

Systematic palaeontology (Vertebrate palaeontology)

# A new stem-sperm whale (Cetacea, Odontoceti, Physeteroidea) from the Latest Miocene of Peru

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## Abstract

A finely preserved skull with mandible and teeth associated, from the Latest Miocene beds (ca. 6 Ma) of the Pisco Formation, Sud-Sacaco, Peru, represents a new physeteroid genus and species, *Acrophyseter deinodon*. This moderate size sperm whale is characterized, among others, by: the short rostrum, the mandible distinctly curved upwards, large teeth very close together (12 on each upper tooth row and 13 on each lower tooth row), the lateral margin of the maxilla along the rostrum base much lower than the orbit roof, a wide supracranial basin dorsally overhanging the right orbit and limited to the cranium and a large temporal fossa dorsomedially elevated. A preliminary cladistic analysis provides a phylogenetic position of *Acrophyseter* nested within the stem-Physeteroidea, more basal than the clade Kogiidae + Physeteridae. The morphology of the oral apparatus and of the temporal fossa suggests that *Acrophyseter* was able to feed on large preys. **To cite this article:** O. Lambert et al., C. R. Palevol 7 (2008). © 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## Résumé

**Un nouveau cachalot basal (Cetacea, Odontoceti, Physeteroidea) du Miocène terminal du Pérou.** Un crâne très bien préservé, avec mandibule et dents associées, découvert dans les couches du Miocène terminal (ca. 6 Ma) de la Formation Pisco, Sud-Sacaco, Pérou, représente un nouveau genre et une nouvelle espèce de Physeteroidea, *Acrophyseter deinodon*. Ce cachalot de taille moyenne est caractérisé, entre autres, par : le rostre court, la mandibule distinctement recourbée vers le haut, de grandes dents rapprochées les unes des autres (12 sur chaque rangée supérieure et 13 sur chaque rangée inférieure), le bord latéral du maxillaire le long de la base du rostre bien plus bas que le toit de l'orbite, un bassin supracrânien large surplombant dorsalement l'orbite droite et limité au crâne cérébral et une vaste fosse temporale élevée dorsomédialement. L'analyse cladistique préliminaire indique une position phylogénique de *Acrophyseter* au sein des stem-Physeteroidea, plus basale que le clade Kogiidae + Physeteridae. La morphologie de la région orale et de la fosse temporale suggère que *Acrophyseter* était capable de se nourrir de proies de grande taille. **Pour citer cet article :** O. Lambert et al., C. R. Palevol 7 (2008).

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**Mots clés :** Odontoceti ; Physeteroidea ; Cachalot ; Miocène terminal ; Pérou

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## 1. Introduction

Sperm whale (Physeteroidea, Odontoceti) teeth, isolated or associated with jaw fragments, are relatively common in the Neogene strata and have often been used to describe new taxa both in the past [4,8] and recently [12]. The significant intraspecific variation in the morphology and size of physeteroid teeth has led to an artificial proliferation of species. Significant fossil remains of physeteroids are instead relatively rare but essential to clarify the history of this diverse odontocete group. The recent discovery of an almost complete physeteroid skeleton from Late Miocene strata of South Italy, *Zygophyseter* Bianucci and Landini, 2006 [2], further demonstrated the low diagnostic value of fragmentary remains like isolated teeth and allowed a first phylogenetic analysis of this cetacean group [2]. In this analysis, *Zygophyseter* was shown to belong, together with other archaic sperm whales, in the stem-Physeteroidea, basal to the crown families Kogiidae and Physeteridae.

Apart from the kogiid *Scaphokogia* Muizon, 1988 [19], remains of physeteroids are rather rare and difficult to excavate in Peruvian localities, contrasting with other odontocetes. The scope of this paper is the description of a new fossil stem physeteroid from the Latest Miocene strata of the Pisco Formation, at Sud-Sacaco, Peru. This specimen is a finely preserved skull with the mandible and teeth associated. A preliminary parsimony analysis of the phylogenetic relationships of this new taxon is undertaken.

## 2. Material and methods

### 2.1. Institutional abbreviations

IRSNB: Institut royal des Sciences Naturelles de Belgique, Brussels, Belgium; MAUL: Museo dell'Ambiente, Università di Lecce, Italy; MLP: Museo de La Plata, Argentina; MNHN: Muséum national d'Histoire naturelle, Paris, France; USNM: United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

### 2.2. Specimens

In addition to MNHN SAS 1626 we have directly examined for comparison the following fossils of physeteroids: *Aulophyseter morricei* Kellogg, 1927 [14] USNM 11230; '*Aulophyseter*' *rionegrensis* Gondar, 1975 [9] MLP 62-XII-19-1; holotype of *Diaphorocetus poucheti* (Moreno, 1892) [18]; *Eudelpis mortezelensis* (Du Bus, 1872) [5] IRSNB M.523;

*Orycterocetus crocodilinus* Cope, 1868 [6] USNM 22926, USNM 14730, and USNM 22931; *Physeterula dubusi* Van Beneden, 1877 [23] IRSNB M.527; *Placoziphius duboisi* Van Beneden, 1869 [22] IRSNB M. 530; *Thalassocetus antwerpiensis* Abel, 1905 [1] IRSNB M.525; *Zygophyseter varolai* Bianucci and Landini, 2006 [2] MAUL 229/1.

