3.3 Cetacea indet.

Numerous additional specimens have been recovered over the past decades, but are often too poorly preserved to be identified beyond the level of Cetacea (Fordyce, 1989; Buono et al., 2016). Of these, the most tantalising is MLP 83-V-20-386, a fragmentary skull vertex and

* UCR: University of California Riverside; now housed at the Museum of Paleontology of the University of California, Berkeley, USA

* USNM: United States National Museum of Natural History, Washington DC, USA

right supraorbital process of the frontal resembling a basilosaurid (Figures 5a–5b). The specimen is notably small (maximum width of 184 mm at the level of the frontal) and the interfrontal suture is open, hinting at a juvenile. The outline of the coronal suture is irregular, but approximately transverse. A second cranial fragment (UCR REF-67) was found with the holotype of *Llanocetus denticrenatus*, but does not appear to belong to this specimen, and cannot be confidently placed within the skull.

Also notable are several pachyosteosclerotic postcrania, including a large lumbar vertebra (UCR REF-80) with extensive regions of massive bone in the body (Figure 5c); a smaller thoracic vertebra (UCR 22174/RV 8435) with a massive neural spine (Figure 5d); a distal portion of a right scapula, with a prominent coracoid process (MLP 82-IV-23-69; Figure 5e), a possible seventh cervical vertebra (MLP 83-v-20-80; Figure 5f); and an isolated rib fragment (UCR Zinsmeister 87-113; Figure 5g). The remaining material, including two isolated incisors and further postcrania, is generally unremarkable, but together reveals a

range of body sizes spanning small *Dorudon*-like forms (e.g. cervical vertebra UCR 21800/RV 8440, centrum width 65 mm; Figure 5h) to perhaps *Llanocetus* (e.g. UCR REF-80, centrum width 210+ mm).

4 Discussion

Previous studies have highlighted the role of the Southern Hemisphere in the emergence of modern cetaceans, especially with regards to the Eocene/Oligocene formation of the Antarctic Circumpolar Current, and the attendant increase in nutrient availability (Fordyce, 1977, 1980, 2003; Berger, 2007). Eocene-Oligocene records of cetaceans, once a global ‘problem child’ (Uhen and Pyenson, 2007), have expanded considerably over the past decade, with new records from New Zealand, Australia, South America and Antarctica. The latter is especially significant in this regard, given the antiquity of the fossils from the La Meseta and Submeseta formations.

