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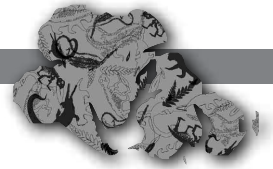Also appearing in this issue:

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Abstract. Basal fully aquatic whales, the basilosaurids are worldwide known from Bartonian−Priabonian localities, indicating that this group was widely distributed during the late middle Eocene. In the Northern Hemisphere, fossils of basilosaurids are abundant, while records in the Southern Hemisphere are scarce and, in some cases (*i.e.,* Antarctica), doubtful. The presence of basilosaurids in Antarctica was, until now, uncertain because most of the records are based on fragmentary materials that preclude an accurate assignment to known archaeocete taxa. Here we report the findings of mandibles, teeth, and innominate bone remains of basilosaurids recovered from the La Meseta Formation (TELM 4 Lutetian−Bartonian and; TELM 7 Priabonian), in Marambio (Seymour) Island (James Ross Basin, Antarctic Peninsula). These findings confirm the presence of Basilosauridae in the marine realm of Antarctica, increasing our knowledge of the paleobiogeographic distribution of basilosaurids during the middle−late Eocene. In addition, one of these records is among the oldest occurrences of basilosaurids worldwide, indicating a rapid radiation and dispersal of this group since at least the early middle Eocene.

Key words. Cetacea. Basilosauridae. Paleogene. Cheek teeth. Mandibles.

Resumen. BASILOSAURIDOS EOCENOS DE LA FORMACIÓN LA MESETA, ISLA MARAMBIO (SEYMOUR), ANTÁRTIDA. El registro fósil de los basilosáuridos está bien documentado durante el Bartoniano−Priaboniano en varias localidades del mundo, lo cual indica que este grupo estaba ampliamente distribuido durante el Eoceno medio tardío. En el Hemisferio Norte, el registro fósil de este grupo es abundante, a diferencia de lo que ocurre en el Hemisferio Sur donde es escaso y, en algunos casos (*i.e.,* Antártida), dudoso. La presencia de basilosáuridos en Antártida es incierta ya que la mayoría de los registros están basados en materiales fragmentarios, lo cual imposibilita su asignación a algún grupo de arqueocetos. En la presente contribución se describen restos de basilosáuridos correspondientes a mandíbulas, dientes aislados y un hueso pélvico, recuperados de la Formación La Meseta (TELM 4 Lutetiano−Bartoniano; TELM 7 Priaboniano), Isla Marambio (Seymour), (Cuenca James Ross, Península Antártica). Este hallazgo confirma la presencia de Basilosauridae en la Antártida, contribuyendo al conocimiento de la distribución paleobiogeográfica de este grupo durante el Eoceno medio−tardío. Finalmente, uno de estos registros se encuentra entre los basilosáuridos más antiguos conocidos, indicando un rápida radiación y dispersión de este grupo al menos desde el Eoceno medio temprano.

Palabras clave. Cetacea. Basilosauridae. Paleógeno. Dientes. Mandíbulas.

THE La Meseta Formation, Marambio (Seymour) Island, NE Antarctic Peninsula, contains one of the world's most diverse Eocene fossil assemblages, including both marine and terrestrial mammals (Reguero *et al.*, 2002, 2013; Reguero and Gasparini, 2006; Gelfo *et al.*, 2015). Regarding whales, the La Meseta Formation has produced fragmentary specimens of archaeocetes, a paraphyletic group of basal whales (Borsuk-Bialynicka, 1988; Fordyce, 1989; Fostowicz-Frelik, 2003), and the oldest archaic toothed mysticete, *Llanocetus denticrenatus* Mitchell, 1989. In particular, archaeocete records in Antarctica are based on undetermined material, mostly collected from uppermost levels (TELM 7) of the La Meseta

Formation (Submeseta Formation, according to Montes *et al.*, 2013) and they were tentatively assigned to Basilosauridae (Borsuk-Bialynicka, 1988; Cozzuol, 1988; Fordyce, 1989; Fostowicz-Frelik, 2003). However, some authors considered these materials as too fragmentary to be confidently assigned to a species or family of archaeocetes (Uhen *et al.*, 2011; Uhen, 2013). Therefore, the presence of this group of archaeocetes in the Eocene of Antarctica remains unclear.

Fieldwork conducted in Marambio (Seymour) Island during the past 30 years, organized by the Dirección Nacional del Antártico–Instituto Antártico Argentino and Museo de La Plata, resulted in the collection of numerous cetacean remains. Here, we report new findings of basilosaurid remains recovered from the La Meseta Formation that confirm the presence of basilosaurid archaeocetes in southern high latitude environments, increasing our knowledge of the paleobiogeographic distribution of basilosaurids during the middle–late Eocene.

Institutional abbreviations. **DPV,** División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina; **IAA,** Instituto Antártico Argentino, Buenos Aires, Argentina; **MLP,** Museo de La Plata, La Plata, Argentina; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **NSFM,** Naturmuseum Senckenberg, Frankfurt am Main, Frankfurt, Germany; **OU,** Geology Museum, University of Otago, Dunedin, New Zealand; **SCSM,** South Carolina State Museum, Columbia, South Carolina, USA; **UM,** University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Anatomical abbreviations. **C,** canine; **I,** incisor; **M,** molar; **P,** premolar.

MATERIAL AND METHODS

The specimens MLP 11-II-21-3, MLP 13-I-25-10, MLP 13-I-25-11 and MLP 84-II-1-568 described here were collected in part by some of the authors of this work during multidisciplinary field trips to Marambio (Seymour) Island, La Meseta Formation over the past 30 years, and are deposited in the Vertebrate Paleontology collection of the Museo de La Plata.

The anatomical terminology is according to Mead and Fordyce (2009) and other more specific for archaeocetes (*i.e.*, Uhen, 2004). The orientation and interpretation of the anatomy of the innominate bone follow Gol'din (2014). The specimens were mechanically prepared using pneumatic chisels and hand tools. Photographs were taken with a Nikon D3000 camera and 55 mm lens.

GEOLOGICAL SETTING

The early Eocene to earliest Oligocene? La Meseta Formation (Elliot and Trautman, 1982) is an unconformity-bounded unit (La Meseta Alloformation of Marenssi *et al.*, 1998a) outcropping in Seymour and Cockburn islands, Antarctica (Fig. 1). This unit is the topmost exposed portion of the sedimentary fill of the Late Jurassic–Paleogene James Ross Basin (Del Valle *et al.*, 1992). The La Meseta Formation rests unconformably on either the late Maastrichtian–Danian López de Bertodano Formation or on the Paleocene Sobral and Cross Valley formations (Sadler, 1988; Marenssi *et al.*, 1998a). The La Meseta Formation is composed of sandstones and mudstones with intercalated shell-rich conglomerates. The unit was subdivided by Sadler (1988) into seven lithofacies (TELMs 1–7) and was later organized into six erosionally based internal units (referred to as Allomembers) that were named as follows (from base to top): Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I, *Cucullaea* II and Submeseta (Marenssi *et al.*, 1998a; Fig. 1.2–3). These units were deposited primarily during the Eocene in deltaic, estuarine, and shallow marine settings, primarily within a northwest-southeast trending incised valley (Marenssi *et al.*, 1998a, b).

Recently Montes *et al.* (2010, 2013) split this formation into two new units: the Submeseta Formation and the La Meseta Formation (Fig. 2). The Submeseta Formation corresponds to the Facies Association III of Marenssi *et al.* (1998b), characterized by a uniform sandy lithology representing a storm-influenced tidal shelf. Three different levels were recognized in this unit and named from base to top: Submeseta I, Submeseta II, and Submeseta III (Montes *et al.*, 2013). Most of the whale fossils were found in the Submeseta II Allomember (level 38). Askin (1997) regarded the age of this unit as late Eocene–earliest Oligocene. However, Dingle and Lavelle (1998) and Dutton *et al.* (2002) reported a $^{87}Sr/^{86}Sr$-derived age of 34.2 Ma and 34.96 Ma respectively for the topmost few meters of this allomember (veneroid shell bank, level 38), assigning it to the late Eocene.

The La Meseta Formation (*sensu* Montes *et al.*, 2013) in-

cludes the Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I and *Cucullaea* II allomembers. Fossil whale remains occur sporadically at the base of the *Cucullaea* I Allomember (*Cucullaea* I shell bank, TELM 4 of Sadler, 1988; Reguero *et al.*, 2013) and other *Cucullaea* and naticid horizons from the overlying TELM 5 (middle and upper part of the *Cucullaea* I Allomember). The age of the La Meseta Formation (*sensu*

