Killer sperm whale: a new basal physeteroid (Mammalia, Cetacea) from the Late Miocene of Italy

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Zygophyseter varolai, a new genus and species of Physeteroidea (Cetacea, Odontoceti), is based on an almost complete skeleton from the Late Miocene (Tortonian) in southern Italy. The extreme elongation of the zygomatic process of the squamosal and the circular supracranial basin (probably for housing the spermaceti organ) delimited by a peculiar anterior projection of the supraorbital process of the right maxilla are the most distinctive features of this bizarre sperm whale. Large body size, large teeth present in both lower and upper jaw, and anteroposteriorly elongated temporal fossa and zygomatic process of the squamosal indicate that this cetacean (for which we suggest the English common name killer sperm whale) was an active predator adapted to feeding on large prey, similarly to the extant killer whale (*Orcinus orca*). A phylogenetic analysis reveals that *Zygophyseter* belongs to a Middle–Late Miocene clade of basal physeteroids, together with ***Naganocetus*** (new genus for the type of '*Scaldicetus*' *shigensis*). Moreover, the phylogenetic analysis shows evidence of a wide physeteroid radiation during the Miocene and that the extant *Physeter* and *Kogia* belong to two distinct families that form a clade representing the crown-group Physeteroidea.   © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, **148**, 103–131.

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INTRODUCTION

Physeter macrocephalus Linnaeus, 1758, the world's largest extant predator, and the similar but dramatically smaller *Kogia breviceps* (Blainville, 1838) and *K. sima* Owen, 1866, are the only living species of sperm whales (superfamily Physeteroidea), a cetacean lineage known since the Late Oligocene (about 25 Ma) (Barnes, 1984; Fordyce & Muizon, 2001; Kazár, 2002).

The fossil record of sperm whales, recently synthesized by Fordyce & Muizon (2001) and Kazár (2002), shows one of the largest diversifications among the odontocetes during the Miocene, represented by at least 12 genera based on significant cranial material. Moreover, fragmentary remains belonging to this odontocete group (mainly teeth) are abundant in several Miocene fossil assemblages, and if we consider these non-diagnostic materials, the number of genera more than doubles. It is likely that the diversity of this superfamily during the Miocene is actually greater than that shown by the well-preserved material. For example, the Rosignano and Vignale assemblages of northern Italy include isolated periotics belonging to at least five physeteroid genera (Bianucci & Landini, 2002), indicating that these odontocetes were already widely diversified in the Burdigalian and Langhian (early Middle Miocene).

Despite their wide diversification, fossil sperm whales have received little recent attention, and their phylogenetic relationships and some adaptations deserve reappraisal.

The aim of this article is to describe an almost complete physeteroid skeleton, here referred to a new genus and species, from the Late Miocene Pietra leccese sediments in southern Italy, its comparison with other sperm whale taxa, and a first cladistic analysis of this superfamily including the new genus and ten other genera of fossil and extant physeteroids.

Before describing the specimen, it is necessary to explain the circumstances of its discovery and to provide a brief review the genus *Scaldicetus*.

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One of the authors (W.L.) previously collaborated on the description of a new sperm whale, *Scaldicetus degiorgii*, from the Pietra leccese (Varola, Landini & Pilleri, 1988). One isolated tooth kept in the Technical School 'O. Costa' in Lecce, southern Italy, already described by Costa (1853), Gervais (1872) and Capellini (1878), was designated as holotype for *S. degiorgii*. Eight teeth collected in the Cisterna Quarry near Lecce were described in the same paper as paratypes of the new species.

Some months after the publication of this new physeteroid species, the workers of Cisterna Quarry discovered an almost complete skeleton belonging to the same specimen as produced the eight teeth described as paratypes of *S. degiorgii*. This skeleton was extracted over several years and is here described in detail.

Other sperm whale remains discovered in the Pietra leccese sediments include some skulls more or less complete with associated teeth. Our study of these remains, and of some historical materials, supports earlier suggestions (e.g. Kellogg, 1925) that teeth are undiagnostic for physeteroids. We conclude:

1. The 44 teeth described as *Scaldicetus caretti* by du Bus (1867) belong to physeteroids, but are diagnostic neither at the generic nor at the specific level, and consequently the generic and specific names must be restricted only to the original material of du Bus.
2. Other species names based only on isolated teeth and referred to *Scaldicetus* (e.g. *S. degiorgii*, *S. grandis*, *S. inflatus*) must be restricted to their apparently nondiagnostic holotypes.
3. In considering *Scaldicetus degiorgi*, the marked difference in size between the small tooth holotype and the large teeth of the Cisterna Quarry supports them as two distinct species.
4. The almost complete skeleton of the Cisterna Quarry, which earlier produced the paratype teeth of *Scaldicetus degiorgii*, differs from named physeteroids and is here assigned to the new genus and species *Zygophyseter varolai*.
5. The original name *Eudelphis* proposed by du Bus (1872) for *Eudelphis mortselensis* is here re-evaluated. This species, based on significant parts of a fossil skull from the Antwerp Basin and referred by Abel (1905) to the genus *Scaldicetus*, substantially differs from the fossil examined herein. A redescription of the holotype of *Eudelphis mortselensis* is necessary but beyond the scope of this paper.
6. The species *Scaldicetus shigensis* from Japan, recently described on the basis of an almost complete skeleton (Hirota & Barnes, 1995), differs sufficiently from *Zygophyseter varolai* to warrant a new genus *Naganocetus*, and the new combination *Naganocetus shigensis* is here proposed. Diagnosis of this new genus is given below under 'Comparisons'.

MATERIAL AND METHODS

The anatomical terminology used derives mainly from various papers by Kasuya (1973), Muizon (1984, 1988, 1991), Fordyce (1994, 2002), Luo & Marsh (1996), Luo & Gingerich (1999) and Geisler & Sanders (2003). Measurements were taken according to the methods used by Bianucci (1996).

The aim of cladistic analysis was to determine relationships within the Physeteroidea. Accordingly, we selected some taxa with significant preserved material and in particular the extant *Physeter* and *Kogia*, nine other fossil genera among the physeteroids, and *Zygorhiza* and *Squalodon* as outgroups. The characters selected for this analysis were observed directly on the fossil material and/or based on published literature (see Table 1 and Appendices 1 and 2).

The cladistic analysis used PAUP version 4.0 b10 (Swofford, 1998) to obtain a cladogram of minimum length. Analysis used the heuristic search option, considering all characters as unordered and unweighted. We used the exhaustive search option, which guarantees to find the most parsimonious tree(s), with the following options: initial 'MaxTrees' setting = 100, branches collapsed (creating polytomies) if maximum branch length = 0, 'MulTrees' option in effect, topological constraints not enforced.

Anticipating the phylogenetic results, the sperm whale monophyletic group (Physeteroidea) here includes the Physeteridae, the Kogiidae and other more basal odontocetes. The new sperm whale genus described herein is one of these basal physeteroids not belonging to either of the two known families of this large clade.

The following institutional abbreviations are used: IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; ITCL, Istituto Tecnico Costa, Lecce, Italy; MAUL, Museo dell'Ambiente, Università di Lecce, Italy; MBMS, Museo Balseros del Mar del Sur, Salango, Ecuador; MGPUF, Museo di Geologia e Palaeontologia, Università di Firenze, Italy; MGPUP, Museo di Geologia e Palaeontologia, Università di Padova, Italy; MSNTUP, Museo di Storia Naturale e del Territorio, Università di Pisa, Italy; MNHNP, Muséum National d'Histoire Naturelle, Paris, France; MZAFS, Museo di Zoologia, Accademia dei Fisiocritici, Siena, Italy; MZUF, Museo di Zoologia, Università di Firenze, Italy; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA; ZMA, Zoological Museum, University of Amsterdam, Netherlands.

Table 1. Age, locality and main references of cetacean species considered in this paper for comparison and cladistic analysis

Species	Age and Locality	References
Aulophyseter morricei Kellogg, 1927	Middle Miocene; California (USA)	Kellogg (1927, 1931)
'Aulophyseter' rionegrensis Gondar, 1975	Late Miocene; Rio Negro (Argentina)	Gondar (1975), Kazár (2002)
Diaphorocetus poucheti (Moreno, 1892)	Early Miocene; Patagonia (Argentina)	Moreno (1892), Lydekker (1894)
Eudelphis mortselensis (du Bus, 1872)	Miocene; Antwerp (Belgium)	du Bus (1872), Abel (1905)
Ferocetotherium kelloggi (Mchedlidze, 1970)	Late Oligocene; Caucasus (Azerbaidzhan)	Mchedlidze (1970, 1976), Barnes (1985), Pilleri (1986b)
Idiophyseter merriami Kellogg, 1925	Middle Miocene; California (USA)	Kellogg (1925)
Idiorophus patagonicus (Lydekker, 1894)	Early Miocene; Patagonia (Argentina)	Lydekker (1894)
Kogia breviceps Blainville, 1838	Recent; cosmopolitan	Schulte (1917), Kasuya (1973), Ross (1979), Caldwell & Caldwell (1989), Porter & Morton (2003)
Kogia pusilla (Pilleri, 1987)	Middle Pliocene; Tuscany (Italy)	Bianucci & Landini (1999)
Kogia sima Owen, 1866	Recent; cosmopolitan	Kasuya (1973), Ross (1979), Caldwell & Caldwell (1989); Porter & Morton (2003)
Kogia sp.	Pliocene, Tuscany (Italy)	Pilleri (1986c), Bianucci & Landini (1999)
Naganocetus shigensis (Hirota & Barnes, 1995) **nov. comb.**	Middle Miocene; Shiga-mura (Japan)	Hirota & Barnes (1995)
Ontocetus oxymycterus Kellogg, 1925	Late Miocene; California (USA)	Kellogg (1925)
Orycterocetus crocodilinus Cope, 1868	Early Middle Miocene; Maryland (USA)	Kellogg (1965)
Orycterocetus sp.	Miocene, Salento Peninsula (Italy)	Bianucci *et al*. (2004)
Physeter macrocephalus Linnaeus, 1758	Recent; cosmopolitan	Flower (1868), Kasuya (1973), Omura *et al*. (1962), Rice (1989)
Physeterula dubusii Van Beneden, 1877	Miocene; Antwerp (Belgium)	Abel (1905)
Placoziphius duboisii Van Beneden, 1869	Miocene; Antwerp (Belgium)	Kazár (2002)
Praekogia cedrosensis Barnes, 1973	Latest Miocene; Isla Cedros (Mexico)	Barnes (1973)
Preaulophyseter gualichensis Caviglia & Jorge, 1980	Miocene; Rio Negro (Argentina)	Caviglia & Jorge (1980)
Scaldicetus caretti du Bus, 1867 (ND)	Miocene; Antwerp (Belgium)	du Bus (1867), Abel (1905)
'Scaldicetus' degiorgii Varola & Pilleri, 1988 (ND)	Miocene; Salento Peninsula (Italy)	Varola *et al*. (1988)
'Scaldicetus' grandis (du Bus, 1972) (ND)	Miocene; Antwerp (Belgium)	du Bus (1872), Abel (1905)
Scaphokogia cochlearis Muizon, 1988	Late Miocene; Aguada de Lomas (Peru)	Muizon (1988)
Squalodon bariensis Jourdan, 1861	Early Miocene; Bari (France); Libano and Belluno (Italy)	Dal Piaz (1916), Pilleri (1985), Muizon (1991)
Squalodon bellunensis Dal Piaz, 1916	Early Miocene; Libano and Belluno (Italy)	Dal Piaz (1916), Pilleri (1985)
Squalodon calvertensis Kellogg, 1923	Early Miocene; Maryland (USA)	Kellogg (1923)
Squalodon sp.	Miocene; Salento Peninsula (Italy)	Bianucci *et al*. (1994a)
Thalassocetus antwerpiensis Abel, 1905	Miocene; Antwerp (Belgium)	Abel (1905)
Zygorhiza kochii Reichenbach *in* Carus, 1847	LateEocene; Alabama (USA)	Kellogg (1936)

*The holotypes of the type species of these two genera are dubiously diagnostic single isolated teeth (respectively *Orycterocetus quadratidens*Leidy, 1853 and *Ontocetus emmonsi* Leidy, 1859); we maintain the two genera because the genera are nominally represented by significant specimens referred to the two species reported in this table (see also Fordyce & Muizon, 2001).
ND, non-diagnostic.

SYSTEMATICS

ORDER CETACEA BRISSON, 1762
SUBORDER ODONTOCETI FLOWER, 1867
SUPERFAMILY PHYSETEROIDEA GRAY, 1821

Emended diagnosis: A superfamily of Odontoceti characterized by the following combined characters of the skull, ear bones and mandible: presence of a supracranial basin; strong asymmetry of skull emphasized by the posterior edge of the right premaxilla extending more posteriorly than the left; right premaxilla transversely widening and passing to the left side of the skull (character lacking because of reversal in the Kogiidae); left premaxillary foramen either very small or absent, and one or two nasal bones lacking; antorbital notch deeply incised; frontal–maxilla suture, with skull in lateral view, angled posterodorsally and lateral exposure of frontal thickening posteriorly; zygomatic process of the squamosal triangular in lateral view with the dorsal margin dorsally bending in its posterior portion; anterior bullar facet of the tympanic bulla absent or very small; accessory ossicle present and partially fused with the anterior process of the periotic; involucrum with an evident central concavity, visible in ventral and medial views; fovea epitubaria of the periotic large and rectangular owing to the anteroposterior elongation of the accessory ossicle; anteroposteriorly elongated mandibular foramen; mandibular condyle located near the ventral margin. Moreover, the following combination of soft-tissue features characterizes the extant species: presence of a spermaceti organ; nasal passages not confluent distally to bony nares and characterized by a developed distal sac and by a proximal sac evolved into a frontal sac.