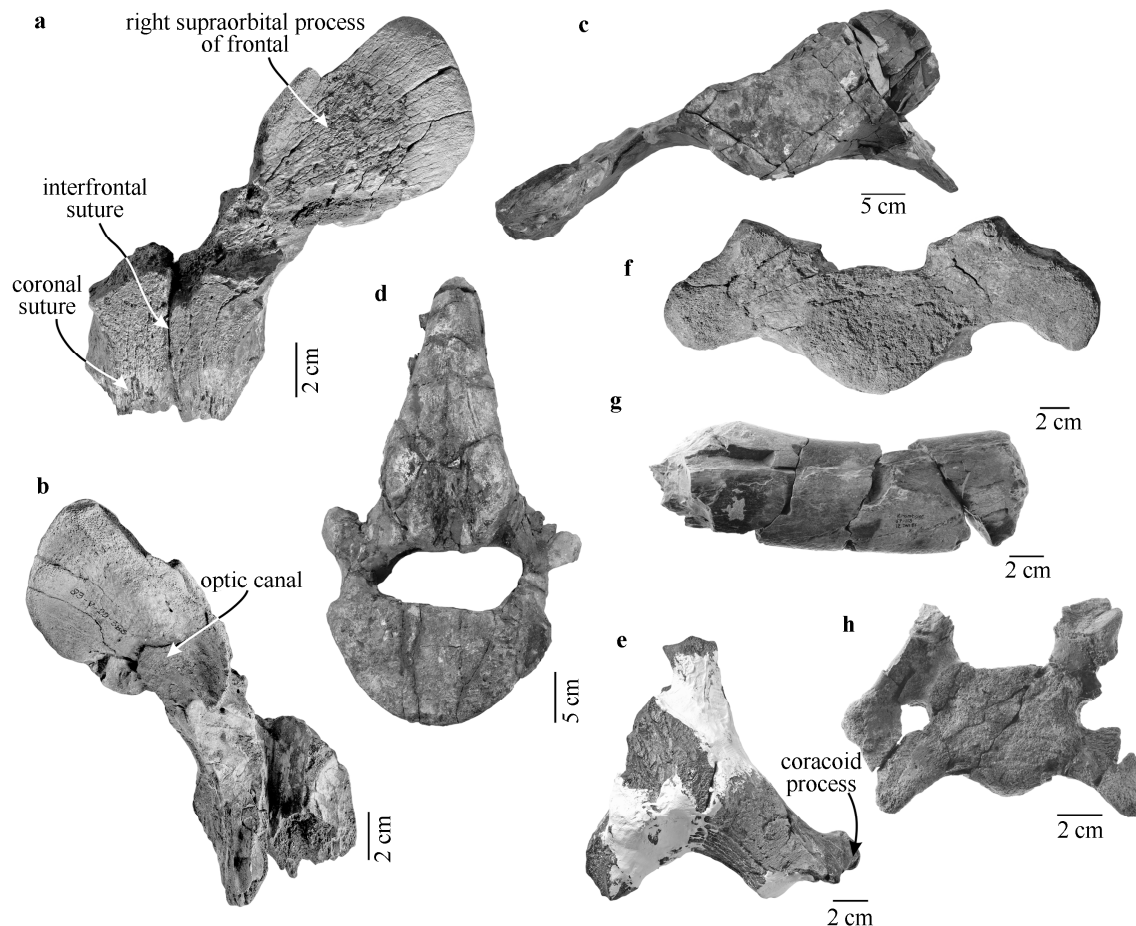


Figure 5 Indeterminate cetacean fossils from the La Meseta and Submeseta formations. **a**, Skull vertex (MLP 83-V-20-38) in dorsal (**a**) and ventral view (**b**); **c**, Lumbar vertebra (UCR REF-80) in anterior view; **d**, Thoracic vertebra (UCR 22174/RV 8435) in posterior view; **e**, Distal portion of right scapula (MLP 82-IV-23-69); **f**, Seventh cervical vertebra (MLP 83-V-20-80) in anterior view; **g**, Isolated rib fragment (UCR Zinsmeister 87-113); **h**, Cervical vertebra (UCR 21800/ RV 8440) in anterior view.

Table 1 Eocene cetacean fossils from the La Meseta and Submeseta formations, Marambio (Seymour) Island, Antarctica