The genus name *Brygmophyseter* Barnes [15] is here preferred to *Naganocetus* Bianucci and Landini, 2006 [2]; although the manuscript by Bianucci and Landini was accepted before the submission of the manuscript by Kimura et al., it was published one month later.

### 2.3. Phylogeny

The preliminary phylogenetic analysis was undertaken using the character–taxon matrix of Bianucci and Landini [2] (see Appendices A and B for the list of characters and the character–taxon matrix), with Paup 4.0b10, using the branch-and-bound algorithm and the heuristic search option, considering all characters as unordered and unweighted.

## 3. Systematic palaeontology

Cetacea Brisson, 1762 [3]

Odontoceti Flower, 1867 [7]

Physeteroidea Gray, 1821 [10]

*Acrophyseter* nov. gen.

**Etymology.** From Ancient Greek Akros, acute, emphasizing the pointed rostrum of this new taxon, and *Physeter*, extant type genus of the family Physeteridae.

**Diagnosis.** Same as for the type species *Acrophyseter deinodon* nov. sp.

*Acrophyseter deinodon* nov. gen. nov. sp.

**Holotype.** MNHN SAS 1626, a skull associated with the two dentaries and most of the upper and lower teeth. The apex of the rostrum is nearly complete. The left portion of the cranium is missing. The right supraorbital process of the frontal is considerably abraded.

**Etymology.** From Ancient Greek *Deinos*, terrible, and *Odon*, tooth, in reference to the sharp and robust teeth of this sperm whale.

**Type locality.** The specimen is from the locality of Sud-Sacaco [20], approximately at the level of the

km 540 of the south Panamerican highway. Geographic coordinates: 15° 34' 52" S–74° 44' 40" W.

**Type horizon.** Pisco Formation, Montemar Horizon as defined by Muizon and DeVries [20], Latest Miocene (ca. 6 Ma). The specimen was found under the erosive unconformity separating the Miocene and Pliocene levels observed by Muizon and DeVries [20] in the locality of Sud-Sacaco.

**Preliminary diagnosis.** This moderate size physeteroid is diagnosed by the following combination of characters: short rostrum (approximately half the condylobasal length); mandible and ventral margin of the rostrum distinctly curved upwards; upper tooth row with 12 teeth; lower tooth row with 13 teeth; enamel on teeth; posterior mandibular teeth transversely compressed; large teeth (ratio between greatest diameter of root and condylobasal length greater than 0.03); deep longitudinal groove on the right premaxilla along the rostrum; lateral margin of the maxilla along the rostrum base lower than the orbit roof and lower than the premaxilla–maxilla suture; wide supracranial basin anterolaterally developed on the right side of the cranium, overhanging the antorbital notch and orbit but not extended on the rostrum; right dorsal infraorbital foramen outside the supracranial basin; and high dorso-medially extended temporal fossa.

### 3.1. Description

#### 3.1.1. Skull

The skull has a size close to *Orycterocetus crocodilinus* (Figs. 1 and 2). The preserved condylobasal length is 815 mm. Taking account of the length of the dentary, no more than a few cm of the rostrum are missing anteriorly. The length of the latter is estimated at 427 mm, for a width at the rostrum base estimated at 274 mm. The bizygomatic width of the skull is estimated at 466 mm and its total height is more than 368 mm (nuchal crest nearly complete). In lateral view, the ventral margin of the rostrum is distinctly curved upwards (Fig. 1c), a condition more pronounced than in any other physeteroid. In dorsal view the rostrum abruptly tapers anteriorly from its wide base. The supracranial basin is deep and it extends far laterally above the right antorbital notch and orbit. A similar condition is observed in *Zygophyseter*. The temporal fossa is as high as long, anteroposteriorly shorter than in *Brygmophyseter* and *Zygophyseter*. Because of its dorsoventral extension, greater than in other physeteroids, the fossa displaces and narrows the dorsal part of the supraoccipital shield (Fig. 1d). The supraoccipital shield is erected, sloping posteriorly, at an average angle

of 55° with the horizontal plane. The median portion of the elevated nuchal crest overhangs the supracranial basin.