FAMILY INCERTAE SEDIS
ZYGOPHYSETER GEN. NOV.

Diagnosis: As for *Zygophyseter varolai*, the only included species.

Type and only included species: *Zygophyseter varolai* sp. nov.

Etymology: The generic name is a combination of the Latin adjective *zygomaticus*, emphasizing the extreme elongation of the zygomatic process of the squamosal, and *Physeter*, the type genus of the family Physeteridae. Gender masculine.

ZYGOPHYSETER VAROLAI SP. NOV.

Holotype: MAUL 229/1: skull (Figs 3–5) mandible with 22 teeth in place (Fig. 9), 25 loose teeth, some as fragments (Fig. 9), incomplete left periotic and left tympanic bulla (Fig 6, 7), atlas, nine thoracic vertebrae, ten lumbar vertebrae and nine caudal vertebrae, 23 complete or fragmentary ribs; almost complete left scapula and fragment of right scapula (Fig. 10); a small fragment of right radius, one phalanx; all remains of the same specimen. Measurements are given in Table 2.

Etymology: Named in honour of Angelo Varola who discovered, collected and restored the holotype. The species name is also in recognition of the outstanding field, laboratory and research activities on the fossil vertebrates of the Pietra leccese carried on by Angelo Varola in the last 20 years.

Horizon and locality: Cisterna Quarry near Cavallino, Salento Peninsula (Apulia, southern Italy, Fig. 1) in

Table 2. Measurements (mm) of the *Zygophyseter varolai* gen. et sp. nov. holotype (MAUL 229/1)

Skull	
Condylobasal length	1480
Length of rostrum	845
Width of rostrum at base	450
Width of premaxillae at base of rostrum	245
Width of rostrum at 60 mm anterior to base	435
Width of rostrum at midlength	190
Width of premaxillae at midlength of rostrum	150
Width of rostrum at 3/4 length (measured from posterior end)	120
Distance from tip of rostrum to external nares	105
Distance from tip of rostrum to internal nares	116
Length of cranium	635
Greatest antorbital width	690*
Greatest supraorbital width	680*
Greatest postorbital width	710*
Greatest parietal width	300
Width of temporal fossa	420
Width across the occipital condyles	175
Length of orbit	140
Greatest width across zygomatic processes of squamosals	745
Length of upper tooth row	820
Number of teeth of upper tooth row	13
Mandible	
Length of dentary	1300
Height of dentary	190
Length of lower tooth row	820
Number of teeth of lower tooth row	14
Length of mandibular symphysis	620
Ear bones	
Thickness of pars cochlearis	20.1
Length of anterior process of periotic	25.3
Greatest width of tympanic bulla	35.9

*Estimated.

the informally named 'Pietra leccese', which consists of generally massive, uniformly fine-grained biomicrites (Mazzei, 1994). The specimen was collected about 2 m below ground level, in sediments of early Tortonian (Late Miocene) age, about 8.14–10.5 Ma. This age is based on a planktonic foraminiferal association referable to the *Neogloboquadrina acostaensis* zone of Iaccarino & Salvatorini (1982), *sensu* Foresi *et al*. (1998). The Pietra leccese has produced a rich vertebrate fossil assemblage (Capellini, 1878; Pilleri, 1986a; Bianucci, Landini & Varola, 1994a, 2004; Bianucci, 2001), and from the Cisterna Quarry in particular, cetacean (Bianucci, Landini & Varola, 1992, 1994b), sirenian (Bianucci, Landini & Varola, 2003) and fish remains (Carnevale *et al*., 2002) have been recently described.

Diagnosis: A Physeteroidea approximately 6.5–7 m in body length with a skull 1.5 m in condylobasal length and characterized by a short and tapered rostrum, presence of a peculiar anterior projection of the supraorbital process of the right maxilla, circular supracranial basin, extreme anteroposterior elongation of the zygomatic process of the squamosal, relatively small periotic, 13 pairs of large teeth (greatest diameter of root larger than 3% of the condylobasal length of the skull) in the upper jaw and 14 in lower jaw. Similar to *Naganocetus* in body size and large teeth, and in having the following plesiomorphic features: supracranial basin not extended anteriorly, leaving the most part of the rostrum dorsally convex; deep alveoli not reduced in number in the upper tooth row; teeth with enamel crown; and anteroposteriorly elongated temporal fossa. It differs from *Naganocetus* in the shorter rostrum, the probably larger number of teeth, the more elongated jugal articulated with the squamosal, the more elongated zygomatic process and the mandible less robust.

Remarks: We propose the English common name 'killer sperm whale' for this species, considering its probable similar feeding adaptation to the extant delphinid killer whale (*Orcinus orca*).

Description
General features of the fossil skeleton: The fossil skeleton was discovered in a quarry surface of about 16 m². The bones were disarticulated but displaced little from original anatomical position (Fig. 2). As is usual for the Pietra leccese fossils, the bones exhibit a marked compression, particularly evident in the vertebral corpora. Moreover, the dorsal and ventral surfaces of the cranium are not well preserved because the cortical bone is only partially fossilized. The bones, especially the larger elements, were cut into several portions by the saw during stone cutting in the quarry, but almost all the cut portions were recovered.

On the basis of the preserved skeletal elements, the total length of the animal in life is estimated to have been approximately 6.5–7 m, of which 21–23% would have been represented by the head.

General features of the skull: The skull, extracted in nine stone blocks and then restored, is almost complete, lacking only the posterior crest of the supracranial basin and portions of the left side of the exoccipital and of the right orbital area (Figs 3, 4).
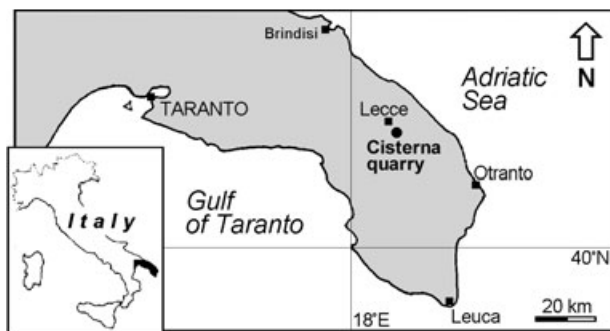

Figure 1. Map of south-eastern Italy showing the location of the Cisterna Quarry, the type locality of *Zygophyseter varolai* **gen. et sp. nov.**
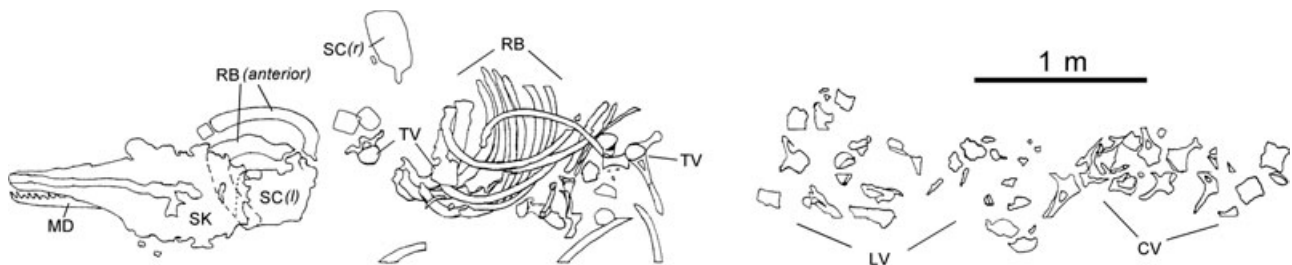

Figure 2. Sketch showing in plain view the relative positions of the skeletal elements of MAUL 229/1, holotype of *Zygophyseter varolai* **gen. et sp. nov.** as they were preserved. CV, caudal vertebrae; LV, lumbar vertebrae; MD, mandible; RB, ribs; SC(l), left scapula; SC(r), right scapula; SK, skull; TV, thoracic vertebrae.
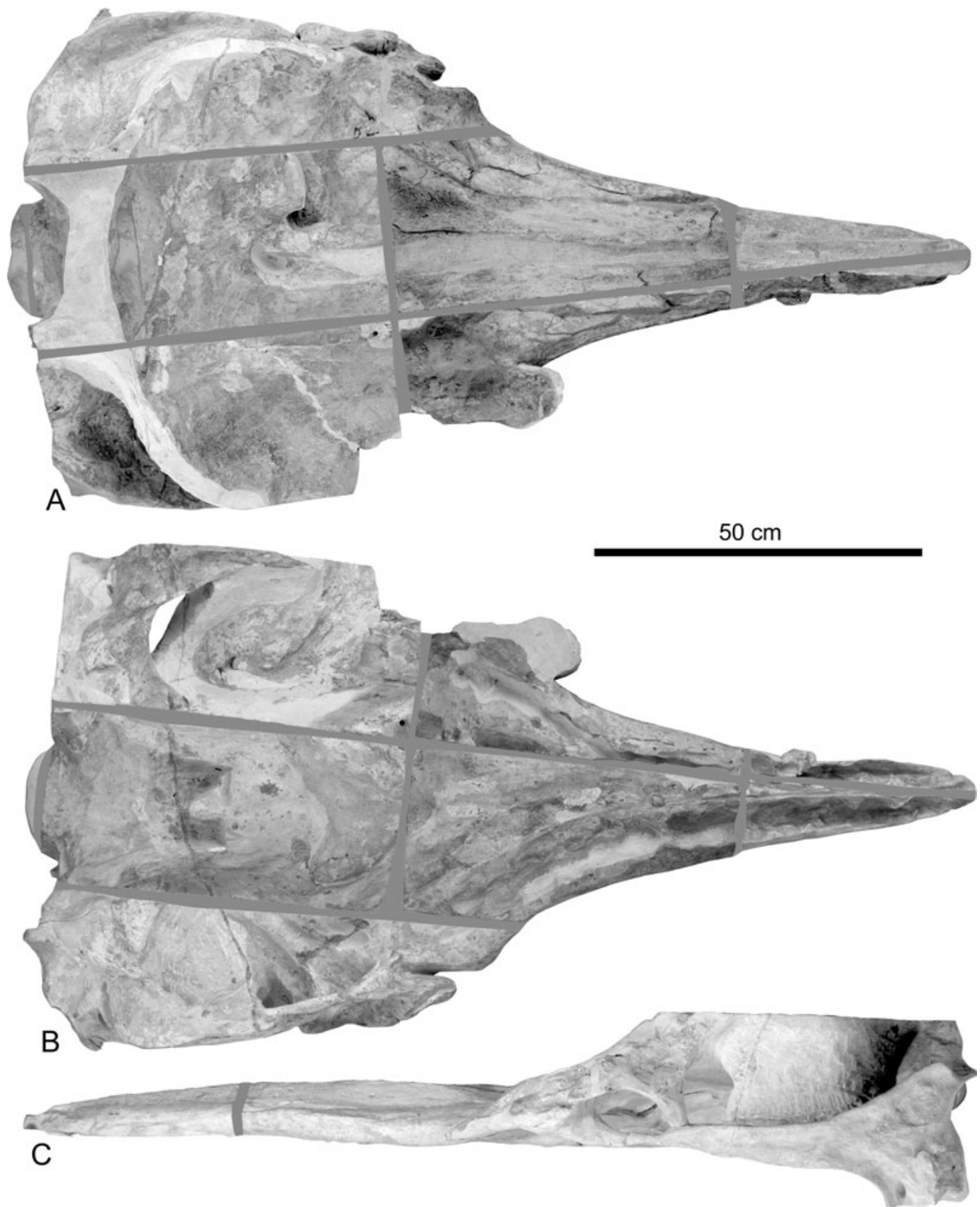
Figure 3. *Zygophyseter varolai* **gen. et sp. nov.** Skull of holotype (MAUL 229/1) in (A) dorsal, (B) ventral and (C) lateral views.
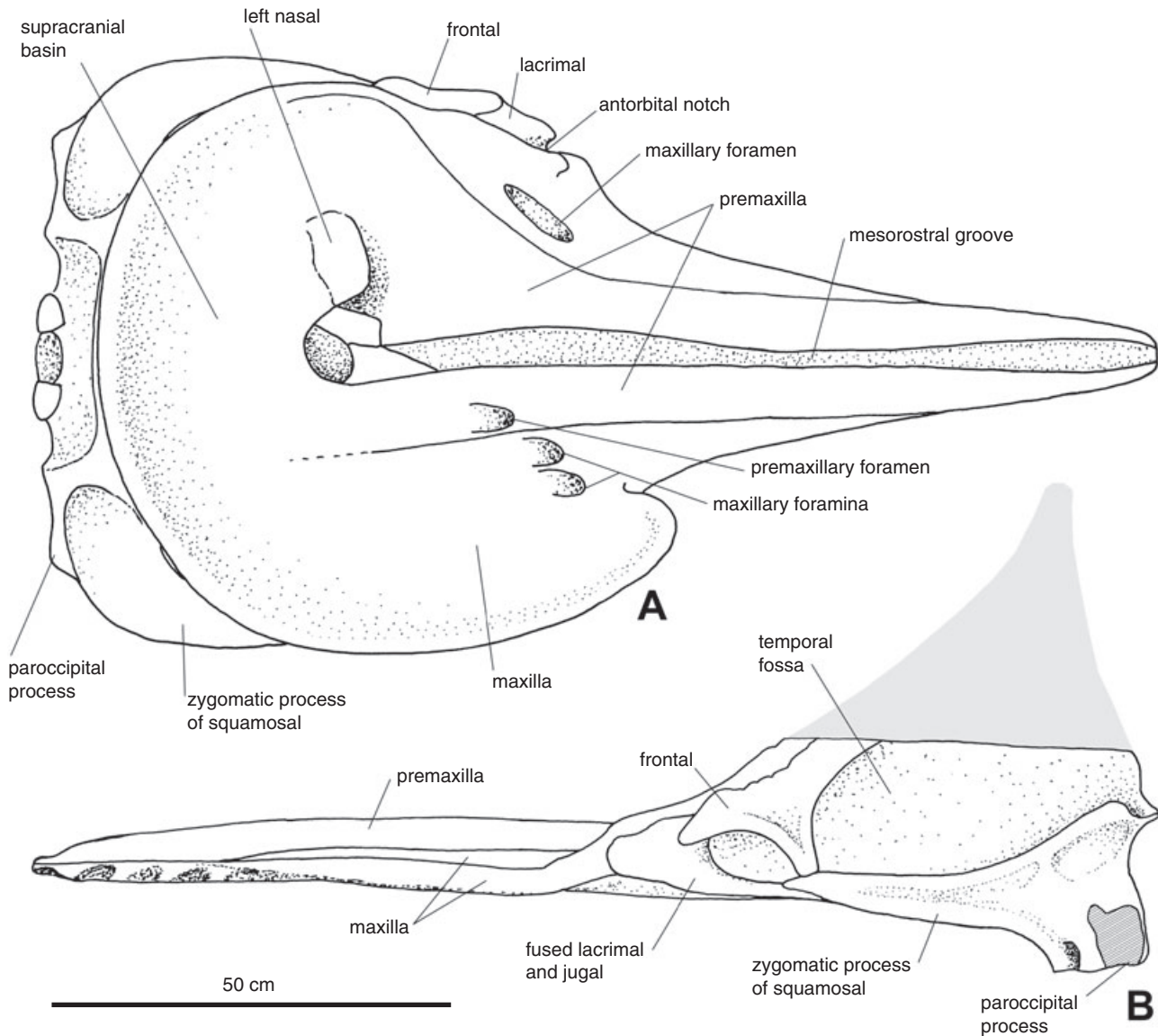
Figure 4. *Zygophyseter varolai* **gen. et sp. nov.** Skull of holotype (MAUL 229/1) in (A) dorsal and (B) lateral views. The non-preserved portion is reconstructed in dorsal view and is shaded in lateral view.

