



FIRST RECORD OF A MACRORAPTORIAL SPERM WHALE (CETACEA, PHYSETEROIDEA) FROM THE MIOCENE OF ARGENTINA

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ABSTRACT – Raptorial sperm whales of the genus *Livyatan* were described from the Miocene of Peru and Chile. Revision of paleontological collections resulted in the finding of isolated teeth belonging to aff. *Livyatan* sp. coming from Early-Middle Miocene strata from Bajo del Gualicho area, Río Negro Province, Argentina. These specimens represent the first finding of this genus in the Southwestern Atlantic Ocean and indicate that *Livyatan*-like forms were more widespread than previously thought. The reasons of the extinction of such predatory whales are still uncertain, but it is not improbable that it may be correlated with competition for food resources with globicephaline delphinids. This hypothesis still rests on weak evidence and should be evaluated through findings of new specimens, as well as detailed analysis of the fossil record.

Keywords: *Livyatan*, Macroraptorial sperm-whales, Argentina, Patagonia, Miocene.

INTRODUCTION

The record of macroraptorial stem-Physeteroidea in South America is composed by two species of the genus *Acrophyseter* (*A. deinodon* and *A. robustus*) and the giant *Livyatan melvillei*, all of them from Late Miocene deposits of the Pisco Formation, Peru (Lambert *et al.*, 2016; Bianucci *et al.*, 2016; Di Celma *et al.*, 2016). Gutstein *et al.* (2015) mentioned the possible presence of *Livyatan* in Chile, represented by an isolated tooth coming from the Bahía Inglesa Formation (Late Miocene/Late Pliocene). In the present contribution, we report the first record assignable to *Livyatan* sp. from Argentina, and we briefly discuss its palaeobiogeographical implications.

MATERIAL

Institutional abbreviations. **BAR**, Museo de la Asociación Paleontológica de Bariloche, San Carlos de Bariloche, Río Negro Province, Argentina; **MML**, Museo Municipal de Lamarque, Vertebrate Paleontology, Río Negro Province, Argentina.

Locality and geological level. The specimens were found near Puesto Picavea locality, in the Gran Bajo del Gualicho area, Río Negro Province, Argentina (Figure 1). Specimens here reported come from the Early-Middle Miocene Saladar Member of the Gran Bajo del Gualicho Formation (Reichler, 2010). Lithologically, the Saladar Member is characterized by the presence of intermixed sandstone, coquina and pelitic levels. It evidences a transgressive environment of shallow waters with an evolution of facies that changes from platform sediments to typical beach deposits (Reichler, 2010). These strata correspond to the *Nodipecten* sp., *Venericor abasolensis* and *Glycymerita camaronesia* biozone (del Río, 2004).

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
ODONTOCETI Flower, 1867
PHYSETEROIDEA Gray, 1821

Livyatan Lambert *et al.*, 2010

aff. *Livyatan* sp.