Each premaxilla bears three deep alveoli for incisors (Fig. 1b). On the lateral side of the rostrum, the premaxilla is erected, roughly vertical for half of its rostral length. The mesorostral groove is wide open dorsally, contrary to the condition in the holotype of *Aulophyseter morricei*, *Idiorophus* Kellogg, 1925 [13] and *Scaphokogia*; only the higher right premaxilla partly covers the groove anterior to the small right premaxillary foramen (transverse diameter 6 mm). Surprisingly, the asymmetry of the premaxillae also extends more anteriorly on the rostrum: the left premaxilla is pierced by two elongated foramina (length of the anterior and posterior foramina, respectively 61 and 22 mm) whereas the right premaxilla is excavated by a deep longitudinal groove starting 60 mm anterior to the right premaxillary foramen at the maxilla–premaxilla suture. At the level of the premaxillary foramen the right premaxilla is constricted by a medial projection of the maxilla. From that point the premaxilla strongly widens posteriorly, covering most of the lateral wall of the supracranial basin, differing on that point from *Zygophyseter* and the kogiids. Along the vomer and towards the bony naris the dorsal surface of the premaxilla remains flat, lacking the deep groove seen in several physeteroids (e.g., *Aulophyseter*, 'A.' *rionegrensis*, *Orycterocetus* and *Placoziphius*). Posterior to the small right bony naris (transverse diameter 21 mm) the right premaxilla is incomplete. However, the outline of the preserved portions suggests that it originally covered most of the right part of the elevated posterior wall of the supracranial basin and that it possibly crossed the sagittal plane of the skull (Fig. 2a). From the posterior left premaxillary foramen, the concave dorsal surface of the left premaxilla deepens towards the large left bony naris (transverse diameter larger than 44 mm), reaching a level 30 mm lower than the right premaxilla. The posterior end of the left premaxilla is not preserved, but anterior to the bony naris the bone does not widen as observed on the right premaxilla.

The maxilla is shorter anteriorly than the vomer, ending 100 mm posterior to the preserved apex of the rostrum. It bears alveoli for nine teeth very near to one another; interalveolar septa are nearly absent. The total count for the upper tooth row is 12 teeth, less than in *Idiorophus* and *Orycterocetus*. The upper dentition is reduced to absent in *Aulophyseter*, *Kogia* Gray, 1846 [11], *Physeter* Linnaeus, 1758 [16], *Placoziphius*, and *Scaphokogia*. The distance between the strongly converging tooth rows is reduced anteriorly; the first left and right maxillary teeth are only separated by 12 mm