Montes *et al.*, 2013) has received much attention by numerous authors (Harwood, 1985, 1988; Coccozza and Clarke, 1992; Stilwell and Zinsmeister, 1992; Askin, 1997, Dutton *et al.*, 2002; Ivany *et al.*, 2008; Douglas *et al.*, 2014). We address this further in the discussion section (see Age of Antarctic basilosaurids).
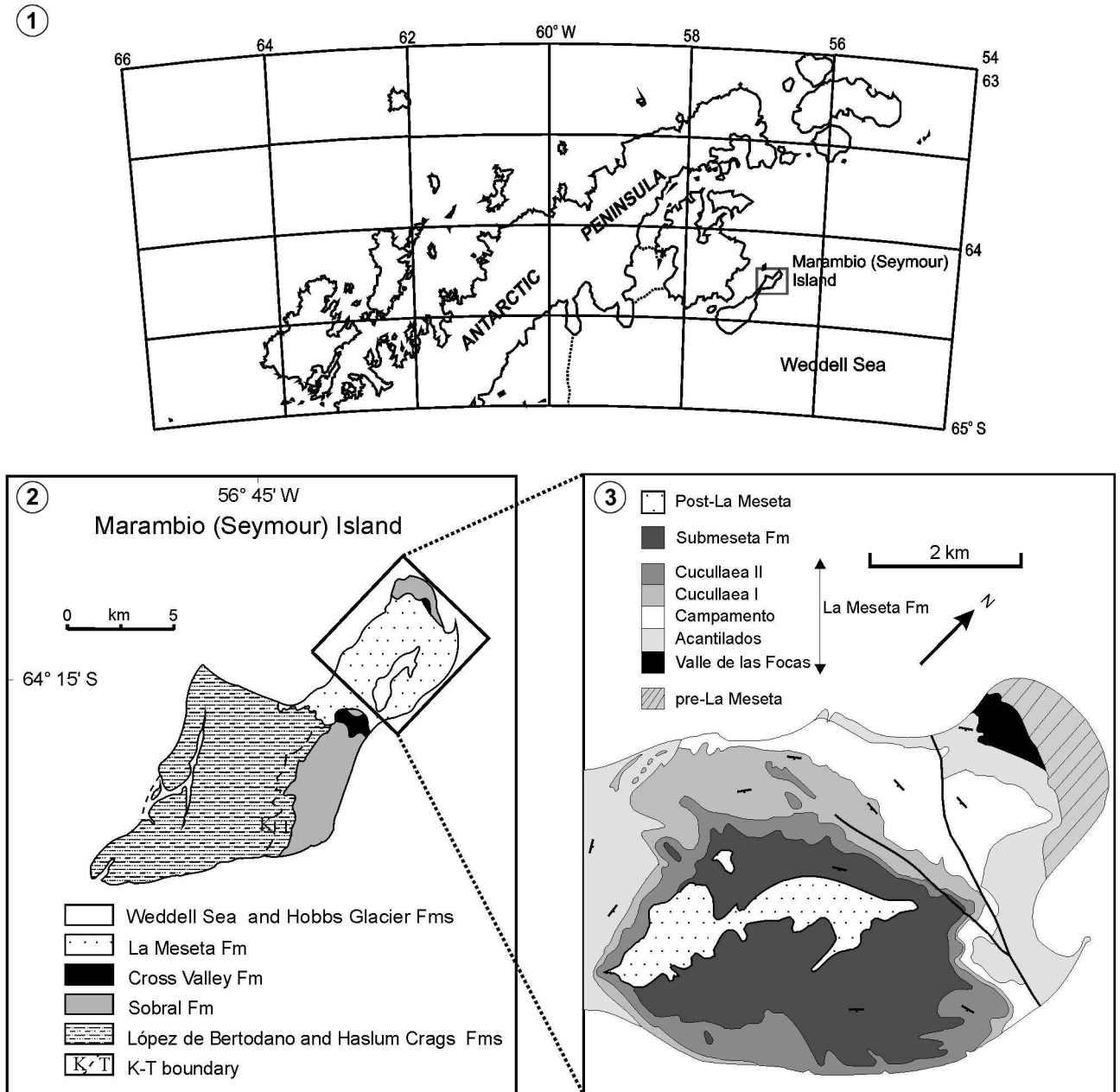

Figure 1. Localization and geological map of Marambio (Seymour) Island (Antarctic Peninsula). **1,** Localization of Marambio (Seymour) Island. **2,** Geological map. **3,** La Meseta Formation units indicating the localities where basilosaurids were collected.

Figure 2. Stratigraphic column of the La Meseta Formation on Marambio (Seymour) Island, Antarctic Peninsula. Chronostratigraphic interpretation for the La Meseta Formation based on dinocyst biostratigraphy and bivalve Sr-isotope signatures (modified from Douglas *et al.*, 2014: fig. S1). Abbreviations: **cu,** *Cucullaea*; **cg,** conglomerates and sandstones; **n,** naticids; **v,** veneroids; **t,** *Turritella*.

SYSTEMATIC PALEONTOLOGY

Order Cetacea Brisson, 1762

Pelagiceti Uhen, 2008

Family Basilosauridae Cope, 1868

Gen. et sp. indet.

Figures 3–4, Tables 1–2

Referred material. MLP 11-II-21-3, incomplete left mandible (from the alveolus of I_3 to M_3) including the P_2 and molar roots.

Geographic provenance. MLP 11-II-21-3 was collected from DPV 2/84 (64° 13′ 53.58″ S; 56° 39′ 13.74″ W), on the northern part of Marambio (Seymour) Island, Antarctic Peninsula (Fig. 1.3).

Stratigraphic provenance. MLP 11-II-21-3 comes from the basal horizon of the *Cucullaea* I Allomember (equivalent to TELM 4 of Sadler, 1988), middle Eocene (Lutetian–Bartonian) (Fig. 2). Specimen MLP 11-II-21-3 was found *in situ* in the shell bank of the *Cucullaea* I Allomember (Supplementary information Fig. S1), no age-diagnostic microfossils were recovered from the matrix around the specimen, but the source horizon is not in doubt. The adhering matrix is composed of coarse sand grains with granules and pebbles characteristic of this shell bank. Furthermore, the mode of preservation (intact, well preserved embedded part, the exposed portion weathered and broken in many pieces) of the mandible indicates that it was not transported after deposition, and there are no other potential source horizons in the immediate vicinity. The specimen was found associated with numerous specimens of *Cucullaea raea* Zinsmeister, 1984, close to the site where the holotype of the astrapothere *Antarctodon sobrali* Bond, Kramarz, MacPhee, and Reguero, 2011, was recovered (Bond *et al.*, 2011). The thanatocoenose of the site is heterogeneous: the bioclastic fraction consists of bivalves (*Cucullaea* sp.), gastropods (struthiolariids, naticids), a variety of other marine invertebrates together with marine (sharks, skates, penguins, etc.) and land (marsupial polydolopids and South American ungulates) vertebrate fossils mixed with fossil plant material (Reguero *et al.*, 2012). The shell bed represents a laterally continuous (several kilometers) horizon with a thicknesses of up to 3 meters. The bearing horizon is composed of thick
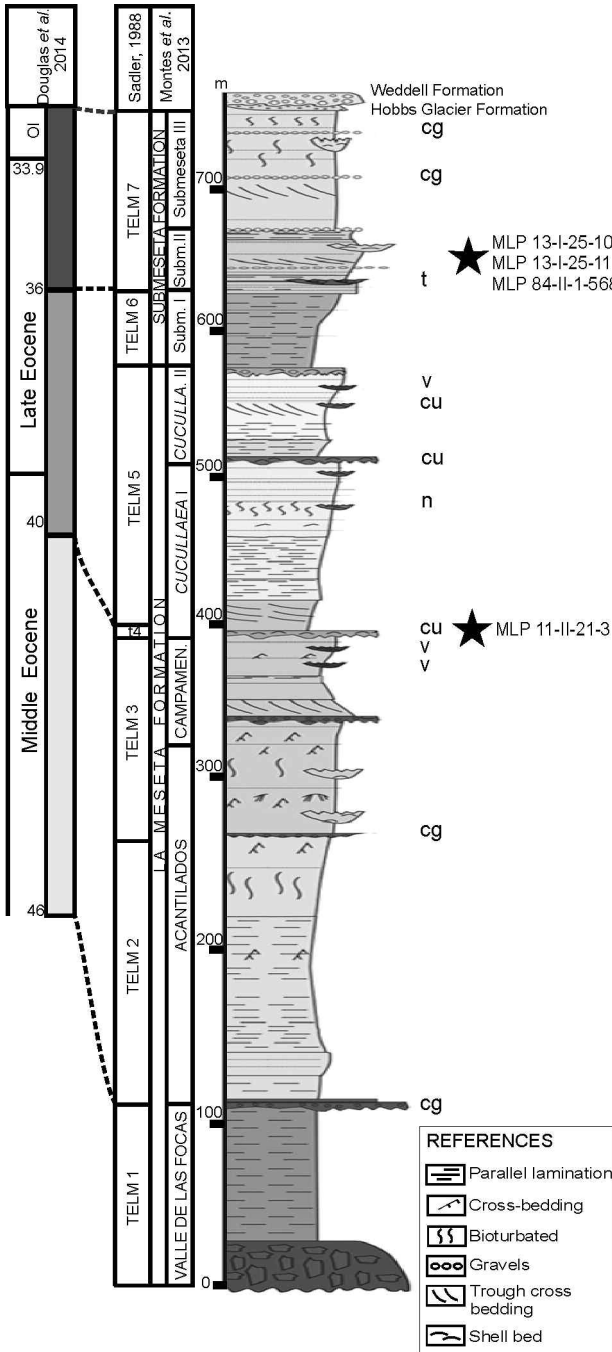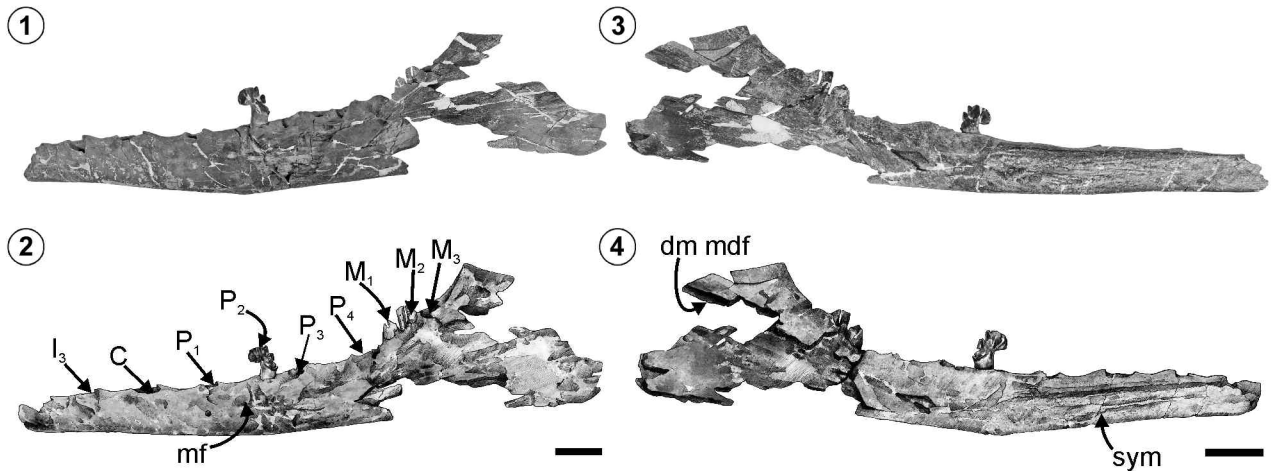
Figure 3. Basilosauridae gen. et sp. indet., left mandible (**MLP** 11-II-21-3). **1–2**, lateral (labial) view; **3–4**, medial (lingual) view. Abbreviations: **C,** canine; **dm mdf,** dorsal margin of mandibular foramen; I_3, incisor 3; $M_{1–3}$, molars 1–3; **mf,** mental foramina; $P_{1–4}$, premolars 1–4; **sym,** mandibular symphysis. Scale bars= 5 cm.