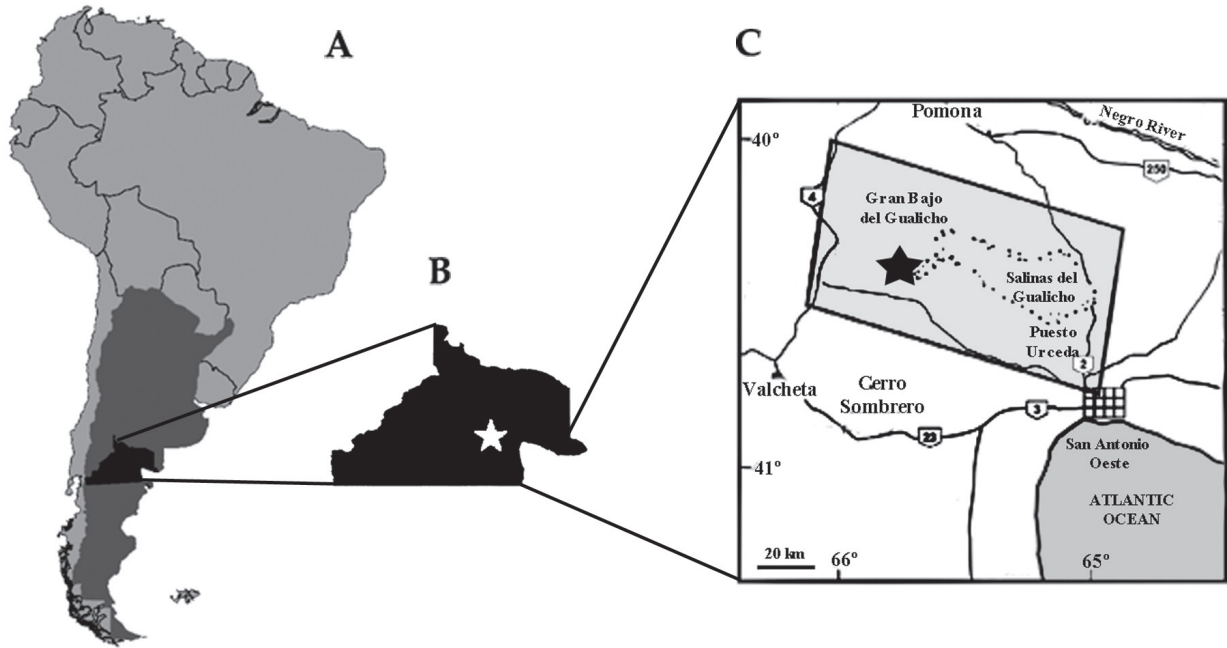


Figure 1. Map showing the location of the fossiliferous locality. **A**, Argentina; **B**, Río Negro Province, the star indicates the Bajo del Gualicho area; **C**, Puesto Picavea fossiliferous locality indicated by a star. Modified from Reichler (2010).

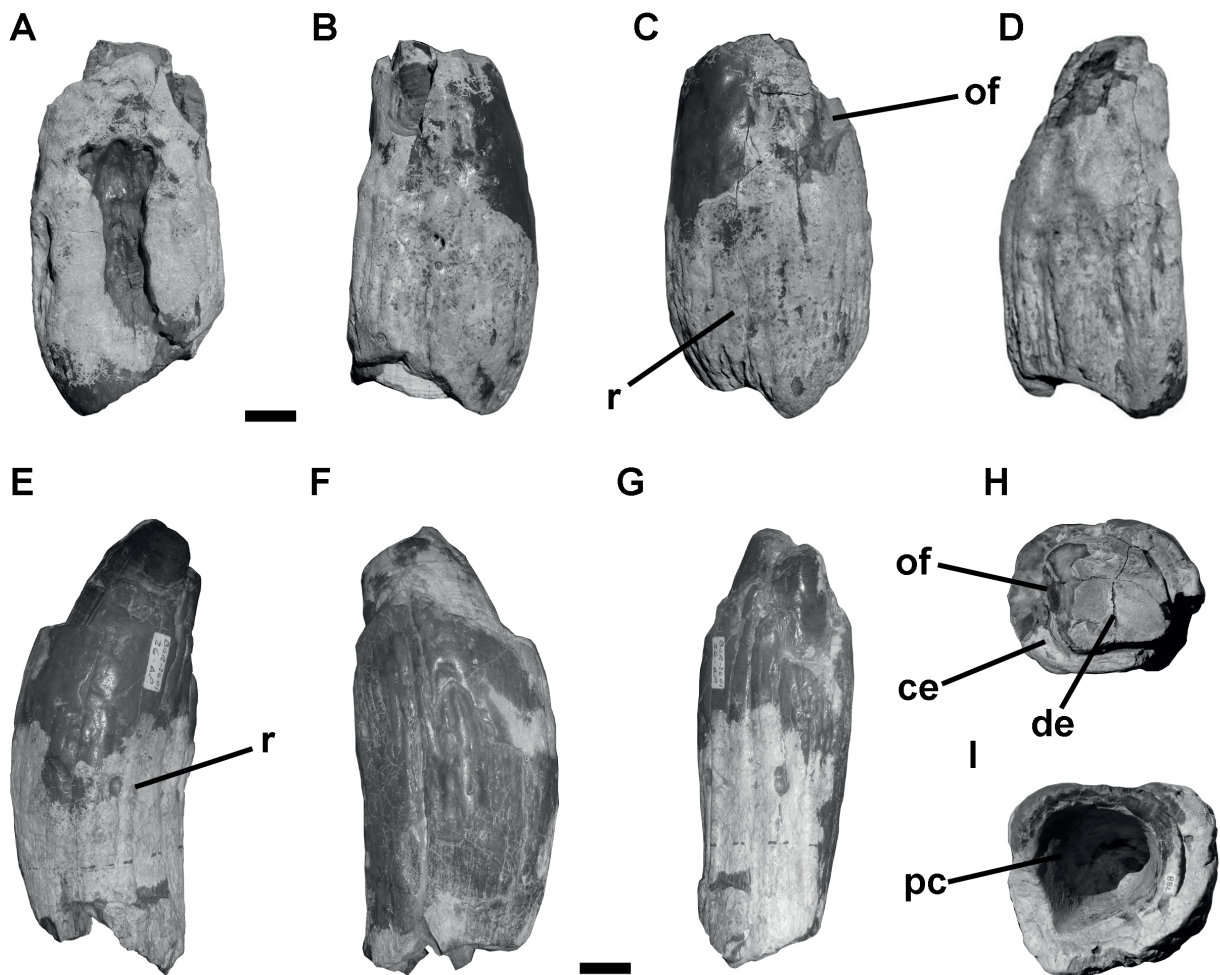


Figure 2. aff. *Livyatan* sp. Isolated teeth **A–D**, **H–I**, MML 882; and **E–G**, BAR-2601. **A**, **C**, **E**, **F**, labial/lingual; **B**, distal and **D**, **G**, mesial views; **H**, apical and **I**, basal views. **Abbreviations:** **ce**, cementum layer; **de**, dentine core; **gc**, gingival collar; **of**, occlusal facet; **pc**, pulp cavity; **r**, apicobasal ridges. Scale bar = 20 mm.