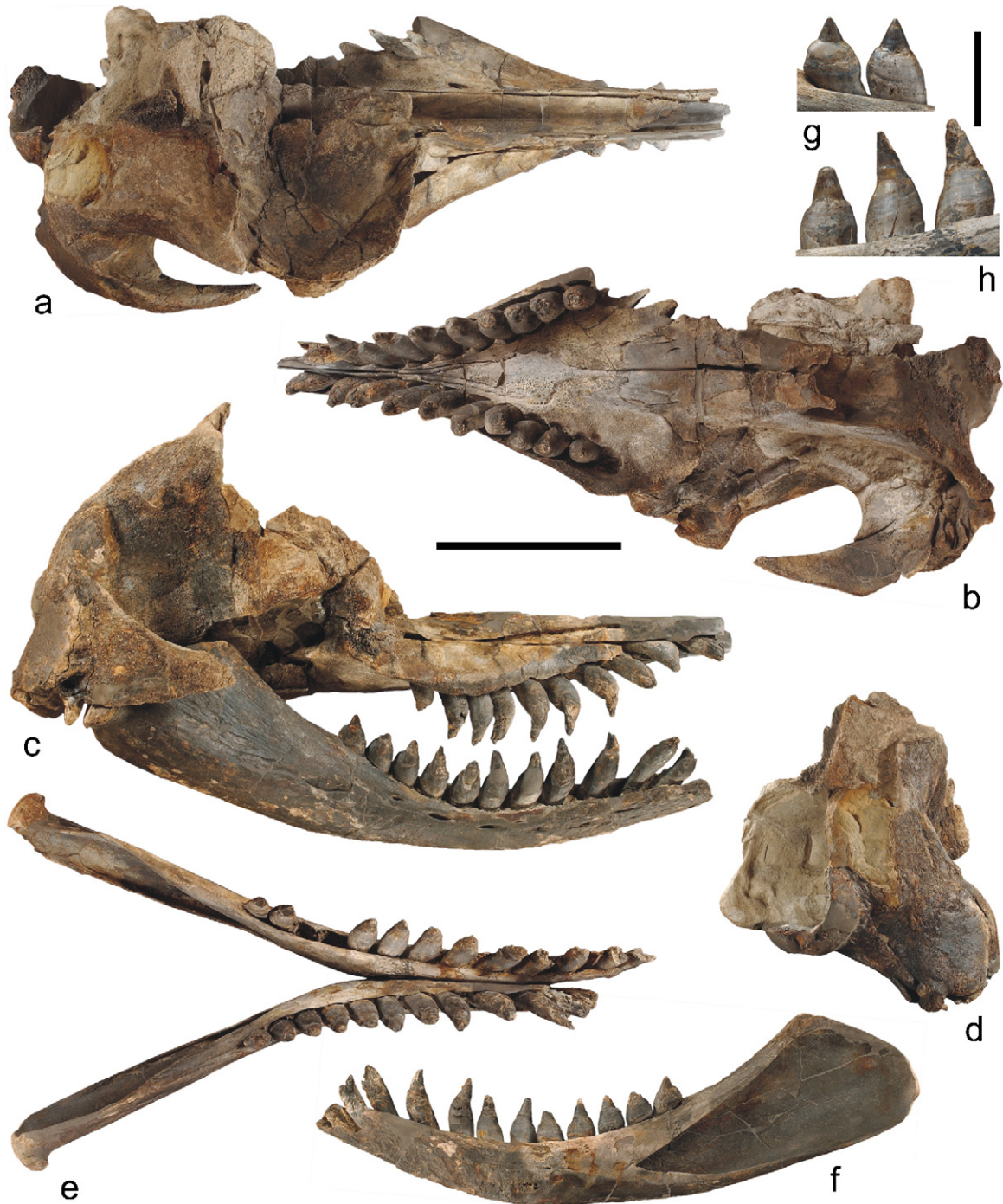


Fig. 1. Skull and mandible of MNHN SAS 1626, holotype of *Acrophyseter deinodon* nov. gen. nov. sp., Pisco Formation, Latest Miocene of Sud-Sacaco, Peru. (a) skull in dorsal view (left part of the cranium missing); (b) skull in ventral view; (c) skull and mandible in right lateral view; (d) skull in posterior view; (e) mandible in dorsal view; (f) right dentary in medial view; (g) 12th and 13rd left dentary teeth in lingual view; (h) 8th and 9th left dentary teeth in lingual view. Scale bar for a–f = 200 mm; scale bar for g–h = 50 mm.

*Crâne et mandibule de MNHN SAS 1626, holotype de Acrophyseter deinodon nov. gen. nov. sp., Formation Pisco, Miocène terminal de Sud-Sacaco, Pérou.* (a) crâne en vue dorsale (partie gauche de la boîte crânienne manquante); (b) crâne en vue ventrale; (c) crâne et mandibule en vue latérale droite; (d) crâne en vue postérieure; (e) mandibule en vue dorsale; (f) dentaire droit en vue médiane; (g) 12<sup>e</sup> et 13<sup>e</sup> dents dentaires gauches en vue linguale; (h) 8<sup>e</sup> et 9<sup>e</sup> dents dentaires gauches en vue linguale. Echelle pour a–f = 200 mm; échelle pour g–h = 50 mm.

