



An enigmatic whale tooth from the Upper Eocene of Seymour Island, Antarctica

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ABSTRACT: An isolated, deciduous incisor of an archaic whale found in the upper part of the La Meseta Formation (Telm7) is tentatively assigned to the Archaeoceti. The strata from which the tooth was recovered are of Late Eocene (Priabonian) age, and previous reports indicate that they contain the remains of Dorudontinae (Archaeoceti) and Llanocetidae (Mysticeti). The tooth is similar in shape, size, and ornamentation to the milk teeth of *Zygorhiza*. The enamel is mostly prismatic, with prism sheaths generally open, except for the outermost layer, which is aprismatic. The Schmelzmuster consists of radial and decussating enamel types. The decussating zone has distinct Hunter-Schreger bands (HSB), usually consisting of 10–12 prisms. It is bordered by an external zone built of radial enamel extending for 22% of the enamel thickness and an internal, starting zone, with less developed HSB, occupying 9% of the enamel thickness. The interprismatic matrix is parallel to the prism direction. An archaeocete origin of the tooth is suggested by its enamel features, typical for the group. However, additional study of the Llanocetidae enamel structure is needed for final identification.

Key words: Antarctica, La Meseta Formation (Eocene), paleontology (Archaeoceti, Mysticeti), enamel microstructure, milk (deciduous) tooth.

Introduction

Five families of archaic whales form the paraphyletic group Archaeoceti (Thewissen 1998, Williams 1998). The oldest and most basal group, Pakicetidae, consists of generally terrestrial, relatively small but long-legged animals, which apparently entered the sea to catch fish (Gingerich *et al.* 1993). The groups Ambulocetidae and Remingtonocetidae were amphibious predators that led a semiaquatic existence in coastal and tidal environments, while the Protocetidae inhabited more open marine areas (Williams 1998). In line with the latest discoveries by Gingerich *et al.* (2001a) and Thewissen *et al.* (2001), the earliest archaeocetes are regarded as closely related to primitive artiodactyls. The latest of the archaeocetes,

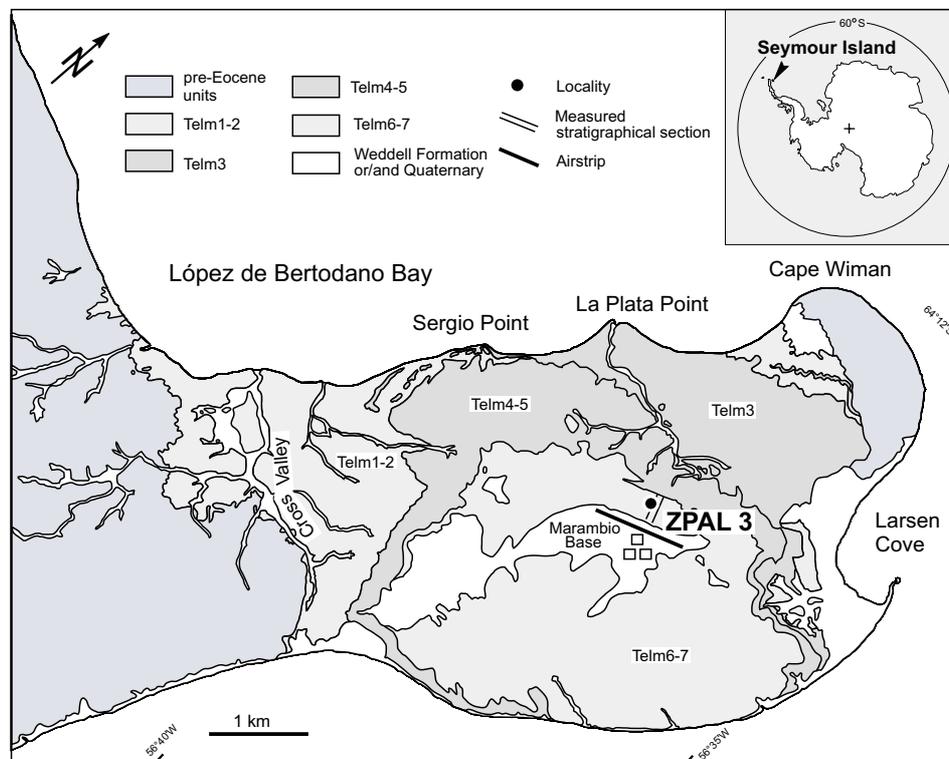


Fig. 1. Location map of the La Meseta Formation on Seymour Island, showing the locality (ZPAL 3) where the cetacean tooth was collected. Distribution of stratigraphic units according to Sadler (1988). Arrow on inset shows the location of Seymour Island in Antarctica.

the Basilosauridae, appeared in the middle Eocene and included fully aquatic, large sea animals (Uhen 1998, Berta and Sumich 1999). There are numerous specimens assigned to this family known from North Africa, Europe, Pakistan and India, North America, New Zealand, and Seymour Island in the Antarctica (Wiman 1905, Barnes and Mitchell 1978, Fordyce 1989, McKenna and Bell 1997, Köhler and Fordyce 1997, Uhen 1998, Williams 1998, Gingerich *et al.* 2001b). The group persisted until the end of the Eocene, and coexisted with the first heterodont mysticetes, such as the Llanocetidae (Fordyce 1989, Mitchell 1989).

Geological setting, stratigraphy, and fossil biota

Seymour Island lies east of the northern end of the Antarctic Peninsula. On the northern part of this small, ice-free island, one finds the La Messeta Formation (Fig. 1). This formation consists of approximately 800 m of tide-influenced

clastic sediments (Doktor *et al.* 1988, Sadler 1988; Porębski 1995, 2000; Marensi *et al.* 1998a, b; Myrcha *et al.* 2002). Based on Sr isotope dating, the La Meseta was deposited during the late Early to Late Eocene, between the very end of the Ypresian and the latest Eocene, Priabonian, 34.2 Ma (Dingle and Lavelle, 1998, see also Dutton *et al.* 2002). The La Meseta Formation was formally described by Elliot and Trautman (1982), who divided the formation into three parts, I–III. In 1988, Sadler, after a detailed study, recognised seven major lithofacies of the La Meseta Formation (Fig. 2) and named the units Telm1–7 (acronym for Tertiary Eocene La Meseta).