The most peculiar features of the skull are the extreme elongation of the zygomatic process of the squamosal (Fig. 5E), the large hemispherical concavity (supracranial basin) in the dorsal surface of the cranium, and the presence of a peculiar plate of the right maxilla delimiting anterolaterally the supracranial basin (Fig. 5B).

The skull exhibits an accentuated asymmetry evident in dorsal view, caused by the displacement to the left side of the external nares, the decrease in size of the right naris, the lack of the right nasal, and the marked difference in shape and size between the right and left premaxillae and maxillae.

The rostrum is triangular, tapered, relatively narrow in its anterior portion (one-third of the rostrum length) and relatively short, being about one-third of the condylobasal length. Its dorsal surface is convex for the whole anteroposterior extension, except its most posterior 10 cm where the dorsal surface slopes anteromedially to delimit anteriorly the supracranial basin. In dorsal and ventral views the lateral margins of the rostrum are concave, particularly in the posterior portion, except the most posterior 10 cm which is rectilinear and parallel to the sagittal plane. The apical portion (4 cm long) of the rostrum consists exclusively of the
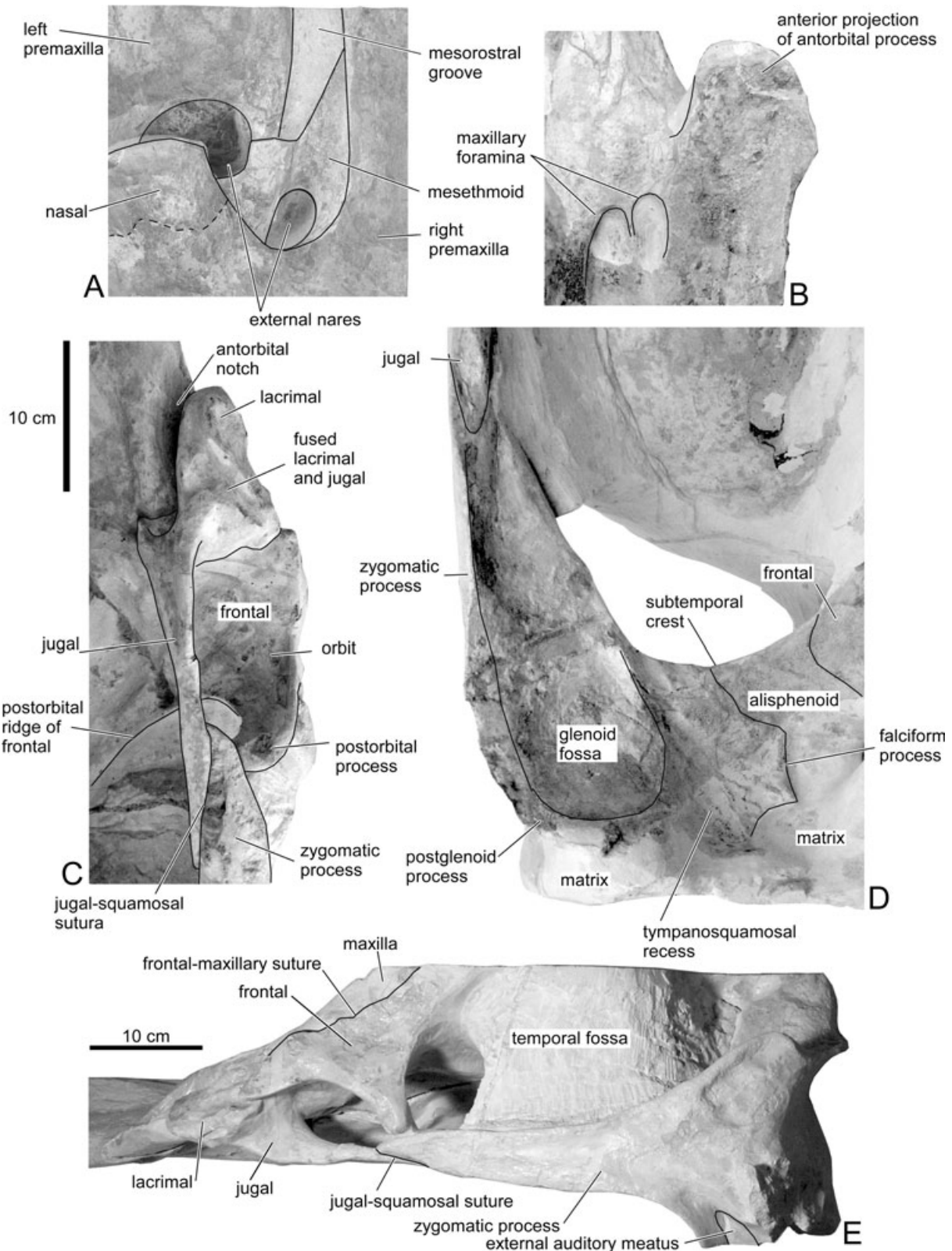
Figure 5. *Zygophyseter varolai* **gen. et sp. nov.** Details (A–D) and lateral view (E) of the cranium of the holotype (MAUL 229/1). A, narial area in dorsal view; B, foramina and antorbital lamina of maxilla in dorsal view; C, left orbital area in ventral view; D, posteroventral surface. The vertical scale bar refers to A–D.

premaxillae and exhibits a peculiar dorsoventral compression.

In lateral view the rostrum is straight, except the dorsoventrally compressed apical portion, it increases in height slightly from the anterior to the posterior portion, and it is rather low at the base.

In dorsal view the cranium is slightly wider than long and in lateral view, considering the missing dorsal portion (Fig. 4B), it greatly increases in height posteriorly.

Dorsal view of the skull: The premaxillae are widely exposed on the dorsal surface of the rostrum and completely cover the maxillae in the 27-cm-long distal portion of the rostrum. The width of the premaxillae is approximately the same along the whole length of the rostrum.

The two premaxillae are medially separated by a continuous mesorostral groove, the width of which decreases about half way alsong the length of the rostrum.

The exposed dorsal surface of the maxilla is almost parallel to the horizontal plane; by contrast, the dorsal surface of the premaxilla is ventrolaterally bent. The left antorbital notch is deep and U-shaped (Fig. 5C), delimited medially by the lateral margin of the rostrum and laterally by the anterior edge of the antorbital process. Both margins are rectilinear and parallel to the sagittal plane. As discussed below, the left antorbital notch is more posteriorly located than the right notch. We conventionally consider as base of the rostrum the transverse line passing through the left antorbital notch.

In the right lateral margin of the rostrum, about 15 cm anteriorly to the rostrum base, the maxilla exhibits a peculiar lateral extension that seem to represent an anterior projection of the supraorbital process of the maxilla (Fig. 5B). Consequently, the right maxillary portion of the rostrum terminates more anteriorly than the left one and the right antorbital notch is a narrow slit (as in *Kogia*) clearly anterior to the left antorbital notch.

Medially to the left antorbital notch, a large and anteroposteriorly elongated infraorbital foramen is present in the left maxilla and at the same level two large foramina are in the right maxilla (Fig. 5B). A large premaxillary foramen is also present in the right premaxilla near and slightly posterior to the two right maxillary foramina, although apparently there is no left premaxillary foramen.

The cranium exhibits a circular supracranial basin extending on most of its dorsal surface and only in the posterior portion of the rostrum. The walls and floor of this basin consist almost exclusively of both maxillae and premaxillae widening in the cranium. This fossa on the right side is anterolaterally delimited by the anterior projection of the supraorbital process of the maxilla.

The width of the right premaxilla remains constant posteriorly to the external nares, while the width of the left premaxilla increases considerably posteriorly, and, at the level of the external nares, the left premaxilla reaches the lateral margin of the cranial fossa.

Because of the poor preservation of the dorsal surface of the supracranial basin, the sutures are not clearly visible posterior to the external nares (Fig. 4A), and, consequently, the posterior extension of the premaxillae and of the maxillae, and any possible posterior dorsal exposure of the frontals, cannot be described.

The external nares lie near the centre of the supracranial basin and are placed slightly to the left with respect to the midline (the right narial passage is crossed by the sagittal plane). The left narial passage is clearly larger than the right one, even if the poor preservation does not permit us to evaluate the true original dimensions of these openings. The two nares are separated by a wide mesethmoid and the left one is partially covered dorsally by a large rectangular bony plate that might represent the left nasal (Fig. 5A). The posterior suture between this supposed nasal and the left premaxilla is not distinguishable. The right nasal bone is missing and was probably absent originally.

The left maxilla does not completely cover the supraorbital process of the frontal, which is clearly visible in dorsal view. By contrast, the right maxilla probably completely covered the right orbit (not preserved), producing an asymmetrical extension of the supracranial basin.

The posterior crest of the supracranial basin was in a stone block lost in the quarry during fossil collection. Nevertheless, its elevation is estimated to have been about 35 cm beyond the uppermost preserved portion, based on the observations made by us before the stone block was lost.

The occipital shield had a narrow anteroposterior dorsal extension, judging by the narrow cut surface of the posterior crest and by its short preserved posterior portion.

Lateral to the occipital shield, the large and elongated zygomatic processes of the squamosals are widely visible in dorsal view with an anteromedially directed apex and a convex lateral margin delimiting the wide temporal fossa.

Lateral view of the skull: The fused lacrimal and jugal are triangular, with a wide anterodorsal portion that contributes to form the antorbital process and a thin and elongated posterior portion articulating with the zygomatic process of the squamosal (Fig. 5E). The jugal–squamosal suture is anteroposteriorly

elongated and obliquely orientated with respect to the major axis of the skull.

The orbit is anteroposteriorly short and somewhat arched. It is at the same height as the dorsal margin of the rostrum and is dorsally delimited by a thick supraorbital process of the frontal that becomes higher posteriorly. The postorbital process is relatively narrow and elongated and it is posteroventrally directed toward the zygomatic process.

The frontal–maxilla suture is angled posterodorsally forming an angle of 35° from the axis of rostrum, and the lateral exposure of the frontal slightly widens posteriorly (Fig. 5E).