shelly conglomerates, well-sorted sands, and interlaminated sand/mud channel fills with thin shelly conglomeratic intervals, supporting matrix composed by bioclasts and some gravels immersed in a coarse-sand with some granules. Internally each bed is massive, with through cross bedding or rarely with parallel bedding. Sadler (1988) interpreted it as a transgressive lag characterized by abundant phosphate pebbles and glauconite. This TELM 4 shell bank is conformably overlain by non-fossiliferous sediments of the base of TELM 5. The fact that the fossil content of TELM 4 includes a significant number of reworked shells and shark teeth could explain the similarity of their strontium ratios to those of TELM 3 (Ivany *et al.*, 2008).

Description. MLP 11-II-21-3 consists of an incomplete left mandible from the alveolus of I_3 to the M_3 including the P_2 and the roots of molars (preserved length= +600 mm) (Fig. 3). The mandible is slender, and it is lower (46 mm) and thinner (31 mm) anteriorly than posteriorly. In lingual or medial view, the mandibular symphysis is long (approximately 43% of total length of the mandible) and it extends to the posterior margin of the anterior root of P_2. It has a rugose symphyseal surface defined by numerous longitudinal ridges, suggesting a sutured mandibular symphysis. In labial or lateral view there are three small mental foramina and six well-defined embrasure pits for the occlusion of the upper dentition, similar to those observed in *Zygorhiza kochii* Carus, 1847 (Kellog, 1936; USNM 11962) and *Dorudon atrox* An-

drews, 1906 (Uhen, 2004). The anteriormost pits, between the alveolus of I_{2-3}, I_3–C and C–P_1, are shallow and lie on the dorso-lateral surface of the mandible and correspond to the occlusion of I^2, I^3 and C respectively. The pits between P_{1-2}, P_{2-3} and P_{3-4} are deep and close to the dorsal margin of the mandible and correspond to the occlusion of P^1, P^2 and P^3 respectively. The pit for the occlusion of P^4 was not preserved and there are no pits for the occlusion of upper molars. In dorsal view, the labial surface is slightly convex and turns outward strongly behind the P_2. Six complete and three incomplete alveoli are found in the dorsal margin of the mandible (Fig. 3.2). Alveoli from I_3 to P_1 are for singled-rooted teeth, whereas the alveoli from P_2 to M_3 are for double-rooted teeth. The dental formula was presumably 3.1.4.3, like in other basilosaurids (Uhen, 2004). The alveolus of I_2 is broken. The alveolus of I_3 is almost circular and not as long as the alveolus of C. The alveolus of C is the largest of the single-rooted series; it is deep and anteroposteriorly longer than transversely (Tab. 1). The third alveolus is for P_1, it is smaller than the alveolus of C and both represent the largest diastema of the alveolus series (Tab. 1). The alveolus of P_2 is larger than that of P_1 and it is the first double-rooted of the series. The alveolus of P_3 is anteroposteriorly larger than the alveolus of P_2 and both are separated by a diastema of 13 mm. The anterior part of the alveolus of P_4 is separated from the alveolus of P_3 by a diastema of 7 mm. The posterior part of the alveolus of P_4 is not pre-

served. Towards the coronoid region, there are three double-rooted alveoli for M_1–M_3, two of which have the roots preserved *in situ*. The alveoli of molars are anteroposteriorly smaller than the double-rooted premolars, and therefore there is a decrease in the tooth size towards the coronoid region. In addition, towards the coronoid region there is a reduction of the diastema between alveoli, as the alveoli of molars are closer to each other. The alveolus of M_1 holds a fragment of the anterior root and a better-preserved posterior root. The alveolus of M_2 holds fragments of the anterior and posterior roots (Fig. 3.2).The roots of M_1 and M_2 are not fused along their length that is emergent from the alveoli and roots of M_2 are posteriorly recurved. The posterior portion of the mandible is partially preserved and lacks the mandibular condyle. The partially preserved dorsal margin of the mandibular foramen (Fig. 3.4) indicates that it is as large as those of other basilosaurids (height >105 mm) (Kellog, 1936; Uhen and Gingerich, 2001; Uhen, 2004; Gingerich, 2008; Martinez-Cáceres and de Muizon, 2011), which suggests the presence of a mandibular fat pad by analogy with living odontocetes (Cranford *et al.*, 1996).

The P_2 of MLP 11-II-21-3 is triangular-shaped, transversely compressed, with large accessory denticles on the posterior side of the crown, and double rooted (Fig. 4, Tab. 2). Two accessory denticles are completely preserved, and one is broken at the base. A small tubercle is located at the base of the crown. The accessory denticles have a triangular outline and are oval in cross-section. They are slightly recurved in posterior direction. The principal cusp is slightly larger than the others suggesting a decrease in size towards the base of the crown. There are small accessory tubercles in the posterior margin of the first accessory denticle. The principal cusp is incomplete and has smooth margins on the dorsal surface, indicating that this cusp was broken off and worn during the animal's life. There is no evidence of a protocone. There are well-developed wear facets on the apical surfaces of the posterior accessory denticles. A slightly developed and vertically elongated wear facet is observed only on the lateral surface of the second accessory denticle, and the enamel in this area is not completely worn (Fig. 4.1–4). A well-defined cingulum, U-shaped in dorsal view, is present encompassing the base of the third accessory denticle and the basal tubercle on the lingual and labial side of the crown (Fig. 4.5). The lingual side of the cingulum bears delicate tubercles. The posterior root of P_2 is longer anteroposteriorly (17 mm) than the anterior root (13 mm) and the transverse width of both is about 12 mm. The anterior root is circular in cross-section while the posterior root is oval. The roots are not fused below the crown. The tooth enamel is dark and smooth, and lacks the marked vertical striations on the lingual and labial side of the crown, which are variably developed in some basilosaurids such as *Dorudon atrox* and *Zygorhiza kochii* (Kellogg, 1936; Uhen, 2004; USNM 11962).

Comparisons. MLP 11-II-21-3 differs from the toothed Mysticeti *Llanocetus denticrenatus,* also recovered from the La Meseta Fm., by having comparatively smaller teeth and a dorsoventrally lower mandible, a short diastema between the lower alveoli of premolars (maximum diastema 30 mm between alveoli of P_1 and P_2 in contrast to 106 mm between the only two preserved teeth of *L. denticrenatus*), a mandible that lacks nutrient grooves around the alveoli, a crown of P_2 that lacks a broad palmate structure (the divergence angle between the axis of the principal cusp and the axis of the fourth accessory denticle is smaller, ~35°, than those observed in *Llanocetus denticrenatus*, ~63°; Mitchell, 1989), and the tooth crown is smooth without strong vertical ridges on labial and lingual enamel surfaces.

The morphology of the accessory cusps in the crown resembles that of other heterodont archaeocetes as protocetids such as the *Georgiacetus vogtlensis* Hulbert, Petkewich, Bishop, Bukry, and Aleshire, 1998 and *Pappocetus lugardi* Andrews,1920. These taxa also have accessory cusps in the crown of P_2 but they are markedly smaller and less defined than those present in basilosaurids (Andrews, 1920; Uhen, 2008). MLP 11-II-21-3 further differs from *Georgiacetus vogtlensis* in having the mandibular symphysis extended posteriorly below the anterior root of P_2, whereas in *Georgiacetus vogtlensis* the posterior end of the symphysis ends near the anterior margin of the anterior root of P_3 (Uhen, 2008).