The abundant and very diverse fossil record of invertebrates, vertebrates, and plants of the La Meseta Formation has made this is one of the finer sections for the study of Eocene high latitude faunal and climatic changes (Rinaldi *et al.* 1978, Sadler 1988, Stilwell and Zinsmeister 1992, Baumiller and Gaździcki 1996, Doktor *et al.* 1996, Hara 2001). The majority of vertebrate material comes from Telm5 (called “Mammal Site”) and from Telm7. The latter has yielded numerous remains of marine vertebrates, including fish (Jerzmańska 1988; Jerzmańska and Świdnicki 1992), birds (Vizcaino *et al.* 1997, 1998; Bargo and Reguero 1998, Reguero *et al.* 1998, Myrcha *et al.* 2002), and mammals (Wiman 1905, Borsuk-Białynicka 1988, Fordyce 1989, Marensi *et al.* 1994, Vizcaino *et al.* 1998, Reguero *et al.* 2002). The mammals of Telm7 (unit III of Elliot and Trautman 1982 or Submeseta Allomember of Marensi *et al.* 1998a, b) include the terrestrial Sparnotheriodontidae, a South American ungulate group (Vizcaino *et al.* 1997, Bargo and Reguero 1998; Reguero *et al.* 1998, 2002), and fossil whales (Wiman 1905, Borsuk-Białynicka 1988, Fordyce 1989, Mitchell 1989).

Fossil whales of the La Meseta Formation

The history of investigations of fossil whales from Seymour Island dates back to the Nordenskjöld’s Swedish South Polar Expedition of 1901–1903 and the paper by Wiman (1905), who identified two incomplete vertebrae as *Zeuglodon* (= *Basilosaurus*). The material came from the upper part of the La Meseta Formation that contains an association of bones of penguins and whales (Borsuk-Białynicka 1988, Myrcha *et al.* 2002). In 1936, Kellogg, reviewing Wiman’s specimens, classified them as *Archaeoceti incertae sedis*.

Subsequently, the whale collection from Seymour Island was enlarged by the discovery of a “small whale skeleton (*Zeuglodon*) (?)” during fieldwork in the 1974–1975 by an Argentine-American team (Elliot *et al.* 1975). Part of that material, consisting of a fragment of the dentary with two cheek teeth was described by Mitchell (1989) as a new species, *Llanocetus denticrenatus*, a member of a new family, Llanocetidae. Later investigations allowed for attributing Llanocetidae,

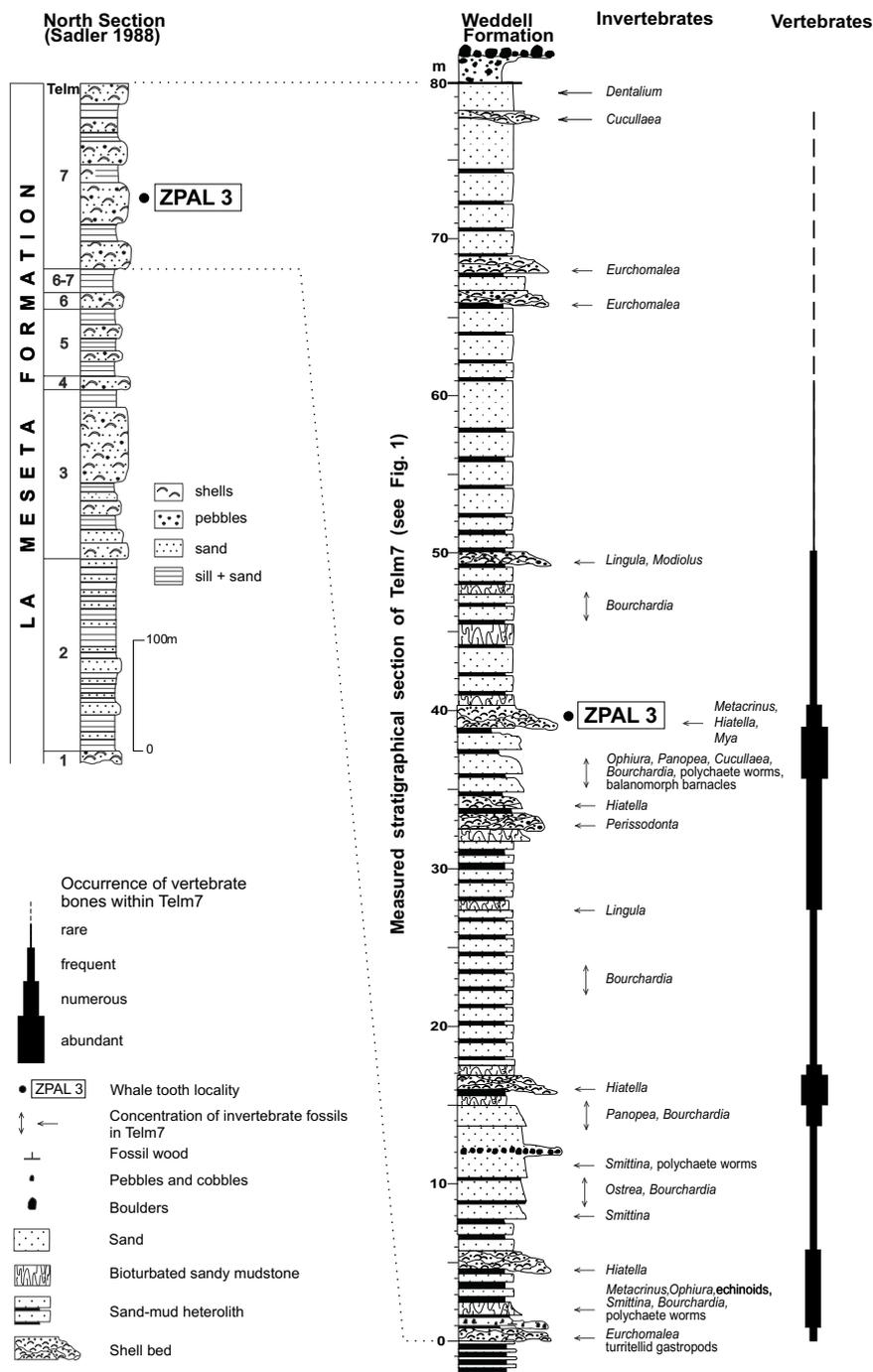


Fig. 2. Stratigraphic section of the Eocene La Meseta Formation on Seymour Island (left column from Sadler 1988) and the measured stratigraphic section of Telm7 (right column, after Myrcha *et al.* 2002). Locality ZPAL 3, at the right of the columns, marks the horizon from which whale tooth was collected.

“representing a morphological stage between Archaeoceti and Mysticeti” (Mitchell 1989) to an early heterodont group of mysticetes (Köhler and Fordyce 1997, McKenna and Bell 1997).

Three isolated vertebrae and a sternal manubrium were found by the Polish members of the Argentine-Polish Field Party in 1985. The material, together with penguin remains, was discovered in the same strata as Wiman’s specimen. It was assigned to Archaeoceti (and probably Dorudontinae) on the basis of “strong posterior protrusion of the postzygapophyseal part of the neural arch” and “shortness of the centrum of the lumbar vertebra” (Borsuk-Białynicka 1988). However, that identification remains uncertain.