The zygomatic process of the squamosal is unusually elongated with respect to other odontocetes and it is rather thin, particularly in its anterior portion where it terminates with a pointed and anteriorly directed apex. In lateral view, the zygomatic process is parallel to the major axis of the skull and its dorsal margin delimits ventrally a very wide, deep and anteroposteriorly elongated temporal fossa. This margin of the zygomatic process has an asymmetrical sinusoidal shape, being concave along almost its entire length, except a strong convexity in its most posterior portion. Overall, the zygomatic process is triangular in lateral view owing to the posterior elevation of its dorsal margin.

The external auditory meatus is clearly visible in lateral view of the skull as a groove separating the postglenoid and the paroccipital process of the exoccipital.

Ventral view of the skull: In ventral view, about 4 cm posterior to the apex of the rostrum, a W-shaped suture separates the premaxillae from the maxillae. The short ventral surface of the premaxillae lacks any alveoli, while each maxilla has 13 relatively deep, single-rooted alveoli. These alveoli are joined one to another forming a gutter with indented lateral and medial margins. A straight suture between the two maxillae is visible along the mid line on the anterior portion of the rostrum ventral surface.

The ventral surface of the anterior portion of the cranium, as with that of the posterior surface of the rostrum, is poorly preserved and consequently it is not possible to estimate the extension of the palatine and pterygoid. By contrast, the ventral surface of the left orbital area is in good condition and the very deep antorbital notch, the large lacrimal fused with the jugal, the elongated and thin lacrimal, and the anteroposteriorly elongated jugal–squamosal suture are clearly visible (Fig. 5C). Moreover, the orbit is posteriorly delimited by an evident curved postorbital ridge.

The preserved posterior ventral surface of the cranium exhibits a relatively narrow basioccipital delimited posteriorly by rather protuberant occipital condyles and laterally by two crests forming an angle of about 30°.

Lateral to the basioccipital crest, the squamosal protrudes well out of the braincase and terminates with a narrow zygomatic process anteroposteriorly very elongated, straight, with its major axis parallel to that of the skull, and with a pointed apex. The ventral surface of the zygomatic process is almost completely occupied by a wide glenoid fossa, posteriorly delimited by a narrow postglenoid process (Fig. 5D). Posteromedially to the glenoid fossa the tympanosquamosal recess is relatively small, and the falciform process (perhaps not completely preserved) appears to be short and wide. A line, slightly in relief, joining the falciform process to the subtemporal crest may represent the squamosal–alisphenoid suture, even if an accurate reconstruction of this important diagnostic area of skull base is not possible because of the poor preservation.

Posterior view of the skull: In posterior view, the exoccipital exhibits an excavated surface dorsally delimited by a protuberant, thin crest. The lateral portion of the exoccipital bends anteriorly, joining the squamosal. The jugular notch is wide and semicircular in posterior view, and the paroccipital process is unusually slender and elongated.

Periotic: Only the left periotic, lacking the posterior process, is preserved (Figs 6A–G, 7). It is relatively small considering the size of the skull.

The anterior process is relatively short and ventromedially bent. The ventrolateral angle (apex) is clearly visible but without a sharp tip. We separated the large accessory ossicle of the tympanic, originally fused with the anterior process of the periotic, and a large and trapezoidal fovea epitubaria is now visible. Medially to this fossa, a narrow but deep groove for the tensor tympani is visible, while anteriorly there is a small and shallow fossa for the outer lip of the tympanic bullar surface. The fossa for the malleus is posteromedially orientated and it is laterally delimited by a large and globose lateral tuberosity. In the posterolateral part of this tuberosity the small facet for the articulation of the sigmoid process of the tympanic bulla is evident.

In its medial surface, the anterior process exhibits a rather large tuberosity visible dorsally and medially but ventrally covered by the accessory ossicle (later detached during preparation; see Fig. 4D). A small but deep groove that may represent a vestige of the anteroexternal sulcus is visible in the lateral surface of the anterior process.

The pars cochlearis (promontorium) is almost spherical with slight dorsoventral compression and it is anteroventrally bent. On its dorsal surface, the internal acoustic meatus is relatively small and exhibits a circular outline with a raised posterior rim. The inter-
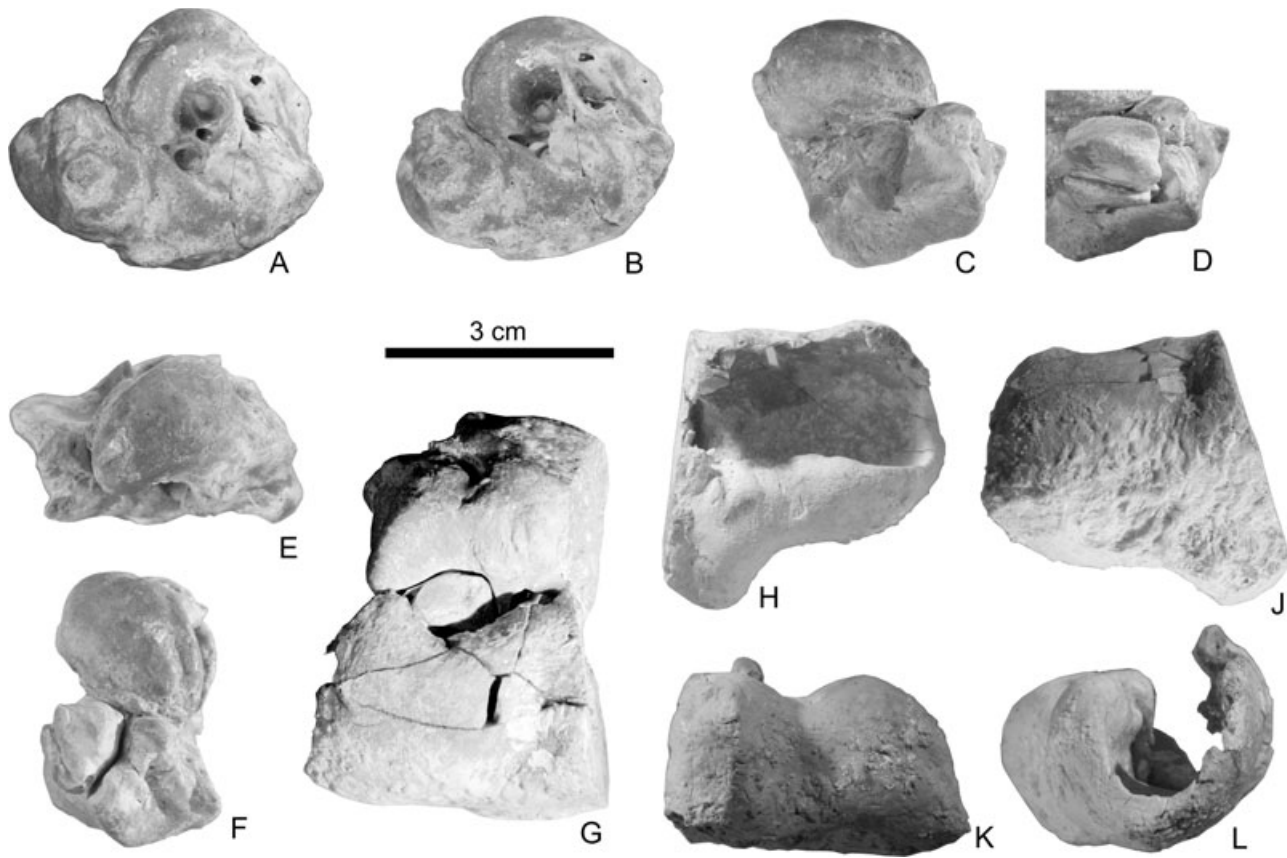
Figure 6. *Zygophyseter varolai* **gen. et sp. nov.** Left incomplete ear bones of the holotype (MAUL 229/1). A–F, periotic in (A) dorsal, (B) dorsomedial, (C, D) ventral, (E) medial and (F) anterior views. G, articulated periotic and tympanic bulla in lateral view; H–L, tympanic bulla in (H) dorsal, (J) ventral, (K) medial and (L) anterior views. D shows detail of the anterior process with the accessory ossicle not removed.

nal opening of the facial canal is separated from the cochlear foramina by a low transverse septum and has a pointed anterior groove, probably for the greater petrosal nerve (Fordyce, 1994). The aperture for the endolymphatic duct is a large, deep fossa inside which there is a narrow fissure divided by a transverse septum. The aperture for the cochlear aqueduct is small, has an almost circular and raised rim, and is slightly medially located with respect to the endolymphatic foramen. The fenestra rotunda is small, semicircular and far from the aperture for the cochlear aqueduct.

An evident pyramidal process is located 15 mm posterolaterally to the aperture of the endolymphatic duct. The dorsal surface of the periotic, laterally to the pars cochlearis (suprameatal region), is slightly concave and delimited laterally by an arched keel representing the dorsal edge of the tegmen tympani.

Tympanic bulla: Only the left tympanic bulla, lacking its posterior portion, is preserved (Fig. 6G–L). In ventral and dorsal view, this bone is wide, without mediolateral compression and shows a posteromedial enlargement of the posterior portion of the involucrum. The ventral surface of the preserved portion of the bulla shows a wrinkled surface without a medial furrow. The anterior margin is rectilinear without an anterior spine. The anterior opening is wide and 'U' shaped in anterior view. The involucrum exhibits an anterior portion dorsally orientated and a pachyostotic posterior portion laterally curved. These two portions are separated by a concavity evident in ventral and particularly in medial view. The preserved portion of the dorsolateral margin of the tympanic bulla is anteroposteriorly in contact with the periotic by a small abruptly elevated outer lip, a large accessory ossicle and a partially preserved sigmoid process.

Teeth: There are 13 teeth in each upper tooth row, all in the maxilla, and 14 teeth in each dentary; in fact, in the lower tooth row an apical tooth is present that is absent from the upper row (Figs 8, 9).

The crowns are relatively small (about 18% of total tooth length, considering also the estimated apical portion of the crown missing as a result of wear),
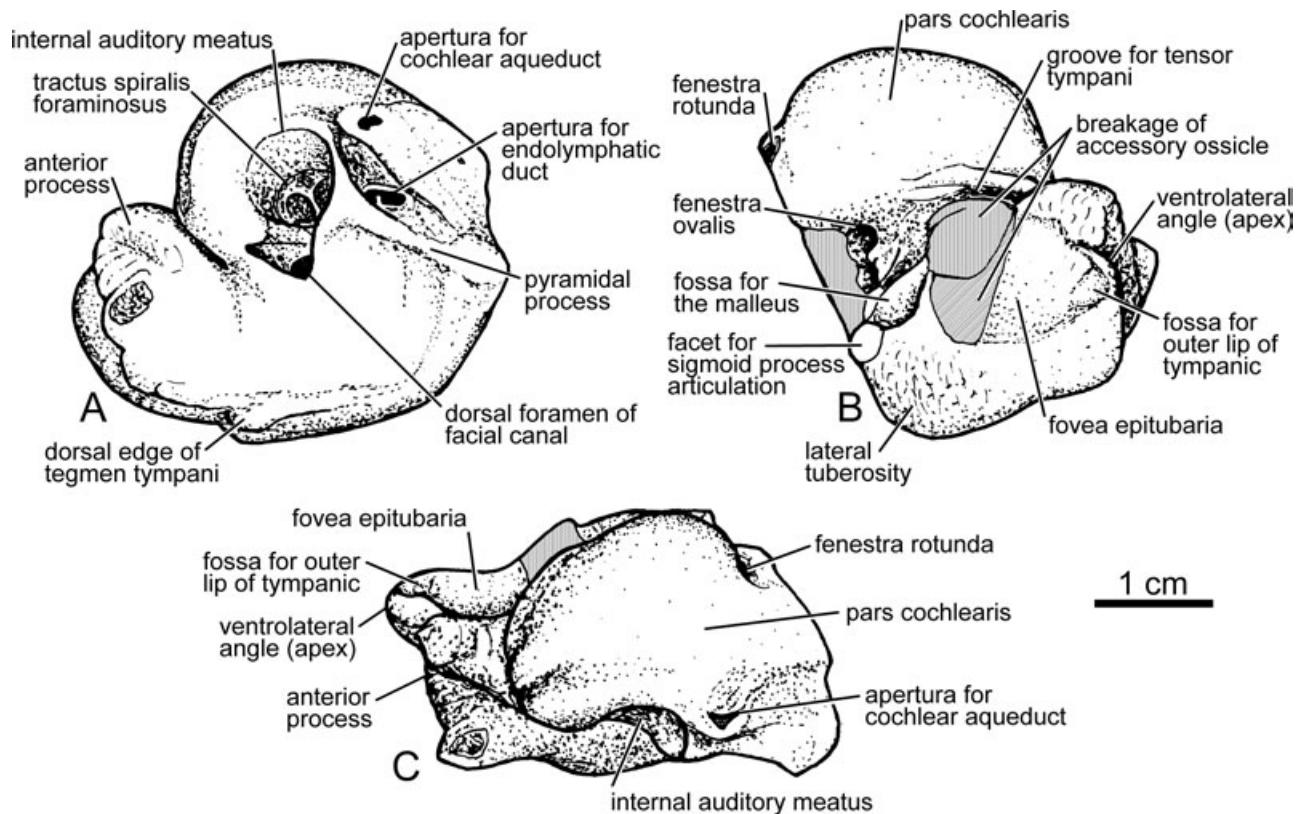
Figure 7. *Zygophyseter varolai* **gen. et sp. nov.** Incomplete left periotic of the holotype (MAUL 229/1) in (A) dorsal, (B) ventral and (C) medial views.
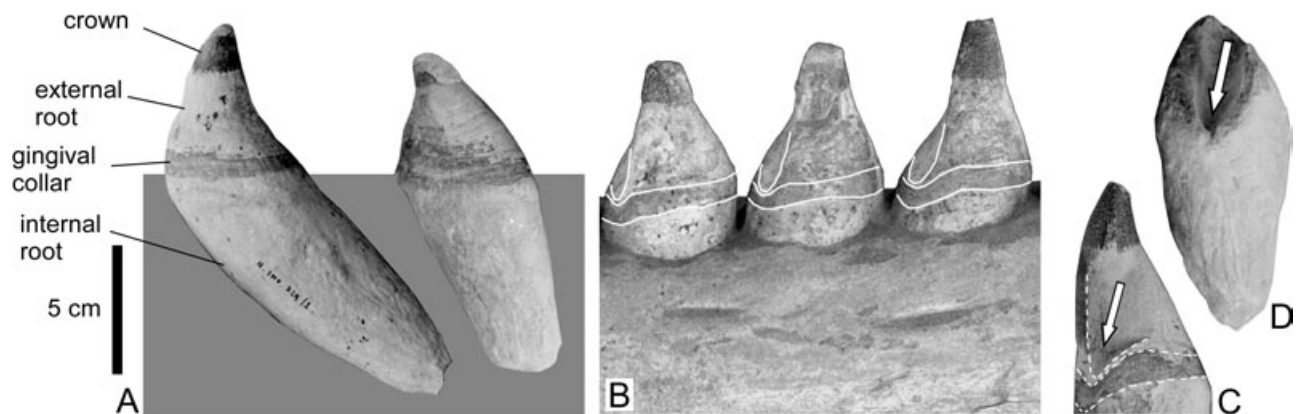