Referred material. MML 882, incomplete tooth; BAR-2601, incomplete tooth (Figure 2).

Description. Specimen MML 882 consists of an incomplete tooth lacking a large portion of the crown and the base of the root. Due to incomplete preservation, it is not possible to discern if an enamel cap was present. The root is subconical, robust and slightly distally curved. It shows a relatively thick layer of cement and a core of dentine. It is subcircular in cross-section, being slightly subrectangular at mid-height and subtriangular towards the base. The root is slightly transversely compressed and tends to converge towards its base. The pulp cavity is remarkably wide. There is a well-developed gingival collar and an occlusal facet at the mesial margin of the tooth. The root shows apicobasal ridges, grooves, and rugosities. This ornamentation becomes attenuated from the base to the tip of the preserved portion of the element. Specimen BAR-2601 is very similar to MML 882. The only difference between the specimens is that BAR-2601 lacks any indication of occlusal facets. However, this may be due to incomplete preservation.

Measurements. MML 882: Maximum apicobasal height (as preserved): 142 mm; Maximum mesiodistal diameter: 74 mm. BAR-2601: Maximum apicobasal height (as preserved): 178 mm; Maximum mesiodistal diameter: 72 mm.

DISCUSSION

Taxonomic assignment of specimens

Traditionally, isolated teeth of physeteroids were considered as being of important value, and allow referral of single elements to the specific level (see Kazár, 2002; Hampe, 2006; Pérez *et al.*, 2011). On the other side, recent contributions suggest that isolated teeth may be not as valuable than previously thought, and are not diagnostic at the specific level, at least (Bianucci & Landini, 2006; Lambert *et al.*, 2016). In spite of that, we sustain that specimens here described have some morphological features that may be useful to determine their taxonomic position with some degree of certainty.

The large size of BAR-2601 and MML 882, together with the presence of an occlusion surface, indicating the presence of functional teeth in both the maxilla and the mandible, and teeth with massive, robust roots, support an attribution of these specimens to stem physeteroids (Kazár, 2002; Reumer *et al.*, 2017). From the same locality and bed were BAR-2601 and MML 882 come, Gondar (1975) described the basal physeteroid *Preaulophyseter gualichensis*. This taxon differs from BAR-2601 and MML 882 in the absence of longitudinal ridges and grooves, and smaller size, among several other features.

The large size and robustness of specimens BAR-2601 and MML 882 suggest their inclusion within “macroraptorial sperm whales” (*sensu* Lambert *et al.*, 2016). Among macroraptorial sperm whales, BAR-2601 and MML 882 are notably large. In fact, in most taxa, the maximum mesiodistal diameter of teeth barely exceeds 50 mm in size (32 mm in *Acrophyseter deinodon*, 34 mm in *A. robustus*, <56 mm in *Zygophyseter varolai*, <40mm in *Brygmophyseter shigensis*; Varola *et al.*, 1988; Hirota & Barnes, 1994; Bianucci & Landini, 2006; Lambert *et al.*, 2016). Further, in spite of the fact that BAR-2601 and MML 882 fall within the size range of *Albicetus*, they clearly differ from the latter in having suboval cross-section, instead of subrectangular (Boersma & Pyenson, 2015).

On the other hand, specimens BAR-2601 and MML 882 approach in size, robustness, and cross-section *Livyatan melvillei* which is the cetacean with the largest known dentition, having disproportionately large teeth that are invariably larger than 80 mm in minimum mesiodistal diameter (Lambert *et al.*, 2010). The combination of characters of specimens BAR-2601 and MML 882 is congruent with *L. melvillei*. However, the teeth of *Livyatan* have a maximum diameter between 100 and 120 mm, the apical tooth having 81 mm (Lambert *et al.*, 2010, 2016), being larger than specimens here described. Because of this, and that only isolated teeth are available, we refrain from referring BAR-2601 and MML 882 to the species level, and we choose for an open taxonomic nomenclature, referring them as aff. *Livyatan* sp.

Table 1. Table summarizing fossil records of macroraptorial sperm-whales.