Subsequent investigations, led by American and New Zealand scientists, resulted in the discovery of an incomplete large skull associated with teeth, parts of mandibles, vertebrae, and ribs (Fordyce 1989). The skull (which is still under preparation) is larger (suggested total length ca. 2 m and exoccipital width ca. 630 mm) than that of any known archaeocete. It could not be assigned to basilosaurines because of the absence of the elongated vertebral centra, which are characteristic of that group (Kellogg 1936, Fordyce 1989, Uhen 1998).

In summary, there are two groups of archaic whales reported from the upper part of the La Meseta Formation: early mysticetes, Llanocetidae (Fordyce 1989, Mitchell 1989), and advanced archaeocetes, probably Dorudontinae (Wiman 1905, Kellogg 1936, Borsuk-Białynicka 1988, Fordyce 1989). The appearance of the latter group is not fully confirmed because of the lack of cranial material (Wiman 1905, Borsuk-Białynicka 1988, Fordyce 1989). However, the presence of Dorudontinae in the sediments of similar age from New Zealand allows us to conclude that they are likely to have been present in the Antarctic waters during the Late Eocene (Fordyce 1989, Köhler and Fordyce 1997).

Material and methods

The isolated tooth ZPAL M. 9/1 was found by Dr A. Tatur, *in situ* in poorly consolidated sediments of the Teln7 at the site ZPAL 3 (Figs 1, 2) during the Argentine-Polish Field Party (1993–1994 austral season). The specimen is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

The tooth is complete, with partly destroyed enamel. The enamel microstructure was examined using SEM. Small fragments of the enamel were embedded in the epoxy resin and cut along the sagittal and transverse axes of the tooth respectively and polished; tangential polishing was also done. The polished surfaces were etched with 1% orthophosphoric acid for 55–65 seconds (Wood 2000), and coated with platinum.

Systematic paleontology

Order **Cetacea** Brisson, 1762
 Suborder **Archaeoceti** Flower, 1883
 Family **?Basilosauridae** Cope, 1868
 Subfamily **?Dorudontinae** Miller, 1923
 Genus et species indet.
 (Figs 3–10)

Material. — Specimen, ZPAL M. 9/1 – complete milk incisor.

Morphological description. — The specimen is an isolated milk tooth (Table 1), most probably I3 (lower left, or upper right). The shape of the tooth is conical, gently laterally compressed and bent backward and slightly inward (Fig. 3). Both anterior and posterior carinae are present, but the anterior one seems to be more developed. The lateral half of the tooth is rounded and convex, but its medial side is delicately concave near the carina. The enamel is partly lacking, in particular on the anterior and lateral parts of the specimen. The remaining portion of the enamel on the medial side is ornamented with thin but distinct vertical striae, slightly anastomosing near the basal margin of the enamel. There are three short ridges located medially to the carina, only slightly smaller than the carina itself. The ornamentation on the lateral side is less expressed and is constricted to the tooth base. The root is relatively short and probably partly destroyed. Its postero-internal portion is deeply hollowed out for the crown of the developing permanent tooth (Fig. 4).

Table 1

Measurements of the milk tooth ZPAL M. 9/1, in mm.

Antero-posterior diameter at the crown base	11.8
Antero-posterior diameter at the widest part of the root	13.1
Medio-lateral dimension at the crown base	8.8
Medio-lateral dimension at the widest part of the root	10.0
Crown length	21.0
Maximal tooth length	38.0

Enamel microstructure. — The enamel is 210 μm thick and has prismatic microstructure, consisting of radial and decussating enamel types (Figs 5, 6). The typical radial enamel is constricted to the outer zone, forming 22% of the enamel thickness. The inner starting zone, covering 9% of the enamel thickness, is formed by the less distinct decussating enamel and resembles the radial one. The most external layer of the enamel, so-called PLEX (acronym for prismless external layer, Martin 1992), lacks prismatic structure. It consists of prismless enamel, constructed of tiny and relatively short crystallites, altered secondarily, and oriented with their long axes perpendicular to the outer enamel surface – OES (Fig. 7).

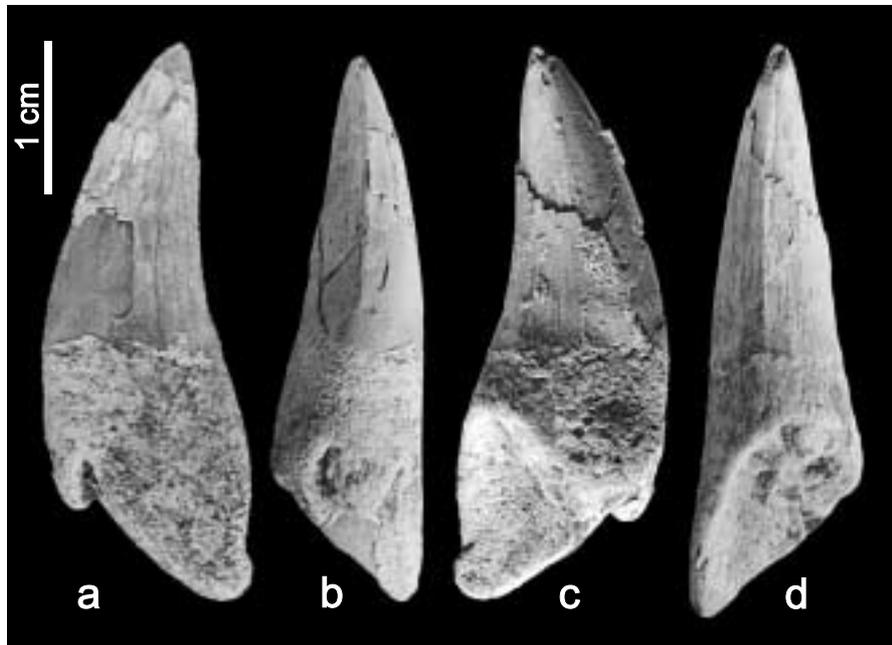


Fig. 3. Milk tooth (? I3), ZPAL M. 9/1 of ? Dorudontinae genus et species indet. from Telm7 of the La Meseta Formation (Late Eocene of Seymour Island, Antarctica).
 a. lateral view, b. anterior view, c. medial view, and d. posterior view.



Fig. 4. The stereophotography of the posterior-basal part of the root of ZPAL M. 9/1, deeply hollowed out for the crown of the underlying, developing permanent tooth.