The mandible of MLP 11-II-21-3 is smaller (although it is incomplete, only a small anterior and posterior portion is missing) than in the large basilosaurids *Basilosaurus cetoides* Owen, 1839 (Tab. 1) and *Cynthiacetus peruvianus* Martínez-Cáceres and de Muizon, 2011 (length= 1170 mm, MNHN.F.PRU 10; Martínez-Cáceres and de Muizon, 2011). However, it is similar in length to some mid-sized basilosaurids (*e.g.*, *Zygorhiza kochii*, length= +718 mm, USNM 11962,

TABLE 1 – *Measurements of the mandibles of MLP 11-II-21-3 and MLP 13-I-25-11 (in mm) and some comparative measurements with other basilosaurids (taken from Kellog, 1936).*

	Basilosauridae indet.		Zygorhiza kochii	Basilosaurus cetoides
	MLP 11-II-21-3	MLP 13-I-25-11	USNM 11962	USNM 4674
Dentary length	+600	+594	+712	+1136
Length of symphysis	+256	-	+315	+415
Vertical height of the mandible at the level of I3 alveolus	46	-	-	71.5
Vertical height of the mandible at the level of C alveolus	51	-	-	80
Vertical height of the mandible at the level of P1 alveolus	54	+30	-	89
Vertical height of the mandible at the level of P2 alveolus	63	-	-	101
Vertical height of the mandible at the level of P3 alveolus	73	-	-	111
Vertical height of the mandible at the level of P4 alveolus	77	+47	67	-
Vertical height of the mandible at the level of M3 alveolus	-	+64	133	-
Transverse width of the mandible at the level of I3 alveolus	31.5	-	-	-
Transverse width of the mandible at the level of C alveolus	34	-	-	-
Transverse width of the mandible at the level of P1 alveolus	39	-	-	-
Transverse width of the mandible at the level of P2 alveolus	40	-	-	-
Transverse width of the mandible at the level of P3 alveolus	45	-	-	-
Transverse width of the mandible at the level of P4 alveolus	46	-	-	-
Transverse width of the mandible at the level of M3 alveolus	-	26	-	-
Antero-posterior length of I3 alveolus	23	-	-	71
Antero-posterior length of C alveolus	30	-	-	74
Antero-posterior length of P1 alveolus	21	26	-	61.5
Antero-posterior length of P2 alveolus	37	42	-	79.5
Antero-posterior length of P3 alveolus	46	-	-	91.5
Antero-posterior length of P4 alveolus	-	-	-	100
Antero-posterior length of M1 alveolus	*26	47	-	-
Antero-posterior length of M2 alveolus	25	43	-	-
Antero-posterior length of M3 alveolus	27	38	-	-
Transverse width of I3 alveolus	20	-	-	-
Transverse width of C alveolus	24	-	-	-
Transverse width of P1 alveolus	18	-	-	-
Transverse width of P2 alveolus[1]	20	-	-	-
Transverse width of P3 alveolus	20	-	-	-
Transverse width of P4 alveolus	15	-	-	-
Transverse width of M1 alveolus	*16	*16	-	-
Transverse width of M2 alveolus	16	*17	-	-
Transverse width of M3 alveolus	14	*14	-	-
Diastema between I3 and C	29	-	34	31
Diastema between C and P1	45	-	38	31
Diastema between P1 and P2	30	31	31.5	27
Diastema between P2 and P3	13	-	26	16.5
Diastema between P3 and P4	7	-	-	-
Diastema between P4 and M1	-	12	-	-
Diastema between M1 and M2	0	0	-	-
Diastema between M2 and M3	0	0	-	-

+ nearly complete; *approximate.
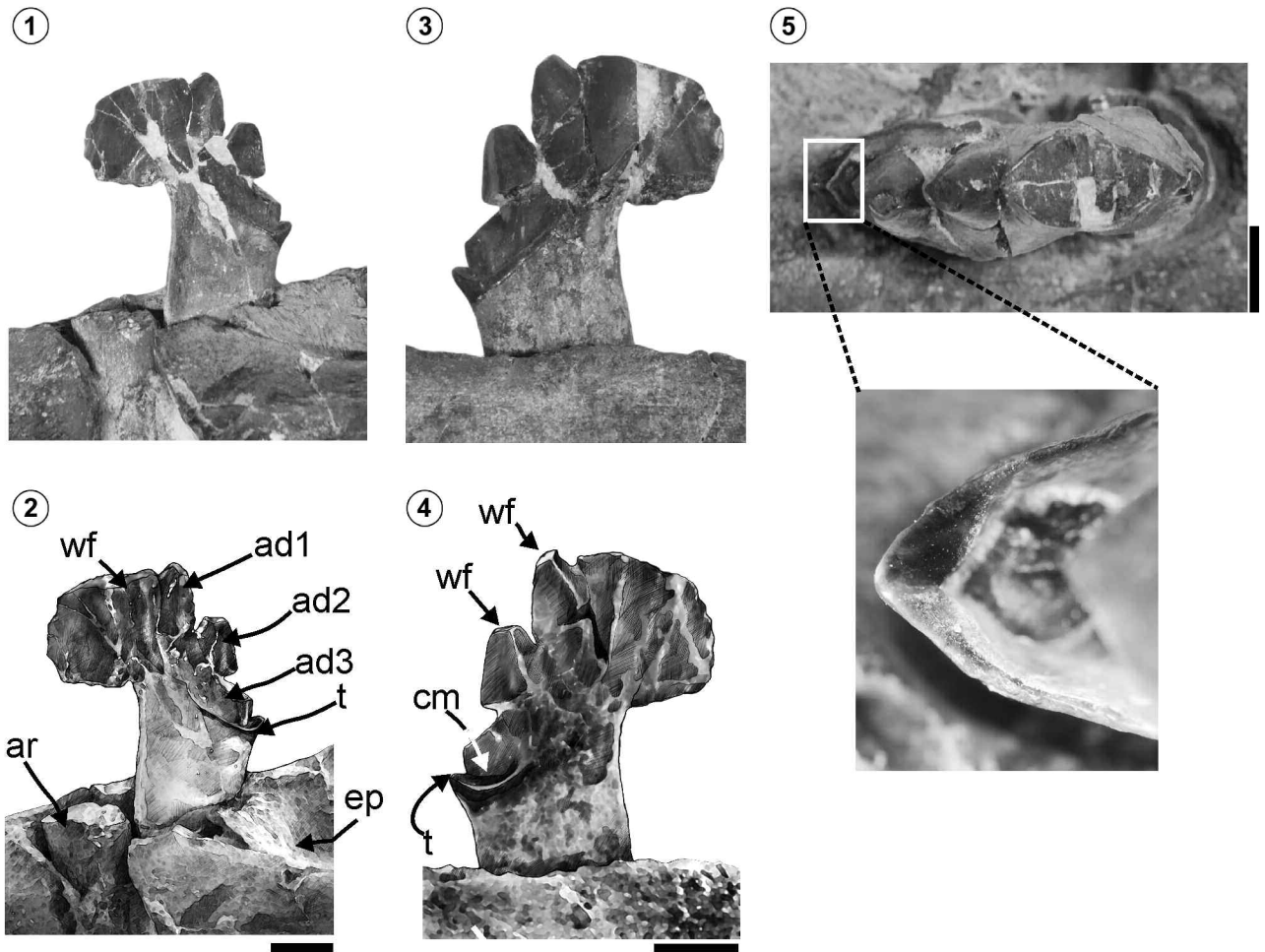[1]In double-rooted alveoli this measure was taken along the maximum width.

Figure 4. Basilosauridae gen. et sp. indet., dental features (**MLP** 11-II-21-3). **1–2,** lateral (labial) view of left lower P_2; **3–4,** medial (lingual) view of left P_2; **5,** dorsal (occlusal) view of left lower P_2 with a detail of the posterior cingulum. Abbreviations: **ad 1–3,** accessory denticles 1–3; **ar,** anterior root; **cm,** cingulum; **ep,** embrasure pit; **t,** tubercle; **wf,** wear facets. Scale bars= 1 cm.

Kellog, 1936; *Dorudon atrox,* length = 850 mm, Uhen, 2004).

The completely erupted permanent teeth and fully developed roots without signs of resorption indicate this specimen is not a juvenile and that the size of this mandible does not result from an early ontogenetic stage. MLP 11-II-21-3 further differs from *Basilosaurus cetoides* in having the crown of P_2 not curved lingually, with smooth enamel, a well-developed cingulum at the base of the crown, and roots less expanded transversely (approximately half the transverse width of the roots of *B. cetoides*) (USNM 4674; Kellog, 1936, p. 34). The specimen MLP 11-II-21-3 differs from *Cynthiacetus* Uhen, 2005, by having a small tubercle on the posterior side of the crown of P_2 (Uhen, 2005; Martínez-Cáceres and de Muizon, 2011). MLP 11-II-21-3 differs from

the basilosaurid *Ancalecetus simonsi* Gingerich and Uhen, 1996, by having a relatively wider diastema between the alveoli of I_3–C, C–P_1 and P_1–P_2, and a smaller size of the alveoli of premolars. MLP 11-II-21-3 differs from *Saghacetus osiris* Gingerich, 1992, by having three accessory denticles on the posterior side of the crown of P_2, rather than two accessory denticles (Gingerich, 2008). Similarly, it differs from *Zygorhiza kochii* by having a well-developed cingulum on the crown of P_2, the crown of P_2 not curved lingually and with smooth enamel, whereas in *Z. kochii* the enamel of the crown is striated vertically on both sides (Kellog, 1936; USNM 11962). It differs from *Dorudon atrox* by having a relatively short diastema between the alveoli of P_2–P_3 and P_3–P_4 (Uhen, 2004). MLP11-II-21-3 differs from *Supayacetus*