Figure 8. *Zygophyseter varolai* **gen. et sp. nov.** Teeth of the holotype (MAUL 229/1). A, reconstruction of the original orientation of two isolated maxillary teeth; B, three mandibular teeth in place showing the gingival collar and the occlusal wear of the roots; C, D, two isolated maxillary teeth (arrows show the wear due to the opposite teeth).

conical, with a circular cross-section and crenulated enamel (Varola *et al*., 1988: Fig. 2). The margin of enamel at the crown base is irregular and interfingered. The roots are fusiform and covered by a 15-mm-thick cement layer (Varola *et al*., 1988: pl. 2). They taper at the lower extremity and, if completely preserved, exhibit some small secondary roots. A dark irregular band, obliquely orientated with respect to the major axis of the teeth, marks the greatest diameter of the roots. This band represents the area of connection between the gum and the teeth and it is here named the 'gingival collar'. The gingival collar separates the tooth into an upper external portion and a lower internal portion. The internal portion is the part
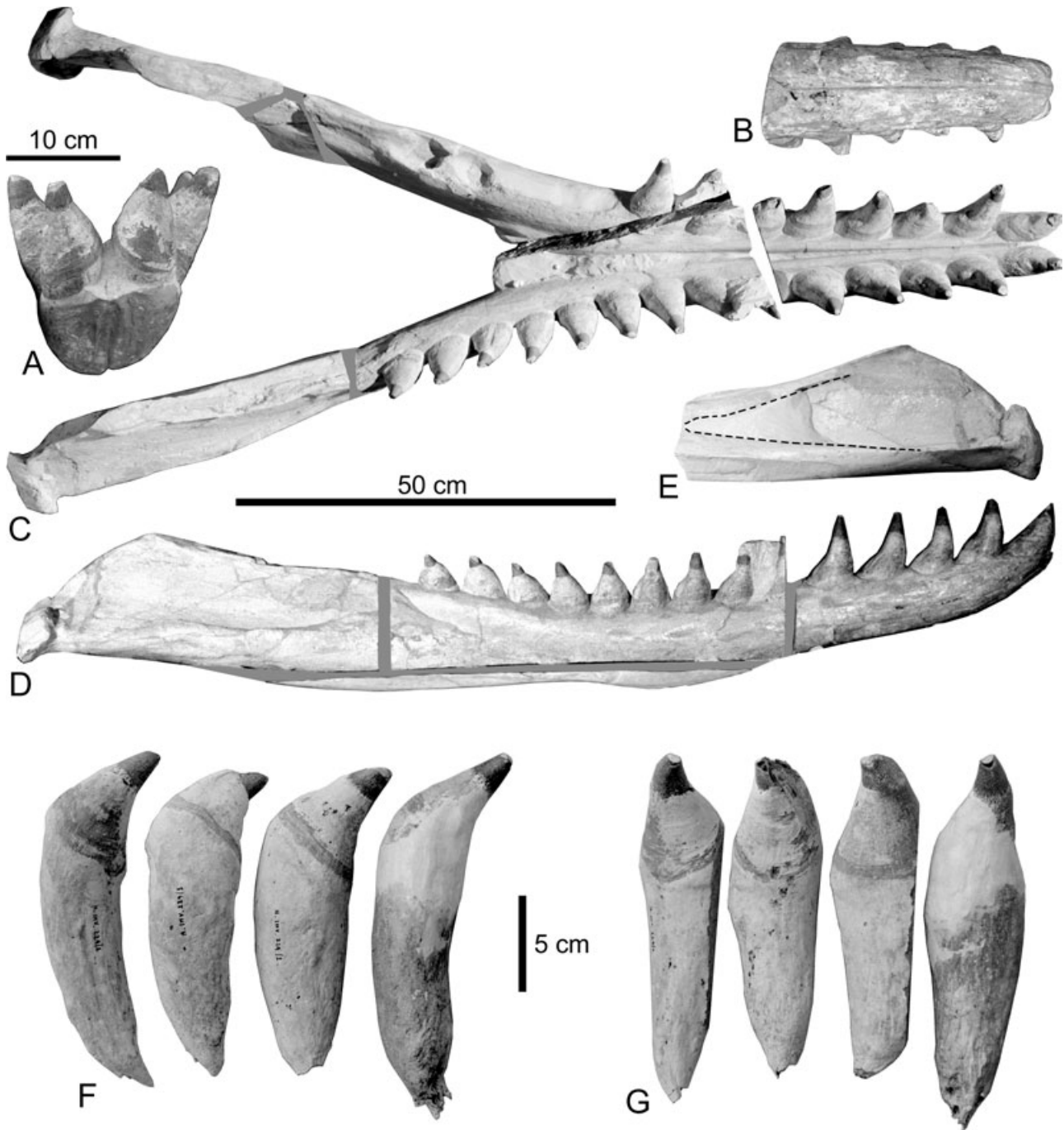
Figure 9. *Zygophyseter varolai* **gen. et sp. nov.** Mandible (A–E) and isolated upper teeth (F, G) of the holotype (MAUL 229/1). A, anterior view; B, ventral view of the anterior portion of the symphysis; C, dorsal view; D, lateral view; E, medial view of left posterior portion of right dentary; F, lateral or medial views; G, posterior views.

of the tooth originally covered by soft tissue and bone. The original inclination of the teeth with respect to the rostrum or mandible can be estimated also in the isolated teeth by orientating the plane that crosses the tooth through the gingival collar, parallel to the horizontal plane (Fig. 8A). In support of this interpretation, the mandibular teeth in places have their gingival collars approximately parallel to the dorsal surface of the mandibular body (Fig. 8B).

The internal portions of the teeth have shallow longitudinal grooves, the function of which was probably to increase the joint between teeth and alveoli.

There is an evident difference in shape and size from anterior to posterior teeth. In fact, examining the mandibular teeth in place (Fig. 9C, D), we can observe that the nine anterior teeth have a root that is circular in cross-section, with the external portion anterolaterally bent. In particular, the apical tooth has an external portion that is strongly anteriorly bent, while the external portions of the other eight anterior teeth have a sinusoidal shape in lateral or medial view. Instead, the internal portion of these nine anterior teeth is strongly posteriorly bent so that each tooth is partially covered by the nearest following tooth. The five posterior teeth are smaller than the nine anterior teeth, and their external portion is posterolaterally bent. The roots of the three most posterior teeth exhibit a strong mediolateral compression.

All external portions of the teeth exhibit various degrees of wear, affecting both the crown and the root. In fact, all crowns lack their apical portion due to wear, and their height is reduced an estimated average of 45% of the original value. In one tooth, the wear caused the total loss of the crown (Fig. 8D). The wear of the roots, due to the opposite teeth (occlusal wear), caused a more or less deep groove in the posterolateral surface of the external portion. The action of the opposite teeth during the life of the animal also caused a lowering of the gum as can be deduced from the folding of the gingival collar (Fig. 8B–D). Wear is more accentuated in the anteriormost teeth.

Mandible: In dorsal and ventral view, the two jointed dentaries appear Y-shaped, with a narrow, cylindrical and relatively elongated symphyseal portion (45% of the mandibular length) and with the two bodies being posteriorly rectilinear and forming an angle of 45° (Fig. 9).

In lateral view, the mandible is arched, with its dorsal profile concave, its ventral profile convex and its anterior portion slightly dorsally bent (Fig. 9D).

The two dentaries are not strongly sutured and in dorsal view they progressively diverge posteriorly. At the posterior margin of the symphysis, the distance between the dentaries is about 3 cm.

Each dentary has 14 teeth, all preserved in place except the six posterior of the left dentary. These teeth are very close to one another and located in an alveolar gutter similar to that in the maxilla. Eight teeth are symphyseal.

The lateral and ventral surfaces of the symphyseal portion of the mandible exhibit shallow longitudinal grooves and exhibit three mental foramina located at the same height and at level of the seventh, eighth and ninth teeth, respectively.

In the postalveolar portion, the coronoid process is not very elevated and the condyle, round in posterior view, is protuberant and located at the posteroventral angle. On the medial surface, there is a large mandibular foramen extending anteriorly 48 cm from the condyle (Fig. 9E).

Vertebrae: Most of the vertebrae are incomplete and were deformed during fossilization (Fig. 10A–E). The atlas is the only cervical vertebra preserved. It has a circular contour in anterior view and exhibits large, semicircular and moderately concave facets for articulation with the occipital condyles. The lower and upper transverse processes join to form a single, short and rather thin process. The neural arch is very low and lacks the neural spine.

Eight thoracic vertebrae are preserved but, considering the number of preserved ribs, we can assume that originally there were at least 12 thoracic vertebrae. The anteriormost preserved thoracic vertebrae have a centrum with reduced anteroposteriorly length and a wide neural arc. Among these, an almost complete and non-deformed vertebra that may represent the fifth thoracic (Fig. 10B) has a centrum that anteriorly measures 92 mm in height and 110 mm in width. Its anteroposterior length is only 60 mm. The neural arch is rather thin and forms a large and pear-shaped neural canal. The neural spine is missing but judging from the small broken area, it was short and thin. The transverse processes, beginning from the lateral margins of the neural arch, are distally wide, as visible in anterior or posterior views, and anterodorsally bent. The width between the transverse processes is 235 mm. A well-preserved posterior thoracic vertebra (Fig. 10D) has a centrum 90 mm high and 100 mm wide and 100 mm anteroposteriorly elongated. Its neural arch is rather high and its neural canal is triangular and 70 mm high. Its neural spine is bent posteriorly and its transverse processes, departing from the dorsolateral margin of the centrum, are relatively wide in dorsal or ventral view, and they are approximately parallel to the horizontal plane. The facets for tubercula of ribs, located at the distal end of the transverse processes, are elliptical. The distance between the two facets is 300 mm.