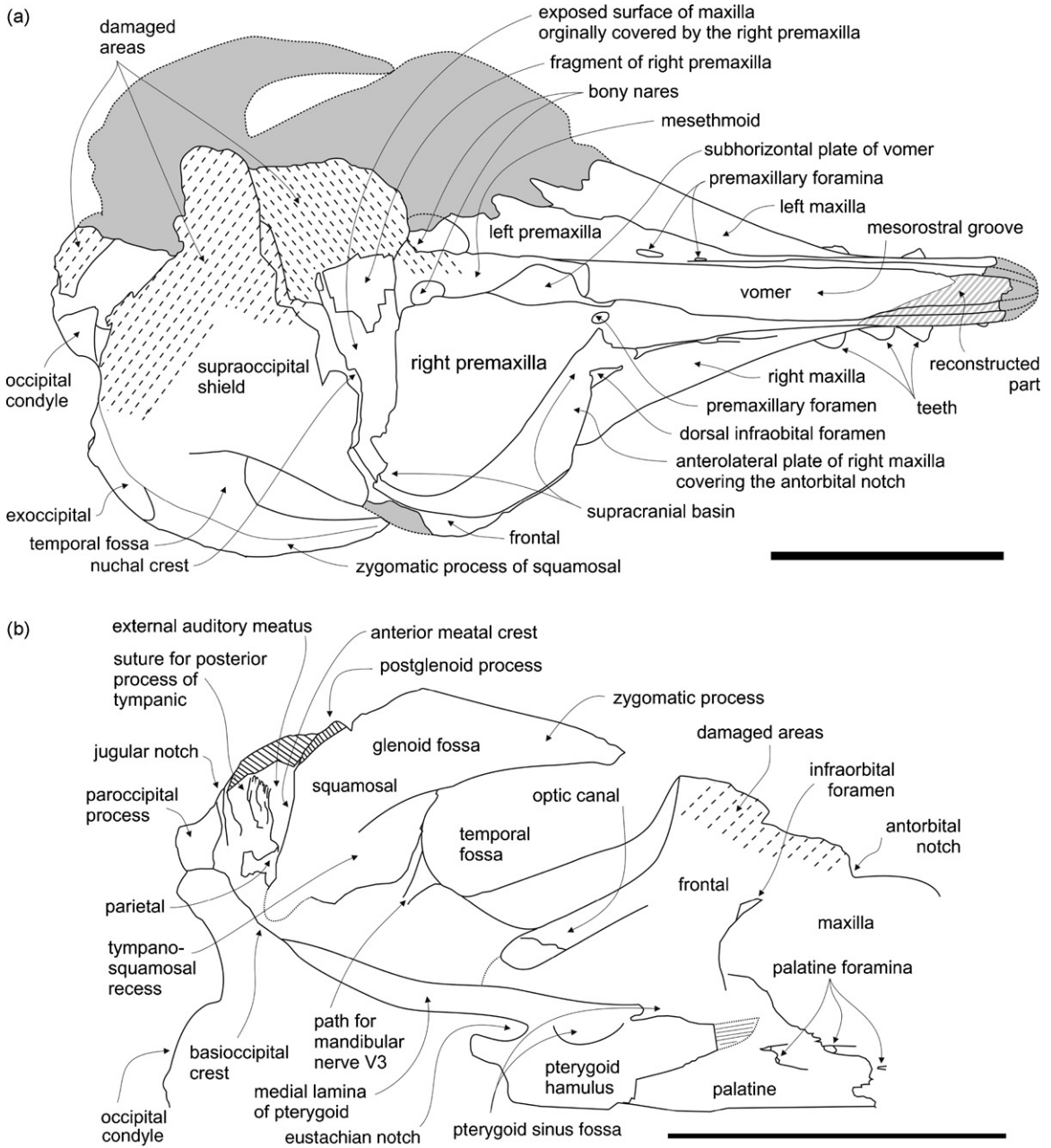


Fig. 2. Explanatory drawings of the skull of MNHN SAS 1626, holotype of *Acrophyseter deinodon* nov. gen. nov. sp., Pisco Formation, Latest Miocene of Sud-Sacaco, Peru. (a) dorsal view; (b) detail of the basicranium and palate in ventral view. Shaded areas correspond to missing parts of the skull. Scale bars = 200 mm.

Dessins explicatifs du crâne de MNHN SAS 1626, holotype de *Acrophyseter deinodon* nov. gen. nov. sp., Formation Pisco, Miocène terminal de Sud-Sacaco, Pérou. (a) vue dorsale; (b) détail du basicrâne et du palais en vue ventrale. Les zones ombrées correspondent aux parties manquantes du crâne. Échelles = 200 mm.

whereas this distance increases to 108 mm at the level of the seventh maxillary teeth and 140.5 mm at the level of the last maxillary teeth. The flat ventral surface of the rostrum between the tooth rows is mostly occupied by the vomer, with a maximum width of 57 mm

at the level of the sixth maxillary tooth (Fig. 1b). In dorsal view the maxilla is visible on the proximal half of the rostrum as a slightly concave surface medially sloping; the lateral margin of the rostrum is therefore considerably lower than the maxilla–premaxilla suture

on the rostrum and than the roof of the orbit (Fig. 1c), contrary to *Aulophyseter*, 'A.' *rionegrensis*, *Brygmophyseter*, *Diaphorocetus*, *Kogia*, *Orycterocetus*, *Physeter*, *Physeterula*, and *Placoziphius*. The antorbital notch is eroded on both sides; on the right side it was originally outside the supracranial basin and much lower than the anterolateral wall of the basin, approximately at the anteroposterior level of the right premaxillary foramen. The supracranial basin is limited anterolaterally by an oblique thin plate of the right maxilla, just posterior to the large dorsal infraorbital foramen. This thin maxillary plate with the lateral slope of the maxilla anterior to the antorbital notch, and the roughly vertical premaxillae along the mesorostral groove on the rostrum are three strong clues for a supracranial basin limited to the cranium, not extending on the rostrum as is observed in *Zygophyseter*. The posterolateral extension of the thin maxillary plate overhangs the supraorbital area and forms the lateral wall of the supracranial basin. No dorsal infraorbital foramen pierces the right maxilla inside the supracranial basin, contrary to *Zygophyseter*. One dorsal infraorbital foramen is preserved on the left maxilla just posterior to the level of the right premaxillary foramen. Either the left maxilla lacks the thin oblique plate described on the right side or it is more posteriorly located and not preserved.

In the mesorostral groove the right lateral wall of the vomer follows the curve of the right premaxilla, partly closing the groove dorsally and covering the ossified posterior portion of the mesethmoid as a subhorizontal plate. As in other physeteroids, the mesethmoid is distinctly tilted towards the left side.