TABLE 2 – *Measurements of the tooth of MLP 11-II-21-3 and MLP 13-I-25-10 (in mm) and some comparatives measurements with other basilosaurids (taken from Kellog, 1936; Köhler and Fordyce, 1997; Uhen and Gingerich, 2001; Uhen, 2004).*

| | Basilosauridae indet. | | | ?Zygorhiza sp. | | Zygorhiza kochii | | | | Dorudon atrox | | | | | | Chrysocetus healyorum | |
| | MLP 11-II-21-3 | MLP 13-I-25-10 | | OU 22222 | OU 22242 | USNM 16639 | USNM 11962 | | | UM 101223 | UM 94811 | UM 83902 | NSFM 4451 | | | SCSM 87.195 | |
	P^2	P^2 or $P_{3(4?)}$	$dI?$	P^3	P^2	dP^2	P^2	P_3	P^2	dI^3	dP^2	dP_3	P^2	P_2	P_3	P^2	P_3
Crown height	+16	30	21	28	40	-	35	45	42	24	26	27	32.5	30	20	29	32
Buccolingual width of the crown	9	10	8		15	10	13	15	15	10	12	11	14	14	15.5	12	12
Antero-posterior length of the crown	+33	46	13	34	45	41.5	45	55	54	17	43	59	52	6	60	42	49
Antero-posterior length of anterior root	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Antero-posterior length of posterior root	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Buccolingual width of anterior root	13	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Buccolingual width of posterior root	12	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Root height	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-

+ nearly complete.
Abbreviations: d, deciduous.

muizoni Uhen, Pyenson, Devries, Urbina, and Renne, 2011 by having a larger and higher mandible (length of the mandible between alveolus of I_3 and P_2 is 219 mm in MLP 11-II-21-3 and ~120 mm in *Supayacetus muizoni*; height of the mandible at the level of the alveolus of P_2 is 63 mm in

Figure 5. **Basilosauridae gen. et sp. indet.**, isolated cheek tooth (P^2 or $P_{3(4?)}$) and incisor (**MLP** 13-I-25-10). **1, 4,** lateral (labial); **2, 5,** medial (lingual) view; **3,** dorsal (occlusal) view of cheek tooth; **6,** ventral view of the deciduous incisor showing the root deeply hollowed. Scale bars= 1 cm.

MLP 11-II-21-3 and ~38 mm in *S. muizoni*; Uhen *et al.*, 2011: fig. 6) and a relatively longer diastema between alveoli of P_1 and P_2.

A combination of teeth and mandibular features allows assigning MLP 11-II-21-3 to Basilosauridae. These include the transversely compressed and triangular-shaped premolar teeth with a large number of high and wide accessory denticles on the posterior side of the crown (not forming a palmate structure), cheek teeth roots not connected by an isthmus below the crown, long, rugose and sutured mandibular symphysis, alveoli for 11 mandibular teeth, a long diastema between alveoli of I_3–C, C–P_1 and P_1–P_2, and a mandible with embrasure pits. Given the fragmentary nature of MLP11-II-21-3 and the lack of autapomorphic features, we refrain from naming a new species and refer it as Basilosauridae gen. et sp. indet. pending future discoveries of more complete specimens.

Gen. et sp. indet.
Figure 5, Table 2

Referred material. MLP 13-I-25-10, isolated incisor deciduous tooth and isolated cheek tooth.

Geographic provenance. MLP 13-I-25-10 was collected from IAA 3/12 (64° 13' 59.5" S; 56° 36' 46.1" W), Marambio (Seymour) Island, Antarctic Peninsula (Fig. 1.3).

Stratigraphic provenance. MLP 13-I-25-10 come from the upper levels of the Submeseta Formation (Submeseta II Allomember, level 38, equivalent to TELM 7 of Sadler, 1988); late Eocene (Priabonian) (Fig. 2).

Description. MLP 13-I-25-10 includes a deciduous incisor or canine and an isolated cheek tooth (Fig. 5.1–6; Tab. 2). In basilosaurids the most remarkable difference between incisors and canine is that the canine is considerably larger than the incisors (Kellog, 1936; Uhen, 2004; Gol'din *et al.*, 2014). The deciduous tooth is similar in size to lower deciduous incisors of *Dorudon atrox* and a deciduous basilosaurid incisor from the La Meseta Formation (Fostowicz-Frelik, 2003; Uhen, 2004) (Tab. 2). Based on this observation we suggest that this tooth probably corresponds to an incisor (more likely an upper left or lower right I3). The crown is almost complete and lacks the anterior and posterior margin; it is conical and the apex is posteriorly and lingually oriented. The labial side of the crown is slightly convex while the lin-
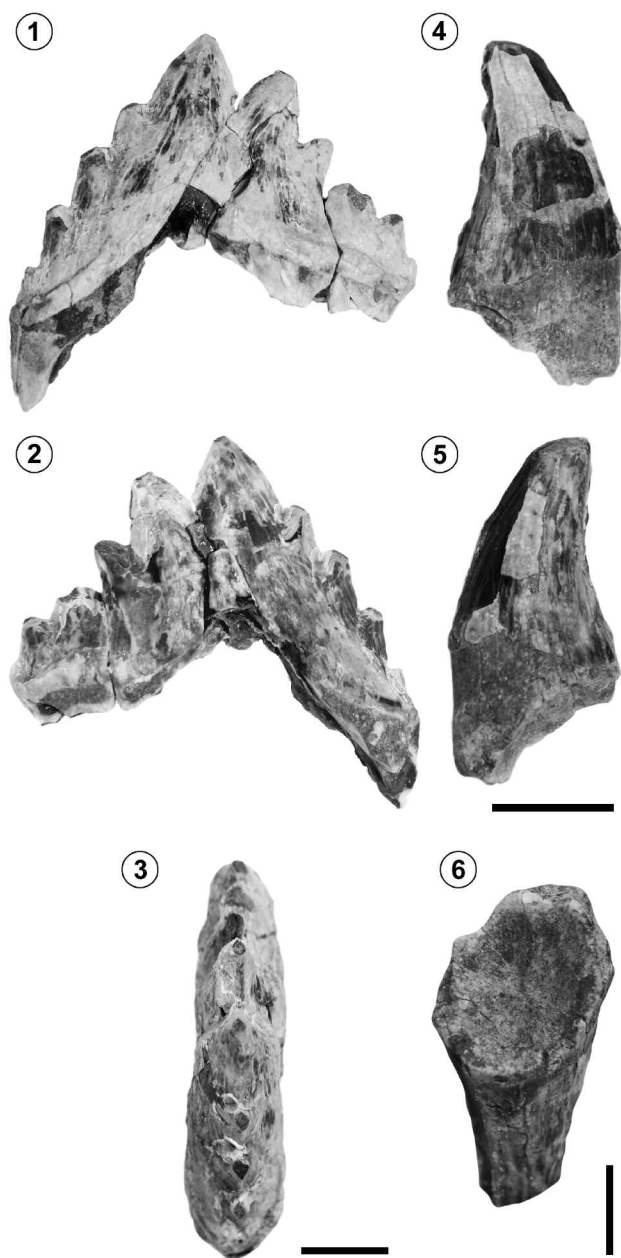
gual side is concave. The enamel is partly preserved, gray-colored, and devoid of ornamentation. The root is short (maximum height= 9 mm; anteroposterior length at the root base=15 mm) and the posterior portion is deeply hollowed suggesting that a resorption of the root was in progress (Fig. 5.6). On the labial side of the root, there is a small notch, which is interpreted as the longitudinal groove present in the deciduous incisor of *Dorudon atrox* (Uhen, 2004, p. 21).

The cheek tooth consists of a premolar with a well-preserved crown and lacks both roots (only the bases of the roots are preserved) (Fig. 5.1–3). The identity of the premolar cannot be determined precisely. It probably represents an upper right P^2 or a lower left $P_{3-4?}$ based on the number of accessory denticles but it is definitely not a P^3 or P^4 based on the lack of the posterior lingual inflation of the root which characterizes these premolars (Kellog, 1936; Köhler and Fordyce, 1997; Uhen and Gingerich, 2001; Uhen, 2004). The small size of the cheek tooth in comparison to permanent dentitions of other basilosaurids (Tab. 2), together with the lack of wear facets, might suggest that this also is a deciduous tooth. The crown is triangular, transversely compressed and longer anteroposteriorly than dorsoventrally high (Tab. 2). There are three accessory denticles and a small tubercle on the anterior side of the crown, and four accessory denticles and a small tubercle on the posterior side. The anterior accessory denticles and the first and fourth posterior accessory denticles are completely preserved, whereas the second and third are broken on the apex. They all have a triangular outline, are oval in cross section, and the posterior accessory denticles are larger than the anterior ones. The anterior accessory denticles are dorsally oriented, while the posterior accessory denticles are posteriorly oriented (Fig. 5.1).There are no tubercles on the margins of the accessory denticles. The apical denticle is slightly posteriorly oriented and is the largest (height= 9 mm, width= 10 mm); however, it is not considerably larger than the first posterior accessory denticle. There is no protocone in this crown. There are indistinct wear facets on the apical surfaces of the accessory denticles and there is no evidence of a vertical wear facet. A weak cingulum is present encompassing the base of the posterior basal tubercle on the lingual side of the crown and there are no small tubercles on the cingulum. In dorsal view, the crown is not curved lingually (Fig. 5.3). Most of the enamel has not been preserved, but a small portion is present on the base of both sides of the crown, where it shows a light coloration and a smooth outer surface. Only the bases of the anterior and posterior roots are preserved and are approximately equal in size.

Comparisons. The cheek tooth of MLP 13-I-25-10 differs from those of *Llanocetus* in its smaller size and the absence of a broad palmate structure (Mitchell, 1989). Moreover, the cheek tooth closely resembles those of the protocetids *Georgiacetus vogtlensis* and *Pappocetus lugardi*. However, the accessory cusps in the crown are markedly larger and more defined than those of these protocetids (Andrews, 1920; Uhen, 2008).