The ten preserved lumbar vertebrae have a centrum anteroposteriorly elongated (110–150 mm) and dorsoventrally compressed due, at least in part, to diagenetic processes, and they lack the longitudinal keel on the ventral surface. Their neural arcs are high and narrow and their neural spines are very elongated and bent posteriorly. The transverse processes, when well preserved, are very elongated, dorsoventrally compressed and anteroposteriorly expanded at their distal end. The distance between these processes ranges between 400 and 420 mm. Only an incomplete caudal vertebra, with a centrum 130 mm in anteroposterior length, has been removed
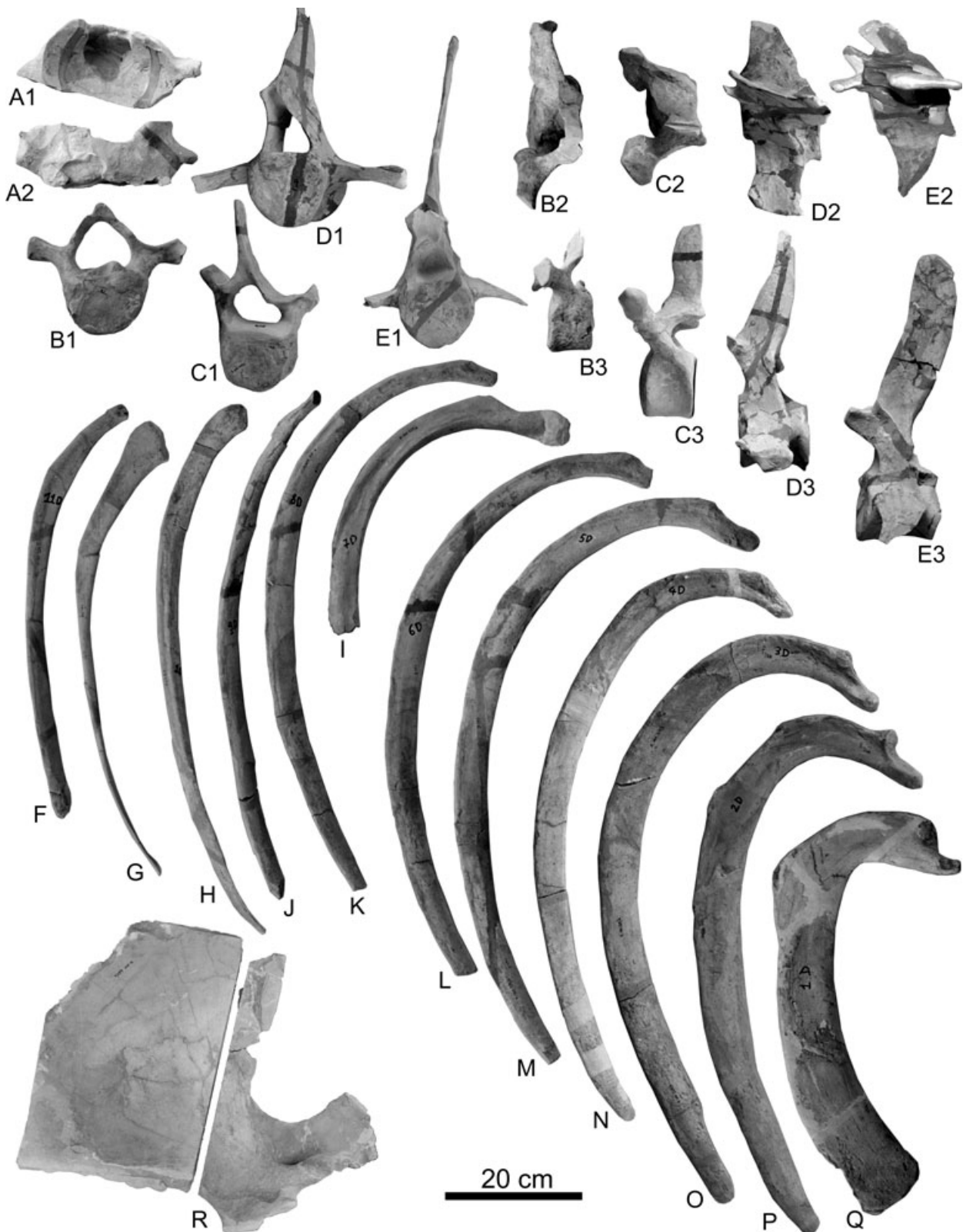
Figure 10. *Zygophyseter varolai* **gen. et sp. nov.** Postcranial skeleton of the holotype (MAUL 229/1). A, atlas; B, D, thoracic vertebrae; E, lumbar vertebra; in (1) anterior, (2) dorsal and (3) lateral views; F–Q, right ribs in lateral view; R, left scapula in medial view.

from the matrix; at least eight caudal vertebrae remain to be removed.

Ribs: Twelve right and 11 left ribs are preserved, some complete and others more or less incomplete (Fig. 10F–Q). In particular, only the proximal portions of the seventh right rib and of the fifth and ninth left ribs are preserved. Moreover, only small fragments of the second and sixth left ribs are preserved and the twelfth left rib is missing. Judging by the gradual variation in shape from the first to the twelfth right ribs and by the shape of the small posteriormost rib, we consider it probable that there were originally 12 ribs. The length increases from the first to the fifth rib and decreases from the fifth to the twelfth rib, while the width progressively decreases from the first to the twelfth rib. As is typical of Cetacea, the first rib is clearly distinguished from the others by its greatest width in anterior or posterior view and by its peculiar 'L' shape due to the strong curvature in its proximal portion. It is anterposteriorly flattened and it widens dorsoventrally in its distal portion. Its tuberculum is relatively small and located in a narrow neck while the capitulum is wide and only slightly protuberant. The second rib is about one-third narrower than the first, is more elongated, shows a more regular curvature and lacks the distal dilation. Moreover, its neck from the tuberculum is more elongated and sturdy and its capitululum is more protuberant. A similar architecture of the proximal portion is also observed in the next six ribs, due to the double articulation with the vertebrae, while the last four ribs lack the capitulum because they were articulated only with the transverse processes of the thoracic vertebrae. Moreover, the tenth and eleventh ribs exhibit a wide and dorsoventrally compressed tuberculum. The curvature is almost the same from the third to the eighth ribs while it decreases considerably in the next four ribs.

Forelimb: An almost complete left scapula, some fragments of the right scapula, a small portion of right radius and one phalanx are preserved.

The left scapula (Fig. 10R) has an elongated and distally expanded acromion and a slender coracoid process. Its straight anterior and posterior margins form an angle of about 90°. Its dorsal margin is not preserved.

The preserved proximal portion of the radius exhibits a large facet for the articulation with the humerus and a smaller posterior facet for the articulation with the ulna. The preserved posterior margin of the radius is slightly concave and the anterior margin is rectilinear. The only preserved phalanx is 72 mm long. It is rather slender and has expanded proximal and distal portions. The wider proximal portion has a convex surface for articulation with the metacarpal.

COMPARISONS

COMPARISONS WITH OTHER PHYSETEROIDS

Zygophyseter varolai shares with all other physeteroids the deep modification in the architecture of the dorsal surface of the cranium, which, judging by homology with the extant *Physeter macrocephalus* and *Kogia* spp., was for housing the spermaceti organ (see the following section). In detail, the cranium of *Z. varolai* exhibits a wide and deep supracranial basin, accentuated asymmetry of maxillae, premaxillae and external nares, and the lack of the right nasal. Besides, as in all other physeteroids, the skull of *Z. varolai* exhibits other derived characters summarized in the diagnosis of this family and described in detail under phylogenetic analysis. Among these characters, the following are observed and/or used for a cladistic analysis for the first time in all sperm whales:

1. Left premaxillary foramen either very small or absent.
2. Fovea epitubaria of the periotic large and rectangular, differing from the elliptical fovea epitubaria of most other odontocetes and from the anteroposteriorly compressed fovea epitubaria of the ziphiids; the large size of the fovea epitubaria in the physeteroids is due to the large accessory ossicle of the tympanic bulla that articulates in this fossa covering almost all of the ventral surface of the anterior process of the periotic (Fig. 11).
3. Zygomatic process of the squamosal triangular in lateral view, due to the posterior elevation of its dorsal margin; this derived condition differs from that of all other cetaceans, which have an 'L'-shaped zygomatic

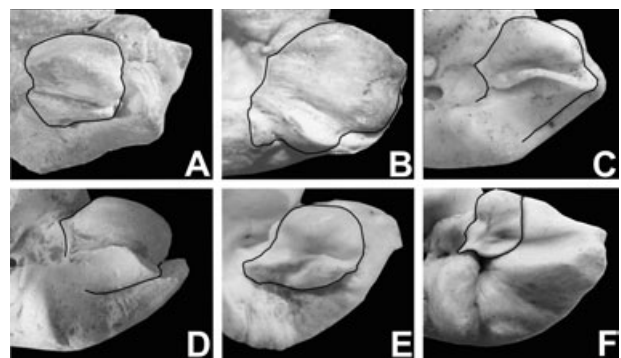**Figure 11.** Anterior process of the periotic of (A) ***Zygophyseter varolai* gen. et sp. nov.** (holotype, MAUL 229/1), (B) *Physeter macrocephalus* (MNHNP 1831), (C) *Kogia breviceps* (MBMS 4000), (D) Physeteroidea indet. from Pietra leccese (MAUL 982/1), (E) *Lagenorhynchus albirostris* (MSNTUP M291) and (F) *Mesoplodon bowdoini* (MSNTUP M269). The black line delineates the accessory ossicle.

process with the dorsal margin ventrally bending or parallel to the horizontal plane in its posterior portion (Fig. 12).

4. Mandibular condyle located near the ventral margin of the mandible: observed in *Physeter*, *Naganocetus*, '*Aulophyseter*' *rionegrensis* and in some (but not in all) examined mandibles of *Kogia* spp. (Fig. 13); among the other fossil genera referred to sperm whales only *Ferocetotherium* has a well-preserved mandible. Unfortunately, the only mandible of *Ferocetotherium* lacks the condyle and the published illustrations (Mchedlidze, 1970: pl. 2, 1976: pl. 1; Pilleri,
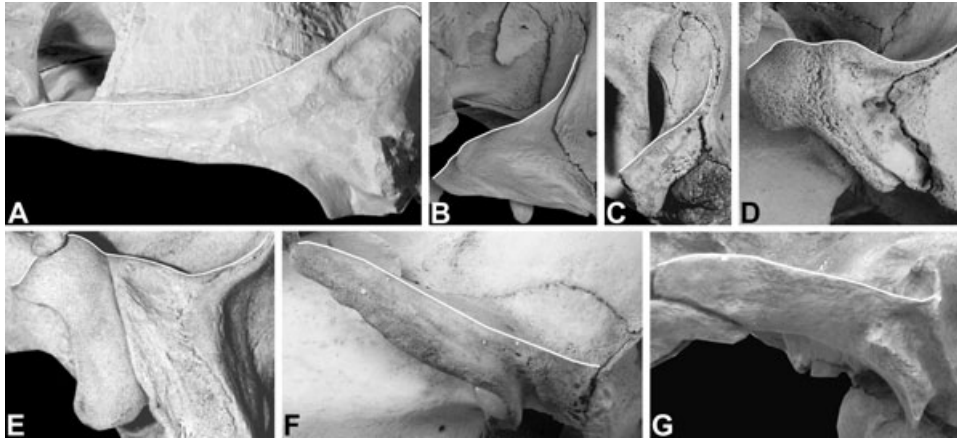

Figure 12. Zygomatic process of squamosal of (A) ***Zygophyseter varolai* gen. et sp. nov.** (holotype, MAUL 229/1), (B) *Physeter macrocephalus* (MSNTUP M266), (C) *Kogia breviceps* (MNHNP 1877-277), (D) *Tursiops truncatus* (MSNTUP M281), (E) *Indopacetus pacificus* (MZUF 1956 M4854), (F) *Pontoporia blainvillei* (MSNTUP M273) and (G) *Zygorhiza kochii* (cast of USNM 11962; mirror image of right side). The white line marks the dorsal margin of the zygomatic process.
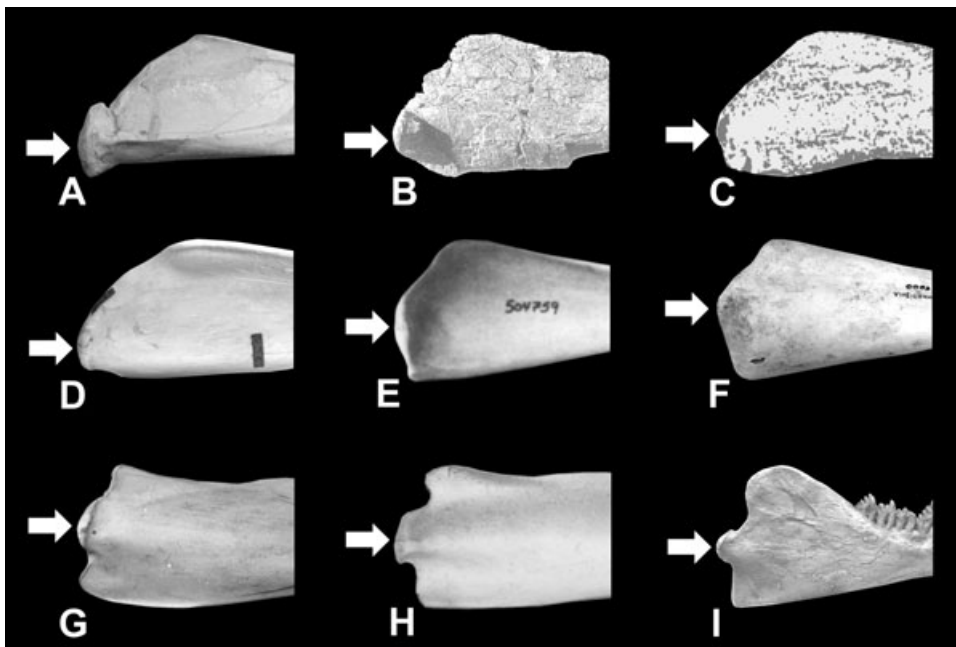

Figure 13. Posterior portion of dentary of (A) ***Zygophyseter varolai* gen. et sp. nov.** (holotype, MAUL 229/1), (B) *Naganocetus shigensis* (from Hirota & Barnes, 1995: Fig. 9), (C) '*Aulophyseter*' *rionegrensis* (from Gondar, 1975: pl. 1, Fig. c), (D) *Physeter macrocephalus* (MSNTUP M267), (E) *Kogia sima* (from Caldwell & Caldwell, 1989: Fig. 6D), (F) *Kogia breviceps* (MBMS 4000), (G) *Mesoplodon bowdoini* (MSNTUP M269), (H) *Delphinus delphis* (MSNTUP M287) and (I) *Zygorhiza kochii* (cast of USNM 11962). A, medial view; B–I, lateral views. The arrows indicate the location of the condyle.