However, it is not obvious if this layer in ZPAL M. 9/1 is original (see Sahni and Koenigswald 1997) or whether it is a byproduct of a weathering process. The area between two radial enamel zones (ca. 70%) consists of relatively well developed Hunter-Schreger bands (HSB). In longitudinal (vertical) section (Fig. 5), these

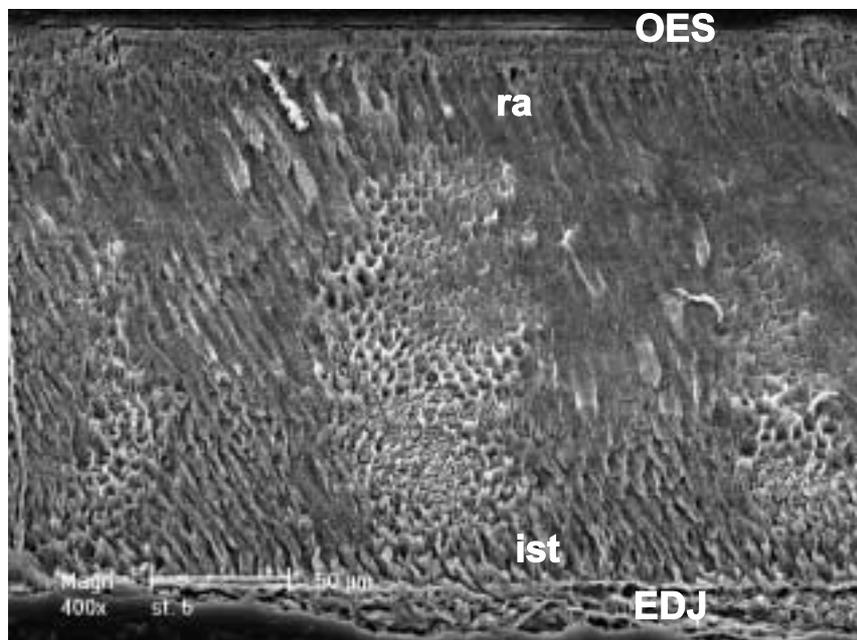


Fig. 5. Vertical (longitudinal) section of the ZPAL M. 9/1 enamel, showing distinct HSB with internal starting zone (ist), and radial layers (ra). OES – outer enamel surface, EDJ – enamel dentine junction. Scale bar 50 μm .

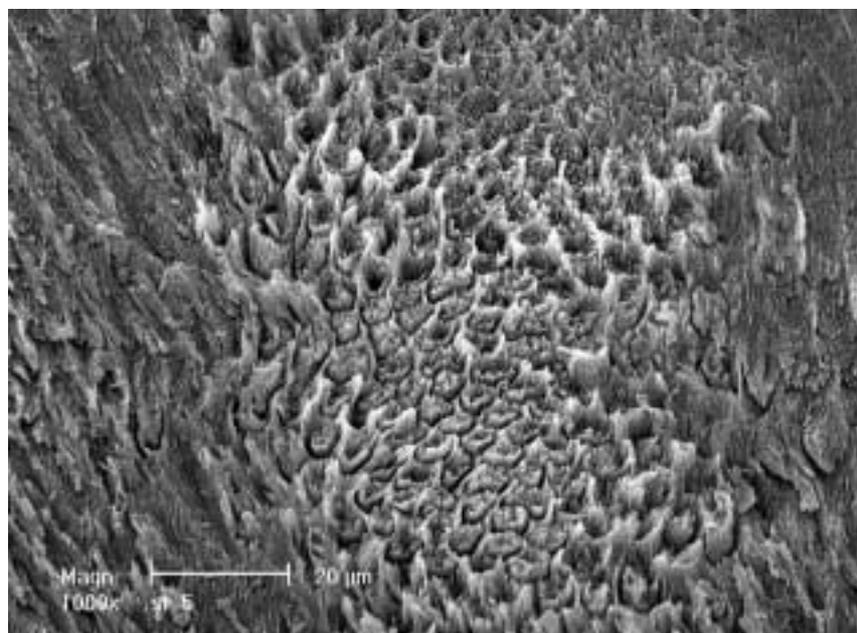


Fig. 6. Decussating enamel in vertical (longitudinal) section of the ZPAL M. 9/1 enamel, the changing of the prism direction toward the OES visible. Scale bar 20 μm .

zones are oriented perpendicularly to the enamel-dentine junction (EDJ) or slightly inclined at the 10–20 degrees. HSB vary in width, but generally consist of 10–12 prisms in width (Fig. 6). The transverse section shows an undulating pattern of the prisms, the result of the transitional zones between the individual Hunter-Schreger bands (Fig. 8). In tangential view, the undulation and occasional bifurcation of Hunter-Schreger bands can also be observed (Fig. 9). Open prism sheaths are dominant and the prisms expressing a keyhole pattern are also present. The closed prism sheaths appear occasionally (Fig. 10) in the external enamel and are much more frequent in the decussating enamel (Fig. 6). The inter-prismatic matrix (IPM) is parallel to the prism direction (Figs 6, 10).

Discussion

Two groups of archaic whales coexisted in the Southern Hemisphere during the Late Eocene. Basilosauridae (mainly Dorudontinae) are known from the Southern Hemisphere from at least late Middle Eocene (Early Bartonian) and are regarded as the earliest whales occurring there (Fordyce 1985, Köhler and Fordyce 1997). The remains of Dorudontinae have been reported from New Zealand (Fordyce 1985, Köhler and Fordyce 1997) and, tentatively, from Seymour Island (Wiman 1905, Kellogg 1936, Borsuk-Białynicka 1988; Fordyce 1985, 1989). The majority of findings from Seymour Island consisted of unspecific highly fragmented postcranial material (Borsuk-Białynicka 1988; Fordyce 1985, 1989; Köhler and Fordyce 1997).

The second group, early toothed mysticetes, inhabited the Southern Hemisphere from at least Late Eocene (Priabonian), and are known from the upper part of the La Meseta Formation on Seymour Island (Mitchell 1989). Generally, the postcranial skeleton of archaeocetes and early members of mysticetes is not very different and discriminating the two groups based on such material is problematic (Fordyce 1989, Köhler and Fordyce 1997). The existence of early mysticetes in the Late Eocene of the La Meseta Formation is confirmed by such findings as *Llanocetus* (Mitchell 1989) and a large skull with broad and flat rostrum typical of mysticetes, mentioned by Fordyce (1989). The presence of Dorudontinae in this area, although not certain, is highly probable (Fordyce 1989, Köhler and Fordyce 1997).

The question arises whether early mysticetes, sharing many features of teeth morphology with archaeocetes, were mono- or diphyodont. The Archaeoceti are heterodont and diphyodont, with the probable exception of *Chrysocetus healyorum* whose subadult specimen did not possess any deciduous teeth (Uhen and Gingerich 2001). As far as we know, the early mysticetes were also heterodont, but no milk teeth assigned to this group are known (Uhen 1998). Until proven to the contrary, we must assume that the specimen ZPAL M. 9/1, which is without doubt a milk tooth as is indicated by a large resorption cavity in its root (Fig. 4), caused by a developing permanent tooth, belongs to Archaeoceti.