The cheek tooth shares a suite of morphological features with Basilosauridae, such as the transversely compressed and triangular tooth shape, with a large number of high and wide accessory denticles on the posterior side of the crown. Among basilosaurids, the cheek tooth is close in size to the deciduous premolars (particularly P^2 and P_3) of *Zygorhiza kochii* and *Dorudon atrox*, as well as to the permanent dentition of the small basilosaurid *Chrysocetus healyorum* Uhen and Gingerich, 2001 (Tab. 2). Additionally, the Antarctic cheek tooth is more similar to deciduous P_3 of *Dorudon atrox* in terms of the number of accessory denticles than to any other basilosaurid. The lack of information on deciduous teeth morphology in other basilosaurids prevents further comparisons.

On the other hand, the morphology of the cheek tooth is particularly close to the specimen OU 22242 from New Zealand referred to *Zygorhiza* sp. (Köhler and Fordyce, 1997). Both specimens share the number and size of accessory denticles, the development of the cingulum, and the smooth enamel. However, the "Antarctic cheek tooth" differs from OU 22242 by having the anterior half of the crown not curved lingually, a smaller crown height (Tab. 2), a smaller apical denticle, and in the lack of small tubercles on the cingulum.

The transversely compressed and triangular shape of the cheek tooth, and the large number of high and wide accessory denticles on the posterior side of the crown (not forming a palmate structure), allows assigning MLP 13-I-25-10 to Basilosauridae. Based on the lack of diagnostic features, we refer it as Basilosauridae gen. et sp. indet.

Family ?BASILOSAURIDAE Cope, 1868

?Gen. et sp. indet.
Figure 6, Table 1

Referred material. MLP 13-I-25-11, incomplete left mandible (from the alveolus of C to alveolus of M_3).

Geographic provenance. MLP 13-I-25-11 was collected from IAA 3/12 (64° 13' 59.5" S; 56° 36' 46.1" W), Marambio (Seymour) Island, Antarctic Peninsula (Fig. 1.3).

Stratigraphic provenance. MLP 13-I-25-11 comes from the upper levels of the Submeseta Formation (Submeseta II Allomember, level 38, equivalent to TELM 7 of Sadler, 1988); late Eocene (Priabonian) (Fig. 2).

Description. MLP 13-I-25-11 consists of an incomplete left mandible with the corresponding mandibular condyle. The preserved portions of the mandibular body include the lingual surface comprising C to M_3 and the labial surface from P_4 to M_3 (Fig. 6.1–2). The ramus of the mandible is poorly preserved and only includes small portions of the lingual and labial surfaces, with the coronoid and angular process missing. The ventral margin of the body and ramus of the mandible are not preserved. The mandible has a preserved length of +594 mm from the alveolus of C to alveolus of M_3. The body of the mandible is short at the level of the premolar alveolar series and continues posteriorly with a slight increase in height until the last alveolus of the molars (Tab. 1). The most abrupt depth increase occurs posterior to the molar series, towards the coronoid region (height at the level of the coronoid region= +69 mm). In lingual or medial view, the only preserved portion of the mandibular symphysis corresponds to a pronounced dorsal ridge and a small portion of rugose bone surface (Fig. 6.2); although most of the mandibular symphysis is missing, the preserved portion allows inferring that it extends posteriorly to the anterior margin of the alveolus of P_2. In dorsal or occlusal view, the alveolar margin is preserved from the alveoli C–M_3. The alveoli of P_3–P_4 are poorly preserved; therefore it is difficult to establish the limits between the alveoli and their size. The alveolus of C is broken; the portion preserved indicates
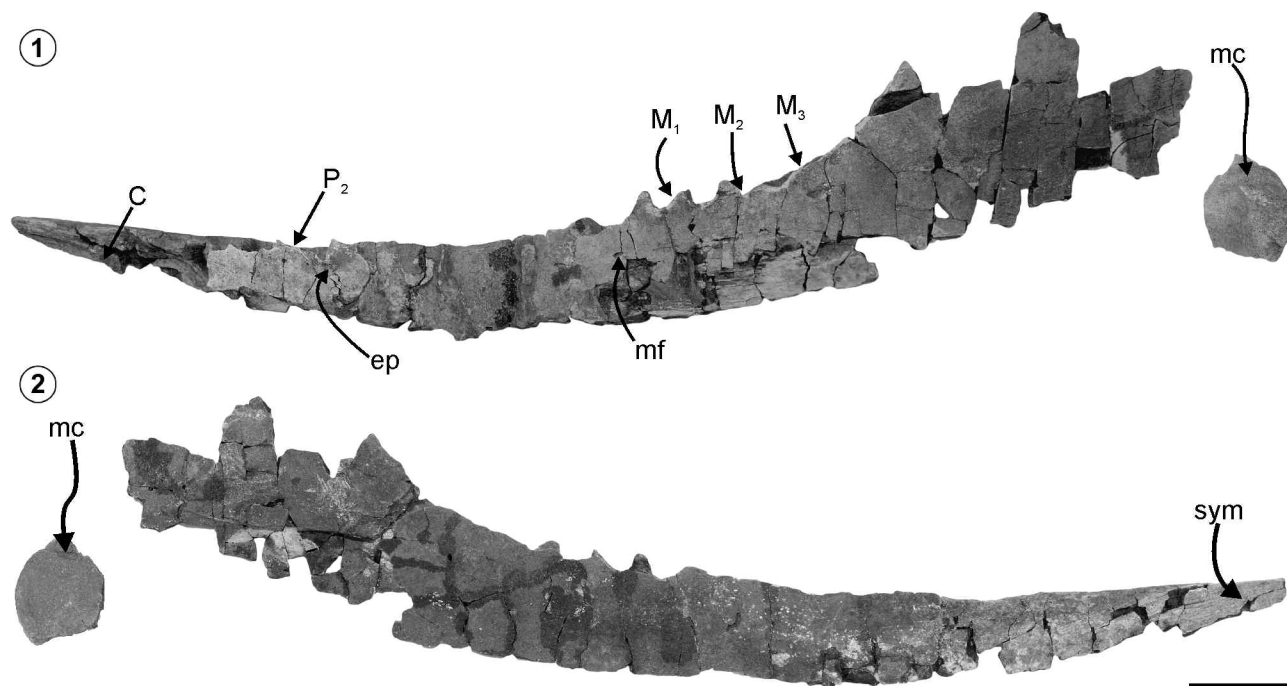

Figure 6. **?Basilosauridae gen. et sp. indet.,** left mandible (**MLP** 13-I-25-11). **1,** lateral (labial) view; **2,** medial (lingual) view. Abbreviations: **C,** canine; **ep,** embrasure pit; **M_{1-3},** molars 1–3; **mc,** mandibular condyle; **mf,** mental foramina; **P_2,** premolar 2; **sym,** mandibular symphysis. Scale bar= 5 cm.

it has a single and curved root. The alveolus of P_1 is circular and for a singled-rooted tooth, whereas the alveoli of P_2–M_3 are for double-rooted teeth. The alveolus of P_1 is the smallest of the series (anteroposterior length= 26 mm) and only the lingual margin is preserved. The alveolus of P_2 is larger (anteroposterior length= 42 mm) than the alveolus of P_1 and both lingual and labial margins are preserved. Only the lingual margins of the alveoli of P_3–P_4 are present. One embrasure pit is observed on the labial margin of the mandible between alveoli of P_2–P_3 (Fig. 6.1). The alveoli of M_1, M_2 and M_3 have an anteroposterior length of 47, 43, and 38 mm and a transverse diameter of 16, 17, and 14 mm, respectively. The diastema between P_1–P_2 is 31 mm and the one between P_4–M_1 is 12 mm; the diastema between P_2–P_3 and P_3–P_4 could not be determined due to the poor preservation of these alveoli. There is no diastema between the alveoli of the molar teeth; as a result the alveoli are very close to each other. The alveoli from P_1–P_2 are slightly laterally oriented, whereas posterior to P_2 the alveoli are dorsally oriented. The preserved lingual surface of the mandible is convex and there is no evidence of labial deflection, although this could be related to a slight diagenetic compression. In labial view there are two small mental foramina below the alveoli of P_4 and M_1 (Fig. 6.1). The coronoid region of the mandible is partially preserved including only the dorsalmost portion of the mandible. The mandible is thin at this level. The mandibular condyle is separately preserved from the body of the mandible; it is higher dorsoventrally (47 mm) than transversely wide (22 mm) (Fig. 6). The articular surface is oval and is markedly convex, with a slight lingual orientation. The mandibular foramen is not preserved.

Comparisons. The mandibular morphology of MLP 13-I-25-11 clearly differs from the toothed Mysticeti *Llanocetus denticrenatus*, also known from the La Meseta Formation, by having a dorsoventrally lower mandible, a short diastema between the alveoli of lower premolars, and a mandible that lacks nutrient grooves around the tooth alveoli (Mitchell, 1989).

The morphology of the mandible can be differentiated from that of the protocetids *Georgiacetus vogtlensis*, *Rhodocetus kasrani* Gingerich, Raza, Arif, Anwar, and Zhou, 1994, *Pappocetus lugardi*, and *Togocetus traversei* Gingerich and Cappetta, 2014, in having a longer diastema between the

alveoli of premolars; from *Georgiacetus vogtlensis*, *Pappocetus lugardi*, and *Togocetus traversei* in having a mandibular symphysis extending up to the level of the alveolus of P_2, whereas in these taxa the symphysis reaches the level of the alveolus of P_3 (Andrews, 1920; Gingerich *et al.*, 1995; Uhen, 2008; Bianucci and Gingerich, 2011; Gingerich and Cappetta, 2014).