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1986b: pl. 3) are uninformative regarding the position of the broken area in the posterior margin of the mandible. The ventral location of the mandibular condyle may be a derived character of the physeteroids related to the wide opening of the mouth.

Among all physeteroids, *Z. varolai* shows closer affinities with *Naganocetus shigensis* by having a wide and anteroposteriorly elongated temporal fossa, large teeth and similar size of the skull. However, *Naganocetus* differs in some substantial characters from *Zygophyseter*, as pointed out by the following diagnosis.

Diagnosis of Naganocetus gen. nov.: A Physeteroidea characterized by a skull at least 1.5 m long, relatively elongated rostrum, maxilla forming a broad, flat-topped supraorbital crest, nuchal crest relatively low and broad, large and robust zygomatic process of the squamosal, probably 12 pairs of large teeth (greatest diameter of root larger than 3% of the condylobasal length of the skull) in each dentary and probably a similar number in each upper tooth row. Similar to *Zygophyseter* in body size, large teeth and in the following plesiomorphic features: supracranial basin not extended anteriorly, leaving the most part of the rostrum dorsally convex; deep alveoli not reduced in number in the upper tooth row; with enamel crown; and anteroposteriorly elongated temporal fossa. Differing from *Zygophyseter* in the probable lesser number of teeth, more elongated rostrum, shorter jugal not articulated with the squamosal, shorter zygomatic process of the squamosal and more robust mandible.

Etymology: The genus name derives from Nagano, the Prefecture of the type locality, and from *cetus*, Latin for whale.

The 44 teeth described as holotype of *Scaldicetus caretti* (for age, locality and references of this and following species, see Table 1) are relatively similar in size and shape to those of *Z. varolai* but the lack of the skull does not allow a more detailed comparison, as for other isolated teeth from various localities described in the past and referred to several nominal taxa.

Ontocetus oxymycterus (described on the basis of an incomplete rostrum and mandible with teeth in place) shows some affinities with *Z. varolai* (in the dorsal outline of the rostrum and in the complete dentition) but it differs in the larger size (probably more than double) and in the closure of the mesorostral groove in the anterior portion of the rostrum.

Eudelphis mortselensis is based on an incomplete skull that differs from that of *Z. varolai* in the smaller size, less tapered rostrum, smaller and more numerous teeth, lesser anteroposterior elongation of the temporal fossa and shorter zygomatic process of the squamosal.

Diaphorocetus poucheti has an apparently less derived skull compared with *Z. varolai* given the marked inclination of the occipital shield and the smaller size. Moreover, the temporal fossa and the zygomatic process of the squamosal in the skull of this physeteroid are not as elongated as in *Zygophyseter*.

Idiorophus patagonicus, only known by an incomplete skull and mandible with several teeth in place, differs from *Z. varolai* in the smaller size, the presence of teeth in the premaxilla and the smaller and more numerous teeth.

The fragmentary skull of *Thalassocetus antwerpiensis* described as 'crane I' by Abel (1905: Fig. 7) differs from *Z. varolai* in the smaller size and in the presence of an evident sagittal crest, similar to that of *Kogia* spp., in the posterior portion of the dorsal surface of the cranium.

Aulophyseter morricei has a skull with some derived characters that are absent in *Zygophyseter*, such as the widening of the premaxillae in the rostrum, the low supraoccipital shield and the lance-like temporal fossa (Kazár, 2002).

'*Aulophyseter*' *rionegrensis*, based on a skull, mandible and fragmentary postcranial elements, differs in several characters from *Z. varolai*, including the smaller size, the shorter zygomatic process of the squamosal and the relatively more slender and numerous teeth. The mandible exhibits the same ventral location of the condyle as in *Z. varolai*, *Naganocetus shigensis* and *Physeter macrocephalus*. As already noted by Kazár (2002), judging by the poor description made by Gondar (1975), '*Aulophyseter*' *rionegrensis* does not seem to be closely related to the other two *Aulophyseter* species.

Ferocetotherium kelloggi, referred to a sperm whale by Barnes (1985), is based on some fragmentary bones including a mandible, differing from that of *Z. varolai* in the larger number and smaller size of the teeth.

Preaulophyseter gualichensis is only based on two teeth and one periotic that differ substantially from those of *Z. varolai*. In particular, the teeth are less robust and have a longer crown and the periotic has a relatively smaller pars cochlearis.

The skulls of extant *Physeter macrocephalus*, *Kogia sima* and *Kogia breviceps* and of the fossil species *Kogia pusilla*, *Orycterocetus crocodilinus*, *Physeterula dubusii*, *Placoziphius duboisii*, *Idiophyseter merriami*, *Praekogia cedrosensis* and *Scaphokogia cochlearis* differ from that of *Z. varolai* in the lacking of enamel in the tooth crowns, the absence of upper teeth or their location in shallow alveoli or in a gutter, the anteroposterior constriction of the temporal fossa and in the short zygomatic process of the squamosal. In fact, in several of the species cited above some of these characters are only hypothesized to be originally present (on the basis of their phylogenetic affinities) but they

have not been observed owing to incompleteness of referred specimens. *Physeter macrocephalus*, *Physeterula dubusii* and *Idiophyseter merriami* also differ from *Z. varolai* in the anterior extension of the supracranial basin onto the rostrum. *Kogia* spp., *Praekogia cedrosensis* and *Scaphokogia cochlearis* also differ from *Z. varolai* in other derived characters such as the small size of the skull, the lack of both nasals and the presence of a sagittal crest on the dorsal surface of the cranium within the supracranial basin.

COMPARISON WITH EXTANT *PHYSETER MACROCEPHALUS* AND MORPHO-FUNCTIONAL IMPLICATIONS

The comparison with the extant *Physeter macrocephalus* displayed the following substantial differences.

Body and skull size
We estimate the total body length of *Z. varolai* to be about 6.5–7 m whereas *P. macrocephalus* attains a maximum length of 18.3 m in the male and 12.5 m in the female (Rice, 1989). The condylobasal length of the skull of *Z. varolai* is 1.5 m and represents about 21–23% of the total length of the body, whereas the condylobasal length of the skull of an adult male *P. macrocephalus* is about 4 m, representing about one-third to one-quarter of the total body length (Rice, 1989).

Skull and head shape
The skull of *Z. varolai* shares with *P. macrocephalus*, in addition to all the derived characters described in the diagnosis of this superfamily, the following plesiomorphic condition: a complete and robust jugal arc fused with the zygomatic process of the squamosal through an elongate and obliquely orientated sutural surface. The major differences between the skull of *Z. varolai* and *P. macrocephalus* are those already mentioned in the comparison with all other physeteroids: specifically, the extension of the supracranial basin, the shape of the temporal fossa and the zygomatic process of the squamosal.

The supracranial basin of *Z. varolai*, not extended onto the anterior portion of the rostrum, suggests that the head of *Z. varolai* probably had a large hemispherical dorsal protuberance and, anteriorly, a short and relatively thin beak (Fig. 14). Consequently, the
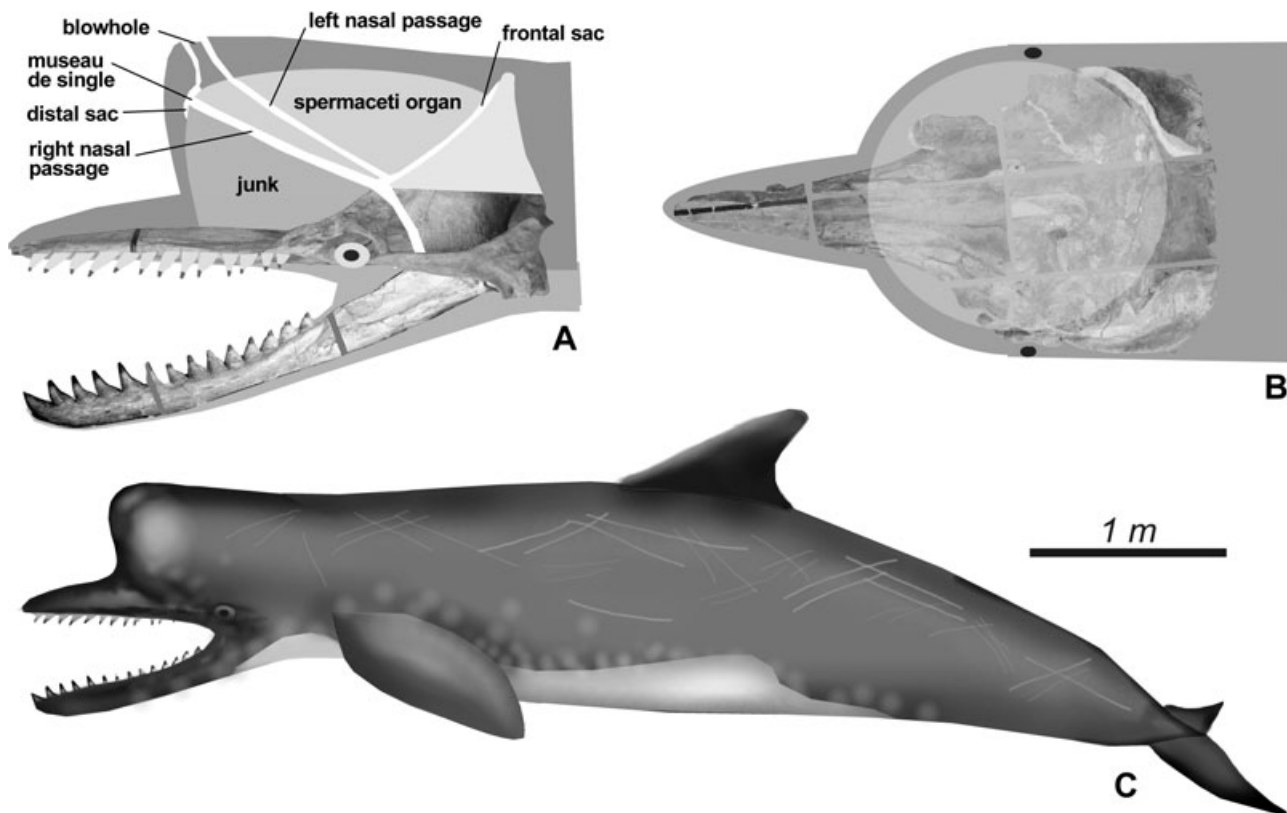

Figure 14. Hypothetical reconstructions of ***Zygophyseter varolai*** **gen. et sp. nov.** A, head in lateral view with a parasagittal section of the nasal area based on *Physeter macrocephalus* (Heyning, 1989: 36); B, head in dorsal view with evidence for the circular supracranial basin of the skull; C, body in lateral view.

external shape of the head of *Z. varolai* was substantially different from that of *P. macrocephalus*, which does not have a distinct beak. The head of *Z. varolai* may have been more similar to that of an adult *Hyperoodon ampullatus* (Mead, 1989: 329) than to extant physeteroids.

The location of external nares of *Z. varolai* is similar to that of *P. macrocephalus* in being placed in a more anterior and lower position compared with the majority of non-physeteroid odontocetes. This suggests that the blowhole of *Z. varolai* was placed anterodorsally to the spermaceti, on the top of the head protuberance, as in *P. macrocephalus* (Fig. 14A, B).

Teeth
Z. varolai has 13 and 14 teeth for each upper and lower tooth row, respectively. *P. macrocephalus* lacks maxillary teeth or has small upper teeth, rarely erupted from the gums. Its mandibular tooth number varies from 17 to 29 pairs (Rice, 1989). The teeth of *Z. varolai* have crenulated enamel on the crown, whereas the teeth of *P. macrocephalus* lack enamel. Moreover, the posterior teeth of *Z. varolai* are mediolaterally compressed whereas the teeth of *P. macrocephalus* all are circle-shaped in cross-section. The teeth of *Z. varolai* are relatively larger than those of *P. macrocephalus*, their greatest diameter being about 3.7% of the condylobasal length, vs. about 1% in *P. macrocephalus*.

Mandible
The mandibles of *Z. varolai* and *P. macrocephalus* are very similar in the following characters: Y-shaped outline, symphyseal portion cylindrical and strongly elongate (45% of the mandibular length in *Z. varolai* and 32–54% in *P. macrocephalus*), mandibular foramen large and anteriorly extended, and condyle ventrally located.