| | Collection number | Specimen | Formation | Reference |
|----------------|---------------------------------|--|--|----------------------------|
| Basilosauridae | Basilosauridae indet. | | | |
| | MLP 11-II-21-3 | Incomplete left mandible and p2 <i>in situ</i> | La Meseta, <i>Cucullaea</i> I Allomember | Buono et al., 2016 |
| | MLP 13-I-25-10 | Isolated teeth | Submeseta, TELM 7 | Buono et al., 2016 |
| | UCR 21797/RV 8405 | Posterior premolar | Unknown | This study |
| | ?Basilosauridae indet. | | | |
| | MLP 13-I-25-11 | Incomplete left mandible | Submeseta, TELM 7 | Buono et al., 2016 |
| | UCR REF-43 | Atlas lacking arch | Submeseta, TELM 7 | This study |
| Mysticeti | <i>Llanocetus denticrenatus</i> | | | |
| | USNM 183022 | skull, partial hyoid apparatus, postcrania | Submeseta, TELM 7 | Fordyce and Marx, 2018 |
| | <i>Llanocetus</i> sp. | | | |
| | MLP 12-XI-1-10 a | Right p4 | Submeseta, TELM 7 | Marx et al., 2019 |
| | MLP 12-XI-1-10 b | Lower left premolar | Submeseta, TELM 7 | Marx et al., 2019 |
| | IAA-PV-731 | Left P3 | Submeseta, TELM 7 | Marx et al., 2019 |
| | ?Mysticeti indet. | | | |
| | MLP 84-II-1-568 | Right pelvis | Submeseta, TELM 7 | Buono et al., 2016 |
| Cetacea indet. | no number | 2 caudal vertebrae | Unknown | Wiman, 1905; Kellogg, 1936 |
| | ZPAL M-VII/1-4 | Isolated lumbar and cervical vertebrae, manubrium of sternum | Submeseta, TELM 6 | Borsuk-Bialynicka, 1988 |
| | MLP 83-V-20-386 | Skull fragment | Submeseta, TELM 7 | This study |
| | MLP 85-V-20-387 | Skull fragment | Submeseta, TELM 7 | This study |
| | ZPAL M. 9/1 | Isolated incisor | Submeseta, TELM 7 | Fostowiz-Frelik, 2003 |
| | MLP 00-I-1-19 | Lumbar vertebrae | Submeseta, TELM 7 | Buono et al., 2016 |
| | MLP 00-I-1-20 | Caudal vertebrae | Submeseta, TELM 7 | Buono et al., 2016 |
| | MLP 12-XI-1-36 | Rib | Submeseta, TELM 7 | Buono et al., 2016 |
| | MLP 82-IV-23-69 | Scapula Fragment | Submeseta, TELM 7 | This study |
| | MLP 83-V-20-80 | ?Cervical vertebra 7 | Submeseta, TELM 7 | This study |
| | MLP 84-II-1-565 | Distal portion of radius | La Meseta, TELM 5 | Buono et al., 2016 |
| | MLP 88-I-1-507 | Partial incisor | Submeseta, TELM 7 | Buono et al., 2016 |
| | MLP 94-III-15-25 | Isolated deciduous incisor | Submeseta, TELM 7 | Buono et al., 2016 |
| | MLP 96-I-5-6 | Isolated deciduous incisor | La Meseta, TELM 5 | Buono et al., 2016 |
| | MLP 96-I-5-99 | Isolated incisor | Submeseta, TELM 7 | Buono et al., 2016 |
| | MLP 96-I-5-100 | Caudal vertebrae | Submeseta, TELM 7 | Buono et al., 2016 |
| | UCR Zinsmeister 87-113 | Pachyosteosclerotic rib | La Meseta | Fordyce, 1989 |
| | UCR 21798/RV 8444 | Rib 1 | Unknown | This study |
| | UCR 21800/RV 8440 | Cervical vertebra 3 or 4 | Unknown | This study |
| | UCR 21801/RV 8419 | Cervical vertebra 4 or 5 | Unknown | Fordyce, 1989 |
| | UCR MOW 8341 | Thoracic vertebra | Unknown | This study |
| | UCR 22174/RV 8435 | Thoracic vertebra, massive pachyosteosclerotic | Unknown | This study |
| | UCR REF-80 | ?Lumbar vertebra, massive pachyosteosclerotic | Submeseta | This study |
| | UCR REF-67 | Skull fragment found with but not belonging to <i>Llanocetus denticrenatus</i> | Submeseta, TELM 7 | This study |
| | UCR REF-31 | Isolated incisor | Submeseta, TELM 7 | This study |

4.1 Origin and Southern Hemisphere dispersal of basilosaurids

Cetaceans originated in the early Eocene Tethys Ocean, in the form of a series of transitional forms with an increasingly aquatic bauplan (Thewissen et al., 1994; Gingerich et al., 2001; Thewissen et al., 2001; Marx et al., 2016a). The earliest cetaceans—pakicetids, ambulocetids, and remingtonocetids—remained restricted to the Tethys (Bebej et al., 2015). Protocetids were the first whales to leave their ancestral ocean, spreading south along the coast of Africa (Gingerich and Cappetta, 2014; Gingerich and Zouhri, 2015), west across the Atlantic to North America (Geisler et al., 2005) and even South America (Lambert et al., 2019). Though geographically widespread, most protocetids retained hind limbs capable of supporting their weight on land, and thus may still have been somewhat tied to the coast (Gingerich et al., 2001). This pattern finally changed with the origin of basilosaurids, the first lineage of obligate aquatic cetaceans (Gingerich et al., 1990).

Concomitant with their aquatic nature, basilosaurids were also the first cetacean lineage to attain a truly cosmopolitan distribution, ranging from the Tethys to western Africa, North and South America, New Zealand and even Antarctica (Köhler and Fordyce, 1997; Uhen, 1998, 2013; Gol'din and Zvonok, 2013; Gingerich and Zouhri, 2015; Buono et al., 2016; Martínez Cáceres et al., 2017). The occurrences from Antarctica and New Zealand are especially significant, as they represent both the earliest evidence for cetaceans in cool high-latitude waters, and—together with a tentatively identified specimen from the Lutetian of Senegal (Élouard, 1966)—the oldest records of the family worldwide (Köhler and Fordyce, 1997; Buono et al., 2016). Nevertheless, the broad temporal and geographical overlap of basilosaurids and protocetids across the Tethys, Atlantic and Pacific oceans, and the lack of protocetids from high latitude localities both suggest that the transition from semi-aquatic to fully aquatic forms occurred in the (sub)tropics. From there, basilosaurids spread across the Southern Hemisphere, reaching Antarctica by 40 Ma (Buono et al., 2016).