MLP 13-I-25-11 shares a suite of morphological features with Basilosauridae, such as a long mandibular symphysis, an elongated intervening diastema between the alveoli of P_1–P_2, and well-developed embrasure pits. Although only a small anterior and posterior portion is missing, MLP 13-I-25-11 is smaller than the large basilosaurids *Basilosaurus cetoides* (Tab. 1) and *Cynthiacetus peruvians* (length= 1170 mm MNHN.F.PRU 10; Martínez-Cáceres and de Muizon, 2011). In turn, MLP 13-I-25-11 is larger than the basilosaurid *Ancalecetus simonsi* Gingerich and Uhen, 1996, as the length of the mandible between the alveolus of C and M_3 is +594 mm in MLP 13-I-25-11 and 415 mm in *Ancalecetus simonsi*, and also has a relatively wider diastema between the alveoli of the premolars (Gingerich and Uhen, 1996, p. 370).

Finally, MLP 13-I-25-11 is close in size (*i.e.*, total length) to the mandible MLP 11-II-21-3 from TELM 4 (this contribution) but it differs by having larger molar alveoli size (Tab. 1). Given the fragmentary nature of MLP 13-I-25-11, it is provisionally identified as Basilosauridae gen. et sp. indet., pending future discoveries of more complete specimens.

?Gen. et sp. indet.
Figure 7, Table 3

Referred material. MLP 84-II-1-568, right innominate bone.
Geographic provenance. MLP 84-II-1-568 comes from DPV 14/84 (64° 14' 55.52" S; 56° 36' 09.05" W), Marambio (Seymour) Island, Antarctic Peninsula (Fig. 1.3).
Stratigraphic provenance. MLP 84-II-1-568 comes from the Submeseta Formation (Submeseta II Allomember, level 38, equivalent to TELM 7 of Sadler, 1988); late Eocene (Priabonian) (Fig. 2).
Description. The specimen corresponds to a right innominate bone of exceptional preservation, containing portions of the three pelvic bones: ilium, ischium and pubis (Fig. 7; Tab. 3). The sutures between these bones are not visible. The innominate bone is longer (preserved maximum length= +205

mm) than wide (maximum width= 68 mm). The dorsal margin is almost straight and the ventral margin is convex; the innominate bone is thin at the level of the ischium and thick at the level of the acetabulum region (Fig. 7.3–4).

The preserved portion of the ilium includes an anterodorsally oriented projection with a broken apex, precluding any observation of the development of the bone. The ilium is dorsoventrally broad and thick proximal to the acetabulum and becomes narrower and thinner toward the apex.

The ischium is almost completely preserved (length=

71 mm) and delimits the posterodorsal margin of the obturator foramen. The ischium broadens posterior to the obturator foramen forming a rectangular blade; in this region the ischium is relatively flat and mediolaterally thin. At this level, the ventral margin of the ischium is concave and the dorsal margin is approximately straight and presents a dorsal rounded projection (Fig. 7.1). The posterior margin is almost complete, convex and with a rough and spongy appearance.

The acetabulum is mostly eroded and can only be differentiated by the presence of a concave surface. The obtu-
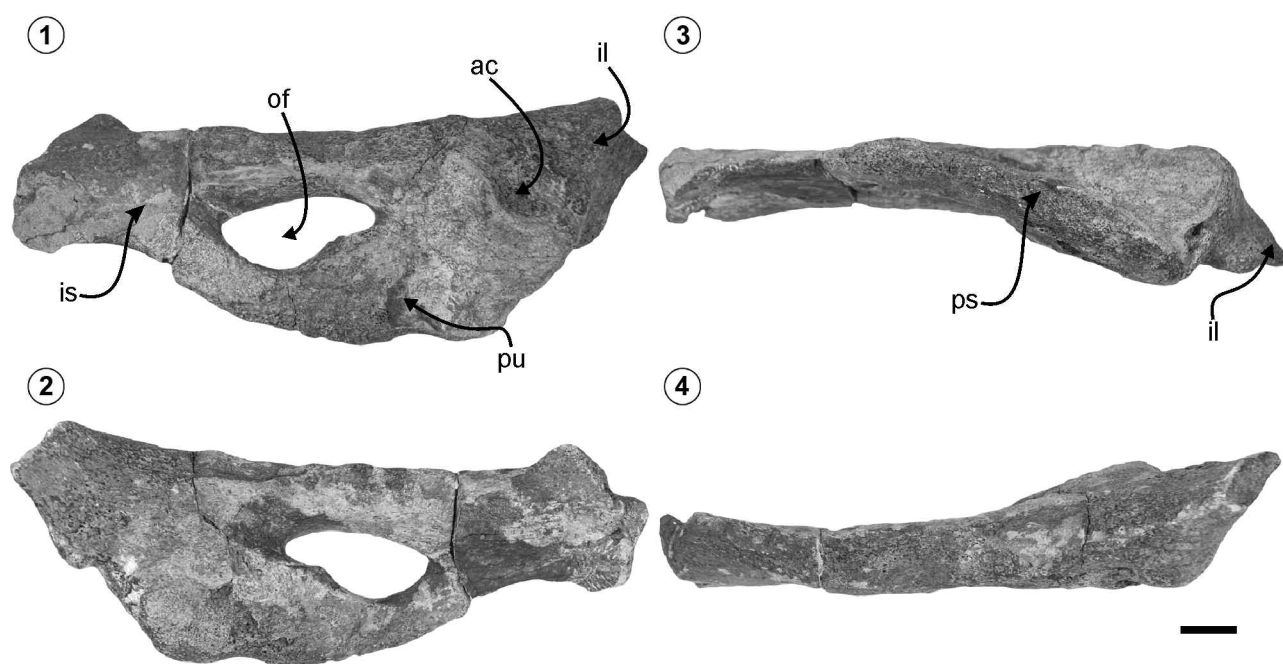

Figure 7. ?**Basilosauridae gen. et sp. indet.,** left innominate bone (**MLP** 84-II-1-568). **1,** lateral; **2,** medial; **3,** ventral; **4,** dorsal views. Abbreviations: **ac,** acetabulum; **il,** ilium; **is,** ischium; **of,** obturator foramen; **ps,** pubic symphisis; **pu,** pubis. Scale bar= 2 cm.

TABLE 3 – Measurements of the innominate bone of MLP 84-II-1-568 and Basilosaurus cetoides *(taken from Kellog, 1936). Measurements in mm.*

	Basilosauridae indet.	Basilosaurus cetoides
	MLP 84-II-1-568	*USNM 12261*
Total length	*+205*	*+234*
Maximum width	68	-
Ischium width	71	-
Obturator foramen height	20	17.5
Obturator foramen length	42	21
+nearly complete		

rator foramen is the most conspicuous character of this bone: it is anteroposteriorly longer (42 mm) than dorsoventrally high (20mm). The dorsal margin is not markedly concave as the ventral margin. Along its ventral margin there is a small projection of bone towards the center of the obturator foramen, which defines two regions: a small anterior portion and a large posterior one. In medial view, a deep and well-defined canal is present towards the anterodorsal margin of the obturator foramen (Fig. 7.2).

The pubis, together with the ischium, delimits the obturator foramen. The ventral margin of the pubis is broader than the ventral margin of the ischium and the anteriormost end is medially oriented. The ventral margin of the pubis corresponds to the symphyseal surface, which has a rough and spongy appearance and indicates there was a cartilaginous contact between the right and left innominate bones (Fig. 7.3).

Comparisons. MLP 84-II-1-568 is different from other previously described cetacean innominate bones. It differs from the protocetids *Rodhocetus kasranii*, *Georgiacetus vogtlensis*, *Maiacetus inuus* Gingerich, Ul-Haq, von Koenigswald, Sanders, Smith, and Zalmout, 2009, *Natchitochia jonesi* Uhen, 2014, and *Qaisracetus arifi* Gingerich, Ul-Haq, Khan, and Zalmout, 2001, by its smaller size (in absolute and relative terms) (Uhen, 2014: tab. 1), the ischium and pubis forming a rectangular blade (*i.e.*, anteroposteriorly longer than dorsoventrally high), an ischium that broadens posteriorly, and a smaller and oval-shaped obturator foramen (which in protocetids is teardrop-shaped and higher than long; Andrews, 1920; Hulbert *et al.*, 1998).

MLP 84-II-1-568 is similar to the condition of basilosaurids (*i.e.*, *Basilotritus wardii* Uhen, 1999, *Basilosaurus isis* Andrews, 1904, *B. cetoides* and *Chrysocetus healyorum*) in both shape and size, and in having a smaller obturator foramen and a wider pubis (Kellog, 1936; Gingerich *et al.*, 1990; Uhen, 1999; Uhen and Gingerich, 2001; Gol'din, 2014). However, MLP 84-II-1-568 shows some peculiarities that differentiate it from other innominate bones of basilosaurids. In MLP 84-II-1-568 the obturator foramen is anteroposteriorly longer (in absolute and relative terms; Tab. 3) than in *Basilosaurus cetoides* and *B. isis* and it has an oval shape with an inward bone protrusion, whereas the foramen is circular in basilosaurids. In addition, the ischium of MLP 84-II-1-568 differs from *Basilosaurus isis, B. cetoides*

and *Chrysocetus healyorum* in being shorter posteriorly, with a constricted neck that is more robust on the ventral margin. Finally, the ilium is wider than in *Chrysocetus healyorum*, and unlike *Basilosaurus* it is anterodorsally oriented (USNM 4676; Kellog, 1936; Gingerich *et al.*, 1990; Uhen and Gingerich, 2001).