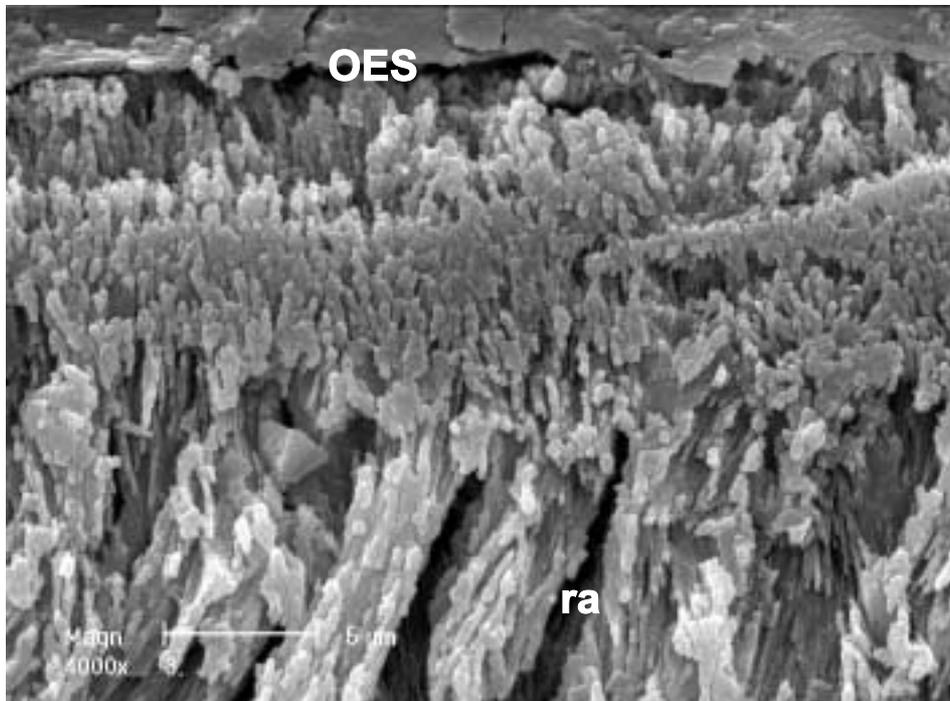


Fig. 7. The outermost aprismatic part of ZPAL M. 9/1 enamel (PLEX). Scale bar 5 μm.

The tooth matches the milk teeth of *Zygorhiza* described by Kellogg (1936) in size, external appearance, and ornamentation. However, all Dorudontinae teeth are similar, and that comparison could not serve as a basis for the generic identification. Although the tooth was found separately and its position in the tooth row cannot be established with certainty, some of its observed features allow the approximate placement. The tooth is curved backward and slightly medially, which is observed only in I3 and canine of Basilosauridae (Kellogg 1936). However, the studied archaeocete canines have roots distinctly larger than those of the incisors. The specimen ZPAL M. 9/1 has a significantly reduced root part, not only due to the state of preservation, but also because of advanced resorption. This suggests that it is one of the incisors, most probably I3.

Enamel problem

The study of enamel structure provides a useful tool for taxonomic and phylogenetic research. However, parallelism is frequently observed due to some biomechanical adaptation and constraints in enamel architecture (Koenigswald *et al.* 1993). There are three main types of enamel investigations, each having different significance for various taxonomic ranks. The first concerns the prism shape,

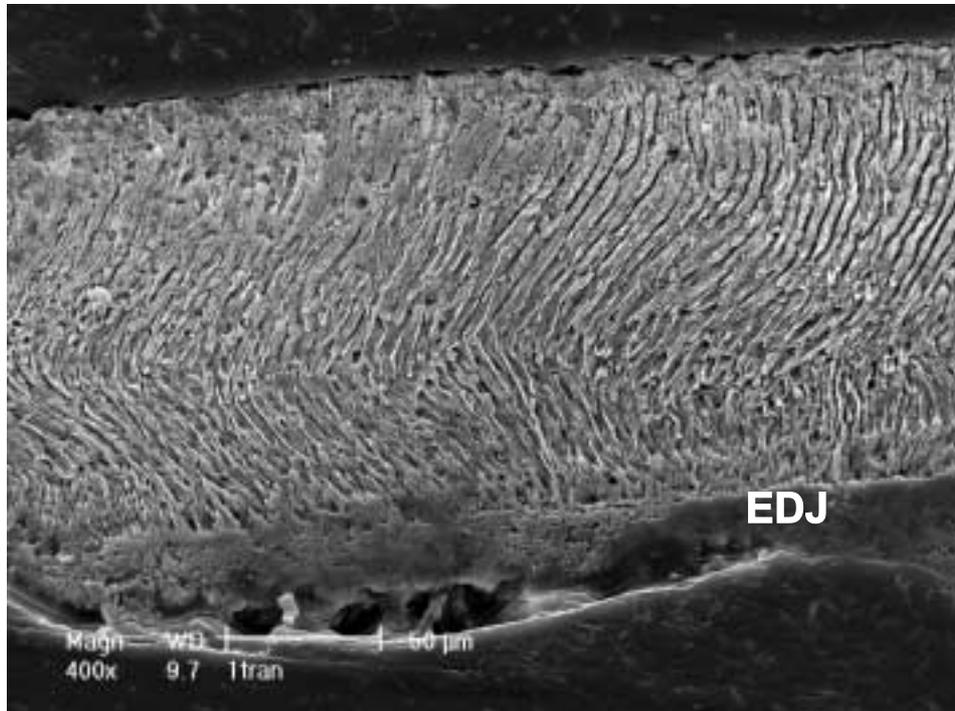


Fig. 8. The transverse section of the ZPAL M. 9/1 enamel, showing the undulating pattern caused by the wide transitional zones of Hunter-Schreger bands. Scale bar 50 µm.

which proves important in describing some mammalian orders. The second refers to the enamel types, and is useful in characterising taxa at about family rank. Finally, the pattern of spatial interrelations of enamel types and the overall organisation of enamel cover, called *Schmelzmuster*, is used in discerning genera (Koenigswald *et al.* 1993, Maas and Thewissen 1995, Koenigswald 1997a, b).

There is a tendency towards the simplification of the enamel pattern and the reduction of the enamel layer in some groups of Cetacea during their evolution (Koenigswald 1997a, Sahni and Koenigswald 1997). In most modern Odontoceti, such as *Stenella* or *Pontoporia*, only radial enamel is found, overlaid by prismless enamel. There are also genera that completely lack the prismatic structure of enamel (Ishiyama 1984, 1987; Koenigswald 1997a).