Species	Formation/Locality	Age	Author
<i>Acrophyseter deinodon</i>	Pisco Fm. (Sud-Sacaco, Peru)	Late Miocene	Lambert <i>et al.</i> (2016)
<i>Acrophyseter robustus</i>	Pisco Fm. (Cerro la Bruja, Peru)	Middle to Late Miocene	Lambert <i>et al.</i> (2016)
<i>Zygophyseter varolai</i>	Cisterna Quarry (Apulia, Italy)	Late Miocene	Bianucci & Landini (2006)
<i>Brygmophyseter shigensis</i>	Bessho Fm. (Shiga-mura, Japan)	Early–Middle Miocene	Hirota & Barnes (1994)
<i>Livyatan melvillei</i>	Pisco Fm. (Cerro Colorado, Perú)	Late Miocene	Lambert <i>et al.</i> (2016)
<i>Livyatan melvillei</i>	Bahía Inglesa Fm. Chile	Late Miocene–Late Pliocene	Gutstein <i>et al.</i> (2015)
aff. <i>Livyatan</i> sp.	Gran Bajo del Gualicho Fm., Río Negro, Argentina	Early–Middle Miocene	Present contribution
cf. <i>Zygophyseter</i> sp.	Undetermined stratigraphic unit, Breskens, Netherlands	?Miocene	Reumer <i>et al.</i> (2017)

Palaeobiogeographical implications

Macroraptorial sperm whales include four different genera, namely *Acrophyseter*, *Livyatan*, *Brygmophyseter* and *Zygophyseter* (Lambert *et al.*, 2016), and probably *Albicetus* (Boersma & Pyenson, 2015). These taxa are recorded in a few localities in the Southern and Northern Hemispheres (Table 1). Among macroraptorial sperm whales, the gigantic form *Livyatan* is only known from Peru (Lambert *et al.*, 2010, 2016) and Chile (Gutstein *et al.*, 2015). It is worth mentioning that up to now the records of *Livyatan* correspond to sites located along the shores of the Pacific Ocean. In the present contribution, we report for the first time a form akin to the genus *Livyatan* from the southwestern Atlantic coast.

On the basis of the scarce fossil record, the distribution of *Livyatan* appears to be restricted to the Southern Hemisphere (Table 1). The absence of fossil remains of a macrophagous form of size and morphology comparable to *Livyatan* in the Northern Hemisphere still lacks a clear explanation. In fact, macrophagous species of the Northern Hemisphere as *Zygophyseter*, *Brygmophyseter*, and *Albicetus* are much smaller and with a much weaker dentition than *Livyatan melvillei* (Hirota & Barnes, 1994; Boersma & Pyenson, 2015; Lambert *et al.*, 2016).

As noted earlier by Davies (1963), by Neogene times the equatorial warm zone constituted an important barrier in the distribution of a large number of cetaceans that have discontinuous distribution (see Bianucci *et al.*, 2016). Based on the fossil record, it is possible that *Livyatan* or a comparable form was not able to cross the warm equatorial zone, and thus, did not reach the Northern Hemisphere. However, we note that the fossil record is still patchy, and more evidence is needed in order to test any hypothesis on the distribution of *Livyatan* and its kin.

It was inferred that gigantic raptorial sperm-whales were mysticete (baleen-whale)-predatory cetaceans, and their appearance in the fossil record coincides with a phase of diversification and size-range increase of the baleen-bearing mysticetes in the Miocene (Lambert *et al.*, 2010). Later, by the late Pliocene, raptorial sperm whales suddenly disappear from the record (Fitzgerald, 2004; Lambert *et al.*, 2016), and thus, by late Pliocene times, the macrophagous niche of cetaceans was probably empty. Fitzgerald (2011) described a large isolated tooth belonging to a large stem-physeteroid from the Pleistocene of Nauru Island (Pacific Ocean). However, this tooth is just 2.5 cm in maximum diameter, being much smaller and weaker than macroraptorial sperm whales, and is no longer considered here.

It is difficult to establish if the diversification of large predatory Globicephalinae Delphinidae by the Late Miocene–Early Pliocene could result in competition by food resources with macrophagous sperm whales. It is not improbable that giant sperm whales were ecologically replaced (Fordyce & Muizon, 2001) or displaced by killer whales of the genus *Orcinus*, which have their first fossil record by the Pliocene of Italy (*i.e.*, *O. citoniensis*; Pilleri & Pilleri, 1982; Heyning & Dahlheim, 1988). Later, by Pleistocene times, *Orcinus* and its kin acquired a global distribution (Taylor *et al.*, 2008).

CONCLUSIONS

Livyatan or a nearly related form is reported for the first time from the Atlantic coast of South America. This reinforces the idea that *Livyatan* and its kin were widespread among southern oceans during the Miocene, and suddenly disappear from the fossil record by Late Pliocene times. Its extinction is still uncertain, but it is probably related with the emergence of globicephaline delphinids. This hypothesis should be tested with finding of novel fossil material and the analysis of quantitative data.

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