The information on pelvic morphology in basal Neoceti is scarce and most informative materials have only been preliminary reported (Fordyce *et al.*, 2000; Martínez Cáceres *et al.*, 2011) preventing further comparisons of MLP 84-II-1-568. The innominate bone is similar to that of basilosaurids in shape and size, a reduced obturator foramen (in comparison to that of protocetids) and a wider pubis, however key innominate basilosaurid characters, such as the reduction of the ilium, could not be determined for this specimen. Based on this we provisionally refer MLP 84-II-1-568 to ?Basilosauridae gen. et sp. indet. pending future discoveries of more complete specimens.

DISCUSSION
Antarctic basilosaurids

Basilosaurids are well known from late middle Eocene to late Eocene in Northern Hemisphere localities (*e.g.*, Gingerich *et al.*, 1990; Gingerich, 1992; Uhen and Gingerich, 2001;Uhen, 2004, 2013; Gol'din and Zvonok, 2013; Zouhri *et al.*, 2014; Gingerich and Zouhri, 2015), while in the Southern Hemisphere their records are scarce (*e.g.*, Fordyce, 1985; Köhler and Fordyce, 1997; Fitzgerald, 2004; Martínez-Cáceres and de Muizon, 2011; Uhen *et al.*, 2011) and, in some cases (*i.e.*, Antarctica), doubtful. The presence of basilosaurids in Antarctica has been uncertain because most previous records are based on materials that did not allow an accurate assignment to known archaeocete families (Borsuk-Bialynicka, 1988; Cozzuol, 1988; Fordyce, 1989; Fostowicz-Frelik, 2003), and should be considered as Cetacea indet. (Uhen *et al.*, 2011; Uhen, 2013). The result of our study shows that two of the materials described here (MLP 11-II-21-3 and MLP 13-I-25-10) clearly differ from other archaeocetes (*i.e.*, protocetids) and basal mysticetes (*e.g.*, *Llanocetus denticrenatus* also reported from the La Meseta Formation) and can be confidently identified as basilosaurids. Other specimens recovered from the La Meseta Formation are more fragmentary and identified as Cetacea indet. (Tab. S1).

The Antarctic basilosaurids reported in this work appear to represent mid-sized forms, such as *Zygorhiza* and *Dorudon.* Comparisons with other basilosaurids from the Southern Hemisphere revealed more similarities with the New Zealand material than with the Peruvian basilosaurids. In particular the cheek tooth morphology of MLP 13-I-25-10 is close to Waihao *Zygorhiza* sp. in the number and size of accessory denticles, the development of the cingulum, and the smooth enamel (Köhler and Fordyce, 1997).The New Zealand specimens were referred to *Zygorhiza* sp. based on the presence of a well-developed crenulated cingulum and an enlarged posterior root on $P^3–P^4$. Both features, however, are also shared with *Chrysocetus healyorum* and *Basilotritus* sp. (Uhen and Gingerich, 2001; Gol'din *et al.*, 2014) and therefore the diagnosis of *Zygorhiza* (as well as the taxonomic identification of the New Zealand specimens) needs to be revised considering other characters, such as the periotic morphology. On the other hand, the mandibular morphology of MLP 11-II-21-3 and MLP 13-I-25-11 differs from the Peruvian basilosaurid *Supayacetus* by having a larger and higher mandible and a greater diastema between the alveoli of $P_1–P_2$. The innominate bone from the La Meseta Formation does not show a close morphology to any other basilosaurid, and in particular the obturator foramen presents a morphology (size and shape) that could be considered intermediate between protocetids and basilosaurids. More and better preserved specimens are necessary to determine the diversity of basilosaurids in Antarctica and their relationship with other taxa reported from the Southern Hemisphere.

Age of Antarctic basilosaurids

Age control within the La Meseta Formation has been based primarily on biostratigraphy and suggests that its deposition spanned during much of the Eocene (Harwood, 1985; Wrenn and Hart, 1988), but there is uncertainty about the precise age of particular units within this formation. In particular, the age of the lower part of the La Meseta Formation (TELMs 2–5), where MLP 11-II-21-3 was collected, is still disputed. Based on the low overall $^{87}Sr/^{86}Sr$ ratios derived from bivalve carbonate, Dutton *et al.* (2002) suggested the deposition of TELMs 2–5 took place during the early–middle Eocene (Ypresian and Lutetian in the chronostratigraphic scheme of Cohen *et al.*, 2013). In contrast, Ivany *et al.* (2008) suggested an early Eocene age (54–48.8 Ma; Ypresian) for these units. TELM 4 includes a significant number of reworked shells, which could have biased the strontium-isotope data. The uncertainty is heightened by the small degree of variance in the global seawater curve for the early to the middle Eocene (McArthur *et al.*, 2001). However, overlying shells from TELM 5 produce ratios that suggest an age for the base of the unit of *ca.* 51 Ma (Ivany *et al.*, 2008). Finally, an early Eocene age of the lower part of the La Meseta Formation is consistent with estimates derived from dinoflagellate (Wrenn and Hart, 1988; Coccozza and Clarke, 1992) and diatom (Harwood, 1985, 1988) biostratigraphy.

A younger age for TELM 4 and TELM 5 has been discussed as a feasible alternative to an early Eocene age in a number of publications (Zinsmeister, 1982; Woodburne and Zinsmeister, 1982; Case *et al.*, 1988; Wrenn and Hart, 1988; Stilwell and Zinsmeister, 1992; Douglas *et al.*, 2014; Kemp *et al.*, 2014). The most recent comprehensive analysis of the La Meseta Formation is a magnetostratigraphically calibrated dinocyst biostratigraphic framework for the early Paleogene of the Southern Ocean, which support a middle Eocene age for TELM 4 (Bijl *et al.*, 2013; Douglas *et al.*, 2014). Samples from La Meseta basal stratigraphic units are characterized by an abundance of Antarctic endemic dinocyst taxa (*Enneadocysta diktyostila*, *Vozzhennikovia apertura*, *Spinidinium macmurdoense*, *Deflandrea antarctica*, and *Octodinium askiniae*; Douglas *et al.*, 2014). The first occurrence of *Enneadocysta diktyostila* (earlier assigned to *Enneadocysta partridgei*), which is dominant in these sediments, has been calibrated to Chron C20r (~45 Ma; Brinkhuis *et al.*, 2003; Williams *et al.*, 2004). Essentially, all dinocyst taxa present in these sediments (*E. diktyostila*, *Vozzhennikovia aperture*) belong to the so-called transantarctic fauna, whose dominance reflects an age near the early–middle Eocene boundary (49 Ma or younger; Bijl *et al.*, 2011).

In summary, considering that $^{87}Sr/^{86}Sr$ ratios provided for TELM 4 might be biased (because of potential reworking and oscillation of the marine Sr isotope curve during the Eocene), we interpret the age of the horizon that produced MLP 11-II-21-3 (*i.e.*, TELM 4) as early middle Eocene (~46–40 Ma; middle Lutetian to early Bartonian based on ICS International Chronostratigraphic Chart 2015; Cohen *et al.*, 2013) and follow the most recent chronostratigraphic interpretation for the La Meseta Formation (Douglas *et al.*,

2014: fig. S1). This age is also more consistent with the published stratigraphic record of basilosaurids elsewhere.

Previous reports of basilosaurids in the Southern Hemisphere come from approximately coeval deposits from New Zealand (39.5–34 Ma, late Bartonian–Priabonian based on recent interpretation of the lower Greensand Member; Marx and Fordyce, 2015) and Peru (41–37 Ma, Bartonian; Uhen *et al.*, 2011). With a middle Lutetian–early Bartonian age, MLP11-II-21-3 predates other basilosaurid records and provides the oldest Pelagiceti record known worldwide, documenting an early global dispersal of basilosaurids.

Paleobiogeographic implication of these findings

The paleobiogeographic distribution of basilosaurids in the Southern Hemisphere is poorly understood due to their scarce fossil record. Recent discoveries of basilosaurids in the middle Eocene of Peru suggest that this group invaded the Southern Hemisphere and spread into the subtropical eastern Pacific realm during the late middle Eocene (Bartonian) (Uhen *et al.*, 2011). More southern records (*i.e.*, subantarctic waters) are restricted to the middle–late Eocene of New Zealand (Köhler and Fordyce, 1997) and late Oligocene of Australia (Fitzgerald, 2004). In particular, the presence of MLP 11-II-21-3 in the Antarctic Peninsula at a nearly middle Eocene age, together with recent reports of protocetids and basilosaurids in subtropical localities of the Southern Hemisphere (*i.e.*, Lutetian localities from South and West Africa, and Bartonian localities from South America; Uhen *et al.*, 2011; Gingerich and Cappetta, 2014; Hautier *et al.*, 2014; Zouri *et al.*, 2014; Gingerich and Zouhri, 2015) could lead to a new understanding of the biogeographic distribution of early whales. These findings suggest a rapid radiation and dispersal of protocetids and basilosaurids into the Southern Hemisphere at least since the early middle Eocene (Lutetian). Basilosaurids show morphological adaptations that have been associated with fully aquatic habits (Uhen, 1998, 2008), therefore it is not surprising that basilosaurids had reached Antarctic waters at an earlier time than previously thought. Testing this hypothesis will require additional exploration of Eocene beds, especially in Antarctica and elsewhere in Southern Hemisphere, and it will lead to better understanding of the paleobiogeographic distribution of this group of archaeocetes.

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