The optic canal forms an angle of 40° with the longitudinal plane; it is more anteriorly oriented than in *Aulophyseter*, *Diaphorocetus*, *Orycterocetus*, and *Physeter*. The palatine is wide anteriorly; it reaches the level of the last alveolus. Several palatine foramina are observed on each side: two in the maxilla, anterior to the palatine–maxilla suture, and two (three on the left side) in the palatine itself. The pterygoid is partly preserved. The anterior portion of the bone is a thin plate, which overlaps the palatine anteriorly. However, the marks of the suture with the palatine indicate an apex posterior to the antorbital notch, but at the level of the anterior edge of the postorbital process. This anterior portion is narrow and distinctly thickened on its lateral edge limiting between the pterygoid and the orbit a shallow fossa, which might correspond to an anterior extension of the pterygoid sinus (Figs. 1b, 2b). A similar withdrawal of the pterygoid is observed e.g., in *Eudelphis* and *Physeter*. The pterygoid is greatly thickened dorsolaterally, especially the part of the bone posterior to the hamular

process (medial lamina), which borders the basioccipital basin. Anterior to the eustachian notch the surface of the pterygoid presents a rounded shallow depression, also possibly related to the pterygoid sinus. The hamular processes are not completely preserved but they clearly indicate the absence of lateral lamina.

The zygomatic process of the squamosal is moderately elongated, less than in *Zygophyseter*, and anteriorly pointed, with a considerable dorsoventral height posteriorly (Fig. 1c). The glenoid surface is weakly demarcated and anteroventromedially oriented. The tympanosquamosal recess is shallow. The postglenoid process is a thin plate anteriorly limiting the wide external auditory meatus. Along the posterior meatal crest is a deeply grooved surface probably corresponding to the area of contact of the squamosal with the enlarged posterolaterally directed posterior process of the tympanic bulla (Figs. 1b, 2b). Only the lateral portion of the alisphenoid could be prepared; the shallow path for the mandibular nerve V3 emerges in the temporal fossa along the squamosal–alisphenoid suture. In the vast temporal fossa, the examination of the sutures suggests that more than one third of the median surface of the fossa is occupied by the parietal, between the frontal and the squamosal. This is wider than in *Aulophyseter* and *Physeter*, more similar to *Idiophyseter* Kellogg, 1925 [13] and probably related to the length of the temporal fossa.

The basioccipital basin is proportionately long, as shown by the elongated and thick medial lamina of the pterygoid from the eustachian notch to the posterior contact with the basioccipital (146 mm long) and posteriorly wide. The robust occipital condyles are not separated from the lateral plate of the exoccipital by a distinct neck.

### 3.1.2. Mandible

The virtually complete left dentary has a total length of 744 mm, with a symphyseal portion of 355 mm. It bears 13 large alveoli, one less than in *Zygophyseter* and distinctly less than in the presumably oldest known physeteroid *Ferecetoherium* Mchedlidze, 1970 [17], *Idiophus*, *Physeter* and *Physeterula*. As for the upper tooth count, this count corresponds to a limited polydonty, with only two teeth in excess over the permanent dentition of the archaeocete *Dorudon* [21]. The posterior limit of the unfused symphysis is at the level of the 9th alveolus (Fig. 1e). The ventral margin of the dentary is strongly and regularly convex. As a consequence, even if the distance between the slender angular process and the mandibular condyle is short, the position of the condyle is elevated relatively to the ventralmost portion of the dentary. The more robust high coronoid process emphasizes the concavity of the dorsal margin



of the bone, matching the outline of the ventral margin of the rostrum. The mandibular fossa is large and distinctly pointed anteriorly (Fig. 1f), a condition particularly marked in young *Physeter* and in *Zygophyseter*. Five mental foramina pierce the right dentary. The alveoli are posteroventrally oriented in the anterior portion of the tooth row; the 9th to 12th alveoli are vertical; and the 13th is anteroventrally directed.

### 3.1.3. Teeth

The teeth are robust, with a swollen root and a relatively short enamelled crown ornamented with shallow grooves (Fig. 1e–h). They are deeply implanted in the alveoli, particularly the anterior upper and lower teeth with an elongated root. The posterior lower teeth are transversely flattened, with a posterior bulge of the root at the limit with the crown, whereas the flattening of the posterior upper teeth is anteroposterior. More anteriorly the upper and lower teeth are more cylindrical.

The apical wear of the crown on the best preserved teeth is weak. On most of the teeth, the anterior and posterior surfaces of the distal portion of the root are marked by deep occlusion facets, due to the short distance between successive teeth. On the anterior upper teeth the occlusion facets are antero- and posterolateral whereas they tend to be more medial in posterior teeth. Small depressions in the maxilla anteromedian and posteromedian to the last posterior alveolus even suggest that the last lower teeth contacted the palate instead of the corresponding upper teeth. A similar condition is observed in *Orycterocetus*. On the sixth maxillary tooth the posterior occlusion surface is transformed in a small pit.