The known distribution of austral basilosaurids suggests two possible dispersion routes to Antarctica: one from northern Africa, across the South Atlantic (Uhen, 1999; Uhen et al., 2011); and another across the Pacific, via New Zealand or western South America. Preliminary comparisons suggest that the Antarctic specimens are closer to those from New Zealand (Köhler and Fordyce, 1997) than those from South America (Uhen et al., 2011; Martínez Cáceres et al., 2017) in terms of their dental and mandibular morphology (Buono et al., 2016), providing some tentative support for a dispersal route via Australasia. Additional material from other southern localities is required to test this hypothesis.

4.2 Toothed mysticetes from Antarctica and the evolution of baleen whales

Southern localities have yielded the two oldest known mysticetes: *Mystacodon* from the Pisco Basin of Peru (36.4 Ma; Lambert et al., 2017), and *Llanocetus* from the La Meseta Formation of Antarctica (34.2 Ma; Fordyce and Marx, 2018). Both appear to be related, and have been included in the single family Llanocetidae (Fordyce and Marx, 2018; but see Lambert et al., 2017). Nevertheless, at an estimated body length of 8–12 m *Llanocetus* was at least twice as large, and suggests that gigantism may have originated more than once in baleen whale evolution (Fordyce and Marx, 2018; Marx et al., 2019). The shape of the isolated mysticete pelvis from the La Meseta Formation (MLP 84-II-1-568) does not match the presumed pelvis of *Llanocetus*, but the latter is fragmentary and uncertainly identified. If MLP 84-II-1-568 does belong to *Llanocetus*, its resemblance with *Mystacodon* may provide further support for the monophyly of Llanocetidae. Alternatively, MLP 84-II-1-568 may indicate the presence of an additional, hitherto unrecognised archaic mysticete in the Eocene of Antarctica.

Thanks to its age and basal phylogenetic position, *Llanocetus* provides crucial insights into early baleen whale evolution. Modern mysticetes are toothless and obligate filter feeders (Pivorunas, 1979). By contrast, most archaic whales had teeth, and their feeding strategy (raptorial, suction, or filtering) remains a matter of debate (Deméré et al., 2008; Marx et al., 2016b; Geisler et al., 2017). *Llanocetus* combines a broad rostrum bearing proportionally small, widely spaced teeth with a notable degree of palatal vascularisation (Fordyce and Marx, 2018). In modern mysticetes, the latter is typically associated with the presence of baleen and filter feeding (Ekdale et al., 2015). In *Llanocetus*, however, the palatal blood vessels are directed towards the alveoli, and thus more likely supplied enlarged gums (Fordyce and Marx, 2018). The molars and posterior premolars of *Llanocetus* are sharp, covered in thick enamel, and show evidence of shearing occlusion, all of which are consistent with prey processing and raptorial feeding (Fordyce and Marx, 2018; Loch et al., 2019; Marx et al., 2019). Nevertheless, the wide spacing and relatively small size of the teeth likely reduced their effectiveness as processing tools and, together with the broad rostrum, suggest that *Llanocetus* may have employed a suction-assisted raptorial strategy.

5 Conclusions

The Eocene La Meseta Formation of Marambio (Seymour) Island has yielded a fragmentary but globally significant assemblage of archaic cetaceans, including the oldest basilosaurid and the second-oldest mysticete. Antarctica is one of just three localities worldwide where stem and crown

cetaceans have been shown to co-occur, the others being Peru and New Zealand. Basilosaurids are represented by small to mid-sized specimens, some of which may represent new species. The antiquity of Antarctic basilosaurids implies an early divergence of the family in the (sub)tropics, followed by relatively rapid dispersal to southern polar waters. Some of the Antarctic forms appear to be different from their Peruvian counterparts, suggesting a possible dispersal via Australasia. Eocene mysticetes from Antarctica provide a crucial window into early baleen whale feeding evolution, and indicate that a suction-assisted raptorial strategy preceded the emergence of filtering. Nevertheless, Eocene mysticetes were among the largest animals of their time, suggesting that gigantism arose repeatedly in baleen whale evolution.

Acknowledgments We thank the Instituto Antártico Argentino and the Fuerza Aérea Argentina, who provided logistic support during field work in Antarctica, as well as the Guest Editors (C. Acosta Hospitaleche, J. Alistair Crame and J. Gelfo) for inviting us to contribute to this special issue. We also thank to the reviewers (O. Lambert and E. Fitzgerald) for their constructive comments.

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