The archaeocete enamel is relatively well known thanks to studies by Sahni (1981, 1984), Maas and Thewissen (1995), and Sahni and Koenigswald (1997). It represents the primitive condition, although more complex than in the majority of extant species, inherited from the cetacean ancestors found among the primitive Artiodactyla (Maas and Thewissen 1995, Gingerich *et al.* 2001a, Thewissen *et al.* 2001). It consists of decussating and often also radial enamel in the outer layer, and shows distinct undulating Hunter-Schreger bands (Sahni 1981, 1984; Maas and

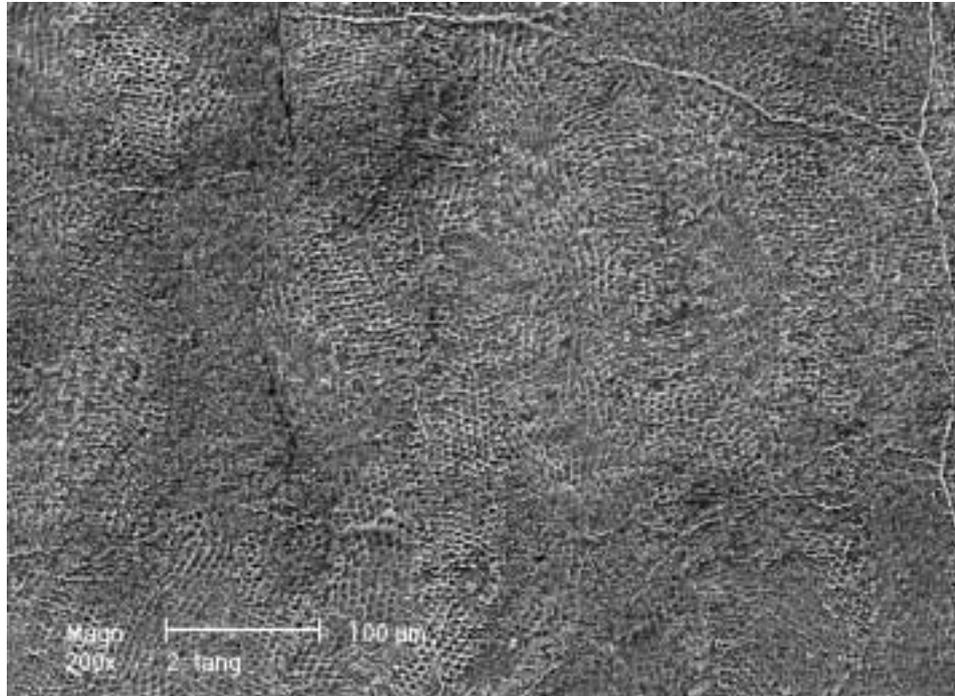


Fig. 9. Tangential polishing of the ZPAL M. 9/1 enamel with marked undulation of the HSB. Scale bar 100 μ m.

Thewissen 1995, Sahni and Koenigswald 1997). The aprismatic enamel type, so common in extant odontocetes, has also been noticed in the most external layer of “premolar of *Archaeocete A*” (Sahni and Koenigswald 1997).

The enamel of ZPAL M. 9/1 specimen shows many features typical of the archaeocete enamel but these characters are of only limited use for more detailed taxonomic purposes.

The enamel layer is relatively thin, about 0.2 mm, which is probably a function of it being a juvenile (deciduous incisor), but the similar, relatively low, enamel thickness was observed in *Saghacetus osiris* (Dorudontinae) from the Upper Eocene of Fayum, Egypt (Gingerich 1992, Sahni and Koenigswald 1997). The majority of other studied archaeocetes (including *Remingtonocetus harudiensis*, *Indocetus ramani*, and two indeterminate archaeocetes, from the lower or middle Eocene of India) have enamel layers which are 0.4 to 0.6 mm thick (Sahni and Koenigswald 1997).

ZPAL M. 9/1 shows a pattern of radial and HSB areas characteristic of archaeocetes, and a comparable width of the inner starting zone, which, if present, does not exceed 10–12% (Maas and Thewissen 1995, Sahni and Koenigswald 1997). The decussating layers of ZPAL M. 9/1 are generally 10–12 prisms wide, which is typical of all known archaeocetes (Maas and Thewissen 1995, Sahni and Koenigswald 1997). The outer radial layer in the specimen is relatively wide, be-

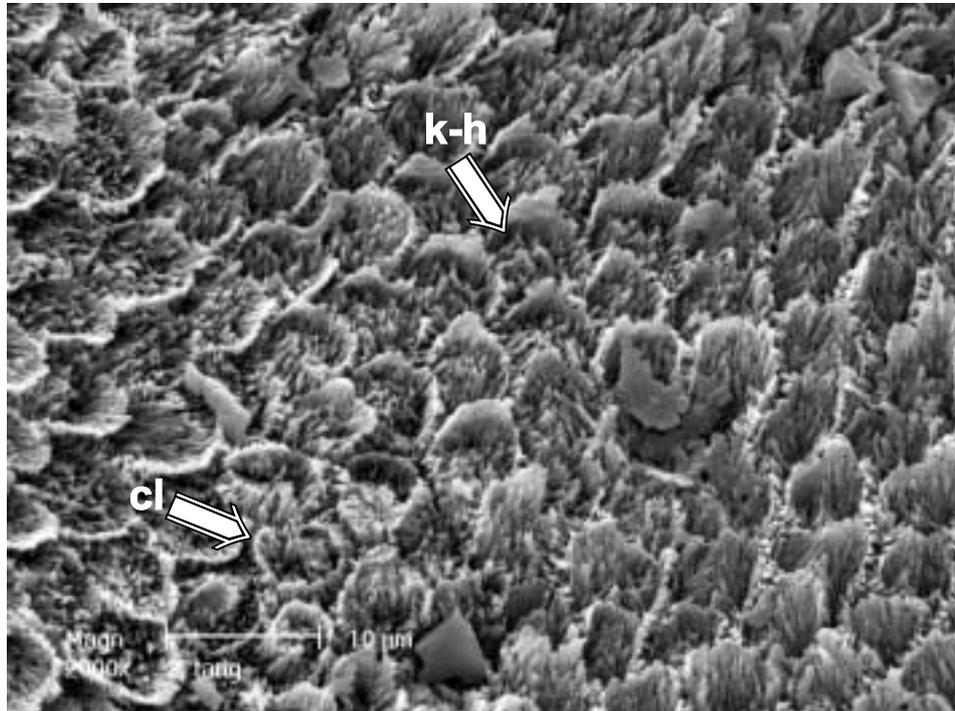


Fig. 10. Superficial enamel of ZPAL M. 9/1 in tangential view. Note that IPM (inter prismatic matrix) is almost parallel to the prisms direction. Most prisms reveal open sheaths; typical keyhole (k-h) and closed (cl) ones are marked by arrows. Scale bar 10 μ m.

coming ca. 20% of the total enamel thickness, which is wider than in the oldest archaeocete, *Pakicetus* (10%), and in the middle Eocene *Remingtonocetus* (15%), but narrower than in *Saghacetus* (25%) from the Upper Eocene beds of Fayum. Other previously studied archaeocetes have the HSB penetrating the whole enamel thickness (Sahni and Koenigswald 1997). However, the HSB are less marked toward the OES (Sahni and Koenigswald 1997).