Even if the wear of the apex of the tooth crown is reduced, considering the filling of the pulp cavity and the depth of the occlusion facets this individual was definitively not a juvenile.

## 4. Phylogeny and discussion

The preliminary phylogenetic analysis (see Section 2 for details) provided two shortest trees (tree length 43; CI 0.84; RI 0.82). The consensus tree is shown in Fig. 3. *Acrophyseter* is more stemward than the Kogiidae + Physeteridae clade (crown-Physeteroidea), due to the retention of enamel on teeth. It is either more closely related to *Brygmophyseter* and *Zygophyseter*, based on the size of its teeth, or more closely related to *Aulophyseter* + crown-Physeteroidea, based on the anteroposterior compression of the temporal fossa.

Interestingly, *Acrophyseter* shares with *Zygophyseter* the supracranial basin anterolaterally developed on the

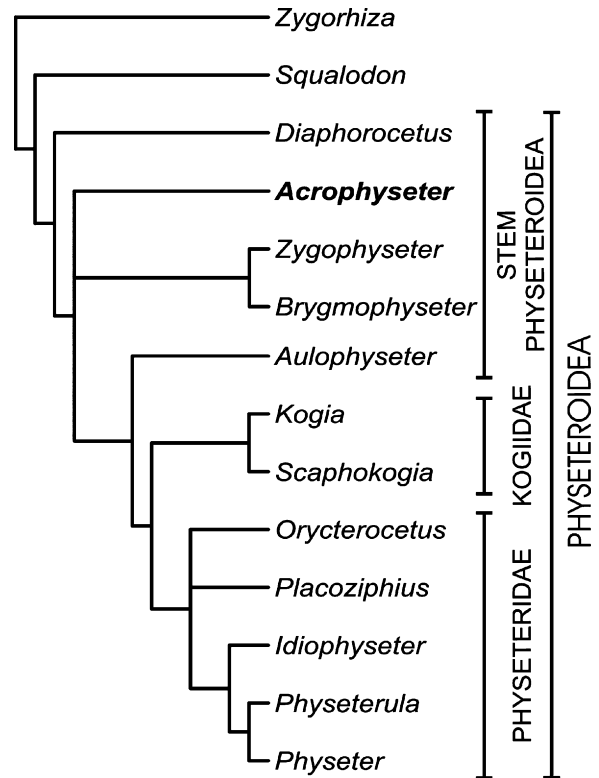


Fig. 3. Consensus tree showing the phylogenetic relationships of *Acrophyseter deinodon* nov. gen. nov. sp. with other physeteroids, more stemward than the clade Kogiidae + Physeteridae (crown-Physeteroidea).

Arbre de consensus indiquant les relations phylogénétiques de *Acrophyseter deinodon* nov. gen. nov. sp. avec les autres physétéroïdés, plus basal que le clade Kogiidae + Physeteridae (crown-Physeteroidea).

right side of the cranium, overhanging the antorbital notch and the orbit. Besides this character, not observed in any other physeteroid and possibly indicating a new lineage, *Acrophyseter* differs fundamentally from the larger *Zygophyseter* in the regularly dorsally curved mandible, the wider right premaxilla in the supracranial basin, the thicker nuchal crest and the shorter zygomatic process of the squamosal and temporal fossa.

In addition to the architecture of the supracranial basin, the oral apparatus of *Acrophyseter* is unusual. The shortened and pointed rostrum associated to the dorsally curved mandible bears very robust teeth, possibly related to predation on large preys. This hypothesis is supported by the important posterodorsal development of the temporal fossa. The transverse compression of the posterior lower teeth might further indicate the retention of some degree of shearing ability. Such a food processing technique would contrast strongly with the suction feeding demonstrated in recent sperm whales, related to the loss of upper teeth [24]. Considering the other faunal ele-

ments of the Montemar Horizon of the Pisco Formation [19,20] and an estimated body length of 3.9–4.3 m for *A. deinodon*, this predator could have fed on small odontocetes (e.g., the phocoenid *Piscolithax* sp.), pinnipeds (e.g., the phocid *Acrophoca* sp.) and seabirds (e.g., the penguin *Spheniscus urbinai*).