The thickening of the outer radial enamel in the late Eocene archaeocetes, together with the relatively low thickness of the enamel layer, initiates the dominance of the radial layer and thus, the evolutionary tendency towards simplification of the enamel microstructure in whales. These advanced characters can be observed both in *Saghacetus* and ZPAL M. 9/1 specimen. The remaining enamel features shared by ZPAL M. 9/1 specimen with archaeocetes are plesiomorphic, and thus insufficient to confirm its archaeocetan status. Until the enamel structure of the earliest mysticetes becomes known, ZPAL M. 9/1 specimen cannot be reliably assigned to either archaeocetes or early mysticetes.

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References

- BARGO M.S., and REGUERO M.A. 1998. Annotated catalogue of the fossil vertebrates from Antarctica housed in the Museo de la Plata, Argentina. I. Birds and land mammals from La Meseta Formation (Eocene–? Early Oligocene). *Asociacion Paleontologica Argentina, Publication Especial, 5. Paleógeno de América del Sur y de la Península Antártica*; 211–221.
- BARNES L.G. and MITCHELL E. 1978. Cetacea. *In: V.J. Maglio and H.B.S. Cooke (eds), Evolution of African Mammals*, 582–602. Harvard University Press, Cambridge.
- BAUMILLER T.K. and GAŹDZICKI A. 1996. New crinoids from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. *In: A. Gaździcki (ed.), Palaeontological results of the Polish Antarctic expeditions. Part II. Palaeontologia Polonica 55*: 101–116.
- BERTA A. and SUMICH J. L. 1999. Cetacean evolution and systematics. *In: A. Berta and J.L. Sumich (eds), Marine Mammals, Evolutionary Biology*, Academic Press, San Diego; 49–85.
- BORSUK-BIAŁYNICKA M. 1988. New remains of Archaeoceti from the Paleogene of Antarctica. *Polish Polar Research 9*: 437–445.
- DINGLE R.V. and LAVELLE M. 1998. Antarctic Peninsular cryosphere: Early Oligocene (c. 30 Ma) initiation and a revised glacial chronology. *Journal of the Geological Society, London*, 155: 433–437.
- DOKTOR M., GAŹDZICKI A., JERZMAŃSKA A., POREBSKI S.J. and ZASTAWNIAK E. 1996. A plant-and-fish assemblage from the Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula) and its environmental implications. *In: A. Gaździcki (ed.), Palaeontological Results of the Polish Antarctic Expeditions. Part II. Palaeontologia Polonica 55*: 127–146.
- DOKTOR M., GAŹDZICKI A., MARENSSI S.A., POREBSKI S.J., SANTILLANA S.N. and VRBA A.V. 1988. Argentine-Polish geological investigations on Seymour (Marambio) Island, Antarctica, 1988. *Polish Polar Research 9*: 521–541.
- DUTTON A.L. and LOHMANN K.C. and ZINSMEISTER W.J. 2002. Stable isotope and minor element proxies for Eocene climate of Seymour Island, Antarctica. *Paleoceanography 17* (2): 6-1–6-14.
- ELLIOT D.H., RINALDI C., ZIMSMEISTER W.J., TRAUTMAN T.A., BRYANT W.A. and DEL VALLE R. 1975. Geological investigations on Seymour Island, Antarctic Peninsula. *Antarctic Journal of the United States 10*: 182–186.
- ELLIOT D.H. and TRAUTMAN T.A. 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula. *In: C. Craddock (ed.), Antarctic Geoscience*, The University of Wisconsin Press, Madison; 287–297.
- FORDYCE R.E. 1985. Late Eocene archaeocete whale (Archaeoceti: Dorudontinae) from Waihao, South Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics*, 28: 351–357.
- FORDYCE R.E. 1989. Origins and evolution of Antarctic marine mammals. *In: J.A. Crame (ed.), Origins and Evolution of the Antarctic Biota*. Geological Society Special Publication 47: 269–281.
- GINGERICH P.D. 1992. Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: stratigraphy, age, and paleoenvironments. *University of Michigan Papers on Paleontology 30*: 1–84.
- GINGERICH P.D., RAZA S.M., ARIF M., ANWAR M. and ZHOU X. 1993. Partial skeletons of *Indocetus ramani* (Mammalia, Cetacea) from the lower Middle Eocene Domanda Shale in the Sulaiman Range of Punjab (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan 28*: 393–416.