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### Appendix A. List of the characters used in the phylogenetic analysis, taken from Bianucci and Landini [2]

1. Size of skull (expressed as condylobasal length): 0, 50–90 cm; 1, 90–120 cm; 2, > 120 cm; 3, < 50 cm.
2. Supracranial basin of the skull: 0, absent; 1, present; 2, extended onto the whole dorsal surface of the rostrum.
3. Antorbital notch: 0, absent; 1, shallow; 2, deeply incised; 3, transformed into a very narrow slit.
4. Maxillae, premaxillae and vomer, all reaching the tip of the rostrum which is not formed only by the premaxillae: 0, no; 1, yes.
5. Frontal–maxilla suture, with skull in lateral view: 0, approximately horizontal, with lateral exposure of frontal, over the orbit, not thickening posteriorly; 1, angled posterodorsally, forming an angle < 20° from the axis of the rostrum, with lateral exposure of frontal thickening posteriorly; 2, as state 1 with an angle of 20–40°; 3, as state 1 with an angle > 40°.
6. Right premaxilla: 0, posteriorly extended as the left premaxilla; 1, more posteriorly extended than the left premaxilla.
7. Right premaxilla: 0, not posteriorly widened; 1, posteriorly widened transversely and passed to the left side of the skull.
8. Left premaxillary foramen very small or absent: 0, no; 1, yes.
9. Increase in size of the right premaxillary foramen: 0, no; 1, yes.
10. Lack of nasals: 0, both nasals present; 1, one nasal absent; 2, both nasals absent.
11. Presence of a sagittal crest: 0, absent; 1, present.
12. Occipital shield: 0, convex and forming an angle of about 40° from the axis of the rostrum; 1, as state 0 with an angle of about 60°; 2, flat or concave forming an angle of about 90°.
13. Fusion of lacrimal and jugal: 0, no; 1, yes.
14. Temporal fossa: 0, anteroposteriorly elongated (width/height > 1); 1, not anteroposteriorly elongated (width/height = 1); 2, anteroposteriorly compressed (width/height < 1).
15. Zygomatic process of squamosal in lateral view: 0, ‘L’-shaped with dorsal margin ventrally bending in its posterior portion; 1, triangular, with dorsal margin dorsally bending in its posterior portion.
16. Anterior bullar facet: 0, very anteroposteriorly elongated; 1, reduced; 2, absent or very small.
17. Accessory ossicle: 0, absent; 1, present; 2 present and partially fused with the anterior process.
18. Posterior extension of the posterior process of the periotic parallel to the general plane of the bone and not ventrally orientated: 0, no; 1, yes.
19. Involucrum with an evident central concavity, visible in ventral and medial views, due to the marked pachyostosis of its anterior and posterior portion: 0, no; 1, yes.
20. Loss of dental enamel: 0, no; 1, yes.
21. Size of teeth (greatest diameter of root expressed as percentage of the condylobasal length of skull): 0, < 3%; 1, > 3%.
22. Upper tooth row: 0, deep alveoli; 1 alveoli shallow or absent.
23. Ventral position of the mandibular condyle: 0, no; 1, yes.

### Appendix B. Character–taxon matrix used in the cladistic analysis, taken from Bianucci and Landini [2]. Matrice caractère-taxon utilisée dans l'analyse cladistique, reprise de Bianucci & Landini [2].



Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Zygorhiza</i>	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Squalodon</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Diaphorocetus</i>	0	1	2	0	1	1	1	1	1	1	0	0	1	1	1	?	?	?	?	?	0	0	?
<b>Acrophyseter</b>	0	1	?	0	2	1	1	1	0	1	0	1	?	2	1	?	?	?	?	0	1	0	1
<i>Zygophyseter</i>	2	1	b	0	2	1	1	1	1	1	0	?	1	0	1	2	2	?	1	0	1	0	1
<i>Brygmophyseter</i>	2	1	2	?	2	1	1	1	1	1	0	1	?	0	1	?	?	?	?	0	1	0	1
<i>Aulophyseter</i>	1	1	2	0	3	1	1	1	1	1	0	1	1	2	1	2	2	0	?	0	0	1	?
<i>Kogia</i>	3	1	3	1	2	1	0	1	0	2	1	1	1	2	1	2	2	1	1	1	0	1	a
<i>Scaphokogia</i>	3	1	3	1	2	1	0	1	0	2	1	1	1	2	?	2	2	1	?	?	?	1	?
<i>Orycterocetus</i>	0	1	2	0	2	1	1	1	1	1	0	2	1	2	1	2	2	0	1	1	0	1	?
<i>Placoziphius</i>	0	1	2	?	2	1	1	1	1	?	0	2	1	2	1	?	?	?	?	1	0	1	?
<i>Idiophyseter</i>	0	2	2	?	2	1	1	1	1	?	0	2	?	2	1	?	?	?	?	?	?	1	?
<i>Physeterula</i>	2	2	2	?	2	1	1	?	?	?	0	2	1	?	?	?	?	?	?	1	0	?	?
<i>Physeter</i>	2	2	2	0	3	1	1	1	1	1	0	2	?	2	1	2	2	0	1	1	0	1	1

0, primitive state; 1–3, derived states; a, variable between 0 and 1; b, variable between 2 and 3; ?, missing character; –, irrelevant character.

0, état primitive ; 1–3, états dérivés ; a, variable entre 0 et 1 ; b, variable entre 2 et 3 ; ?, caractère manquant ; –, caractère non pertinent.

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