- GINGERICH P.D., UL-HAQ M., ZALMOUT I. S. KHAN I. H. and MALKANI M.S. 2001a. Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science* 293: 2239–2242.
- GINGERICH P.D., UL-HAQ M., KHAN I.H. and ZALMOUT I.S. 2001b. Eocene stratigraphy and archaeocete whales (Mammalia, Cetacea) of Drug Lahar in the Eastern Sulaiman Range, Balochistan (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan* 30: 269–319.
- HARA U. 2001. Bryozoans from the Eocene of Seymour Island, Antarctic Peninsula. *In: A. Gaździcki (ed.), Palaeontological Results of the Polish Antarctic Expedition. Part III.* *Palaeontologia Polonica* 60: 33–156.
- ISHIYAMA M. 1984. Comparative histology of tooth enamel in several toothed whales. *In: R. W. Fearnhead and S. Suga (eds), Tooth Enamel IV*, Elsevier, Amsterdam; 432–436.
- ISHIYAMA M. 1987. Enamel structure in odontocete whales. *Scanning Microscopy* 1: 1071–1079.
- JERZMAŃSKA A. 1988. Isolated vertebrae of teleostean fishes from the Paleogene of Antarctica. *Polish Polar Research* 9: 421–435.
- JERZMAŃSKA A. and ŚWIDNICKI J. 1992. Gadiform remains from the La Meseta Formation (Eocene) of Seymour Island, West Antarctica. *Polish Polar Research* 13: 241–253.
- KELLOGG R. 1936. A review of the Archaeoceti. *Carnegie Institution of Washington, Publication* 482. *Carnegie Institution of Washington, Washington*; 366 pp.
- V. KOENIGSWALD W. 1997a. Brief survey of the enamel diversity at the schmelzmuster level in cenozoic placental mammals. *In: W. v. Koenigswald and P.M. Sander (eds), Tooth enamel microstructure*, Balkema, Rotterdam; 137–161.
- V. KOENIGSWALD W. 1997b. Evolutionary trends in the differentiation of mammalian enamel ultrastructure. *In: W. v. Koenigswald and P.M. Sander (eds), Tooth enamel microstructure*, Balkema, Rotterdam; 137–161.
- V. KOENIGSWALD W., MARTIN T. and PFRETZSCHNER H.U. 1993. Phylogenetic interpretation of enamel structures in mammalian teeth: possibilities and problems. *In: F.S. Szalay, M.J. Novacek and M.C. McKenna (eds), Mammal Phylogeny, Placentals*, Springer-Verlag, New York Inc.; 303–314.
- KÖHLER R. and FORDYCE R.E. 1997. An archaeocete whale (Cetacea: Archaeoceti) from the Eocene Waihao Greensand, New Zealand. *Journal of Vertebrate Paleontology* 17: 574–583.
- MARENSSI S.A., REGUERO M.A., SANTILLANA S.N. and VIZCAINO S.F. 1994. Review: Eocene land mammals from Seymour Island, Antarctica: paleobiogeographical implications. *Antarctic Science* 6: 3–15.
- MARENSSI S.A., SANTILLANA S.N. and RINALDI C.A. 1998a. Paleoaambientes sedimentarios de La Aloformacion La Meseta (Eoceno), Isla Marambio (Seymour), Antartida. *Instituto Antártico Argentino, Contribucion* 464: 1–51.
- MARENSSI S.A., SANTILLANA S.N. and RINALDI C.A. 1998b. Stratigraphy of the La Meseta Formation (Eocene), Marambio (Seymour) Island, Antarctica. *Asociación Paleontológica Argentina, Publicación Especial 5. Paleógeno de América del Sur y de la Península Antártica*; 137–146.
- MAAS M.C. and THEWISSEN J.G.M. 1995. Enamel microstructure of *Pakicetus* (Mammalia: Archaeoceti). *Journal of Paleontology* 69: 1154–1163.
- MARTIN T. 1992. Schmelzmikrostruktur in den Inzisivenalt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata Mémoire Extraordiner* 1992: 1–168.
- MCKENNA M.C. and BELL S.K. 1997. *Classification of mammals above the species level*. *Columbia University Press, New York*; 631 pp.
- MITCHELL E.D. 1989. A new cetacean from the Late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 2219–2235.
- MYRCHA A., JADWISZCZAK P., TAMBUSI C.P., NORIEGA J.I., GAŹDZICKI A., TATUR A. and DEL VALLE R. 2002. Taxonomic revision of eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Research*, 23: 5–46.

- POREBSKI S.J. 1995. Facies architecture in a tectonically-controlled incised-valley estuary: La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula. In: K. Birkenmajer (ed.), *Geological Results of the Polish Antarctic Expeditions. Part XI*. Studia Geologica Polonica 107: 7–97.
- POREBSKI S.J. 2000. Shelf-valley compound fill produced by fault subsidence and eustatic sea-level changes, Eocene La Meseta Formation, Seymour Island, Antarctica. *Geology* 28: 147–150.
- REGUERO M.A., VIZCAINO S.F., GOIN F.J., MARENSSI S.A. and SANTILLANA S.N. 1998. Eocene high-latitude terrestrial vertebrates from Antarctica as biogeographic evidence. *Asociacion Paleontologica Argentina, Publicación Especial* 5: 185–198.
- REGUERO M.A., MARENSSI S.A. and SANTILLANA S.N. 2002. Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments; biogeographic relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology* 179: 189–210.
- RINALDI C.A., MASSABIE A., MORELLI J., ROSENMAN H.L. and DEL VALLE R. 1978. Geología de la Isla Vicecomodoro Marambio. Instituto Antártico Argentino, *Contribucion* 217: 5–43.
- SADLER P. M. 1988. Geometry and stratifications of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. *Geological Society of America, Memoir* 169: 303–320.
- SAHNI A. 1981. Enamel ultrastructure of fossil Mammalia: Eocene Archaeoceti from Kutch. *Journal of the Palaeontological Society of India* 25: 33–37.
- SAHNI A. 1984. The evolution of mammalian enamels: Evidence from multituberculata (Allotheria, extinct); primitive whales (archaeocete Cetacea) and early rodents. In: R. W. Fearnhead and S. Suga (eds), *Tooth Enamel IV*, Elsevier, Amsterdam; 457–461.
- SAHNI A. and v. KOENIGSWALD W. 1997. The enamel structure of some fossil and recent whales from the Indian subcontinent. In: W. v. Koenigswald and P.M. Sander (eds), *Tooth enamel microstructure*, Balkema, Rotterdam; 177–191.
- STILWELL J.D. and ZINSMEISTER W.J. 1992. Molluscan systematics and biostratigraphy: lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *American Geophysical Union, Antarctic Research Series* 55: 1–192.
- THEWISSEN J.G.M. 1998. Cetacean origins. Evolutionary turmoil during the invasion of the oceans. In: J.G.M. Thewissen (ed.), *The Emergence of Whales*, Plenum Press, New York; 451–464.
- THEWISSEN J.G.M., WILLIAMS E.M., ROE L.J. and HUSSAIN S.T. 2001. Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. *Nature* 413: 277–281.
- UHEN M.D. 1998. Middle to Late Eocene Basilosaurines and Dorudodontines. In: J.G.M. Thewissen (ed.), *The Emergence of Whales*, Plenum Press, New York; 29–61.
- UHEN M.D. and GINGERICH P.D. 2001. New genus of dorudontine archaeocete (Cetacea) from the middle-to-late Eocene of South Carolina. *Marine Mammal Science* 17: 1–34.
- VIZCAINO S.F., BOND M., REGUERO M.A. and PASCUAL R. 1997. The youngest record of fossil land mammals from Antarctica; its significance on the evolution of the terrestrial environment of the Antarctic Peninsula during the late Eocene. *Journal of Paleontology* 71: 348–350.
- VIZCAINO S.F., REGUERO M. A., GOIN F.J., TAMBUSI C.P. and NORIEGA J.I. 1998. Community structure of Eocene terrestrial vertebrates from Antarctic Peninsula. *Asociación Paleontológica Argentina, Publicación Especial*, 5. *Paleógeno de América del Sur y de la Península Antártica*; 177–183.
- WILLIAMS E.M. 1998. Synopsis of the earliest cetaceans. In: J.G.M. Thewissen (ed.), *The Emergence of Whales*, Plenum Press, New York; 1–28.
- WIMAN C. 1905. Über die alttertiären Vertebraten der Seymour-Insel. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903*, 3: 1–37.
- WOOD C.B. 2000. Tooth enamel microstructure in *Deltatheridium* (Metatheria, Late Cretaceous of Mongolia), with comparison to some other Mesozoic mammals. *Special Publications of the Korea Paleontological Society* 4: 127–152.

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