Vertebrae
The atlas of *Z. varolai*, as with that of *P. macrocephalus*, is not fused to the other cervical vertebrae. The atlas of *Z. varolai* does not have the peculiar robust transverse processes and the dorsoventral compression seen in *P. macrocephalus* and that give to the atlas a rectangular shape in anterior and posterior view in the latter. The lack of the 2nd to 7th cervical vertebrae of *Z. varolai* does not allow us to verify if these vertebrae were all fused, a condition observed only in *P. macrocephalus* among cetaceans. Nevertheless, the fact that the entire sequence of these vertebrae has not been found in the outcropping area may be interpreted as a slight indication of their

possible fusion. The number of thoracic vertebrae is at least one more (12) than in *P. macrocephalus* (11). The neural spine and the transverse processes of the thoracic and particularly lumbar vertebrae are more elongated in *Z. varolai* than in *P. macrocephalus*.

Ribs
The ribs of *Z. varolai* are similar to those of *P. macrocephalus* and, in both genera, the first rib is very robust and has the same 'L' shape and the 2nd–9th ribs have a double articulation. *Z. varolai* had at least one rib more (12) than *P. macrocephalus* (11).

Scapula
The scapula of *Z. varolai* differs from that of *P. macrocephalus* which is unusually higher than wide. Both the scapula of *Z. varolai* and that of *P. macrocephalus* have a very elongated and distally expanded acromion and a slender coracoid process.

Differences in the feeding apparatus between *Z. varolai* and *P. macrocephalus* suggest that *Z. varolai* captured different prey and with different methods. The large and pointed teeth of *Z. varolai* were able to penetrate large prey that may have been seized with the conical and trapping anterior teeth and cut with the mediolateral compressed posterior teeth (Fig. 15). The teeth of *P. macrocephalus*, which are present only in the mandible, not pointed and circular in cross-section, are not suited for cutting (Massare, 1987) and have no evident function in the capture of prey, which is acquired by suction (Werth, 2000). They are probably utilized for social and/or sexual intraspecific interactions (Clarke, Paliza & Aguayo, 1988). To support these observations, the skull of *Z. varolai* exhibits a large temporal fossa and an elongated zygomatic process of the squamosal, indicating large temporal and masseter muscles producing a great biting force. By contrast, a relatively small temporal fossa and short zygomatic process characterize the *P. macrocephalus* skull. The ventral location of the mandibular condyle both in *Z. varolai* and in *P. macrocephalus* favours a wide opening of the mouth that may be related to luring squids in the latter (Werth, 2000; Fristrup & Harbison, 2002) and to capture and cut large prey in *Z. varolai*. In *Z. varolai* the extreme elongation of the zygomatic process of the squamosal favours adduction when the mandible is rotated to a wide angle and the mouth is completely open.

There are no apparent reasons to hypothesize a different function of the supracranial basin of *Z. varolai* other than housing the spermaceti organ, as in the extant *P. macrocephalus* (Raven & Gregory, 1933;

Clarke, 1979; Heyning, 1989; Heyning & Mead, 1990; Cranford, 1999; Klima, 1999). In fact, among the extant cetaceans the spermaceti organ is always associated with the supracranial basin and both structures are present only in *Physeter* and *Kogia*, the two closest extant relatives of *Zygophyseter* (Fig. 16). This fulfils both conditions requested by Witmer (1995) and Geisler & Luo (1998) for the reconstruction of a soft-tissue structure in an extinct taxon with a high degree of confidence: (1) the presence of a unique osteological correlate and (2) the two closest extant relatives of the fossil taxon having both the soft-tissue structure and the osteological correlate.

The complex facial anatomy of *P. macrocephalus*, formed by the spermaceti organ and the nasal passages, is generally interpreted as a sound-generating
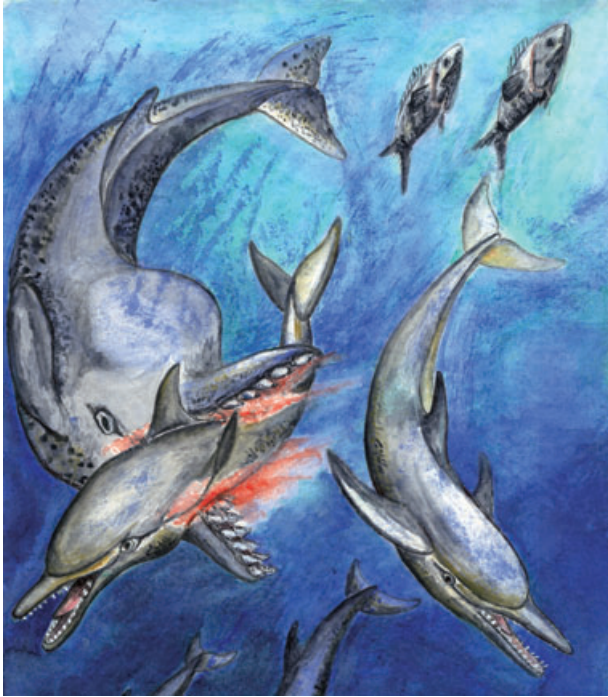

Figure 15. Hypothetical reconstruction of a Late Miocene marine scenario showing the killer sperm whale *Zygophyseter* attacking a kentriodontid (delphinoid). Painting by Giovanni Bianucci.
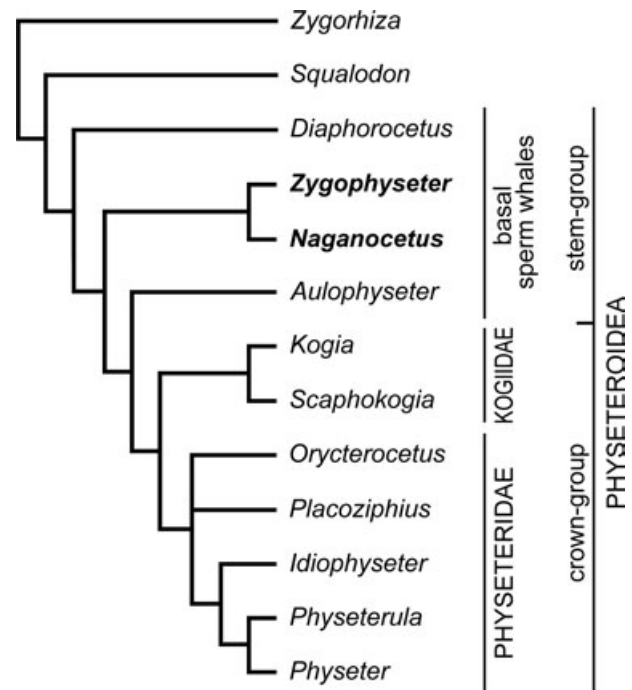

Figure 16. Strict consensus of three most parsimonious trees generated from the cladistic analysis. See text for discussion and Table 3 for character support.

Table 3. Character-taxon matrix used in cladistic analysis. 0, primitive state; 1–3, derived states; a = variable between 0 and 1; b = variable between 2 and 3; ? = missing characters; −= irrelevant characters

Taxa	1	2	3	4	5	6	7	8	90	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Zygorhiza	0	0	0	0	−	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Squalodon	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Kogia	3	1	3	1	2	1	0	1	0	2	1	1	1	2	1	2	2	1	1	1	0	1	a
Scaphokogia	3	1	3	1	2	1	0	1	0	2	1	1	1	2	?	2	2	1	?	?	?	1	?
Zygophyseter	2	1	b	0	2	1	1	1	1	1	0	?	1	0	1	2	2	?	1	0	1	0	1
Aulophyseter	1	1	2	0	3	1	1	1	1	1	0	1	1	2	1	2	2	0	?	0	0	1	?
Diaphorocetus	0	1	2	0	1	1	1	1	1	1	0	0	1	1	1	?	?	?	?	?	0	0	?
Naganocetus	2	1	2	?	2	1	1	1	1	1	0	1	?	0	1	?	?	?	?	0	1	0	1
Physeterula	2	2	2	?	2	1	1	?	?	?	0	2	1	?	?	?	?	?	?	1	0	?	?
Physeter	2	2	2	0	3	1	1	1	1	1	0	2	?	2	1	2	2	0	1	1	0	1	1
Idiophyseter	0	2	2	?	2	1	1	1	1	?	0	2	?	2	1	?	?	?	?	?	?	1	?
Orycterocetus	0	1	2	0	2	1	1	1	1	1	0	2	1	2	1	2	2	0	1	1	0	1	?
Placoziphius	0	1	2	?	2	1	1	1	1	?	0	2	1	2	1	?	?	?	?	1	0	1	?

structure with a function similar to that of other extant odontocetes (Norris & Harvey, 1972; Heyning, 1989; Heyning & Mead, 1990) although two alternative hypotheses have been suggestes: one attributes to this structure a function in buoyancy control (Clarke, 1979), whereas the other asserts that it facilitates evacuation of the lungs and absorbs excess nitrogen (Schenkkan & Purves, 1973).

Based on indirect evidence of the presence of a spermaceti organ we suggest that *Z. varolai* had an echolocation system similar to that of *P. macrocephalus*. Fristrup & Harbison (2002) report that the echolocation system of *P. macrocephalus* differs from that of homologous small odontocetes because it generates clicks with smaller bandwidths and lower centre frequencies and consequently it is not able to discriminate (by reflection) objects smaller than 1 m in diameter. Moreover, they also observed that the tissues of the squids (the main prey item of *P. macrocephalus*) have acoustic properties too similar to seawater to reflect sounds and, consequently, they suggest that extant sperm whales generally do not use echolocation to localize prey, in contrast to the hypothesis of others (Norris & Harvey, 1972; Norris & Møhl, 1983). As the feeding apparatus of *Z. varolai* is suited to capture large prey (probably even longer that 1 m, considering its body size and feeding apparatus), we can hypothesize that, unlike the extant *P. macrocephalus*, this cetacean was able to use echolocation to localize prey, even if its echolocation system was not particularly accurate, as that of extant *P. macrocephalus*. Some characters of the postcranial skeleton seem to confirm *Z. varolai* as a large, active predator that could swim much faster than *P. macrocephalus* (Figs 13C, 14). In fact, the wider and more elongated neural spines and transverse processes of the lumbar vertebrae indicate a great insertion surface for the multifidus and longissimus muscles system. These muscles, used for propulsion in cetaceans (Slijper, 1979; Thewissen, 2002), were probably larger in *Z. varolai* than in *P. macrocephalus*.

PHYLOGENETIC ANALYSIS

The phylogenetic relationships of physeteroids among the other cetaceans has been much debated in the last few years, particularly since the publication of the results of the genetic research by Milinkovitch and colleagues (Milinkovitch, Orti & Meyer, 1993, 1995; Milinkovitch, Meyer & Powell, 1994; Milinkovitch *et al*., 1996) which questioned the monophyly of the odontocetes, and suggested a close relationship between physeteroids and mysticetes. The following studies based on molecular data (Árnason, Gullberg & Widegren, 1993; Árnason & Gullberg, 1994; Gatesy *et al*., 1999; Cassens *et al*., 2000; Nikaido *et al*., 2001; Árnason, Gullberg & Janke, 2004), morphology (Luo & Marsh, 1996; Fordyce, 1994, 2002; Heyning, 1997; Luo & Gingerich, 1999; Geisler & Sanders, 2003; Lambert, 2005) and on both molecular data and morphology (Messenger & McGuire, 1998) contrast the results of Milinkovitch and colleagues, re-establishing the physeteroids within the odontocete clade.

From a palaeontological point of view, the most significant results on this topic are those by Muizon (1991), Luo & Gingerich (1999), Fordyce (1994, 2002), Geisler & Sanders (2003) and Lambert (2005).

Muizon (1991) considered the Physeteroidea (Physeteridae and Kogiidae) as a sister group of the Ziphiidae, and both of these taxa as sister group of a larger clade formed by the Delphinida, Eurhinodelphinoidea and Platanistoidea.

Luo & Gingerich (1999), considering the evolution of the basicranium and of hearing, placed *Physeter* clearly within the odontocete clade in a more crown-ward condition with respect to the Delphinoidea. They considered *Physeter* as the sister group of a clade formed by *Mesoplodon* (Ziphiidae), *Xenorophus* (Xenorophiidae) and *Squalodon* (Squalodontoidea).

Fordyce (1994, 2002) placed *Physeter* and *Kogia* within a wide clade that is more crown-ward with respect to the archaic odontocetes *Archaeodelphis* and *Simocetus*. In accordance with the previous analysis of Muizon (1991), Fordyce considered *Physeter* and *Kogia* as a sister group of the Ziphiidae.

Geisler & Sanders (2003), in their cladistic analysis of cetaceans based on 54 taxa and more than 300 morphological characters, confirmed the monophyly of the clade formed by Physeteridae (*Kogia*, *Physeter* and *Orycterocetus*) and Ziphiidae. The cladogram presented by these authors differs from those of Fordyce (1994, 2002), not only by the larger number of taxa considered, but also by the more basal position of *Prosqualodon*, *Squalodon*, *Notocetus* and *Waipatia*, which are removed from the Platanistoidea.

Lambert (2005) rejected the supposed sister-group relationship between physeteroids and ziphiids and placed the sperm whales in a more basal position.

Recent cladistic analyses based only on molecular data (Cassens *et al*., 2000; Nikaido *et al*., 2001; Árnason, Gullberg & Janke, 2004), agree with Lambert's results in considering the physeteroids as basal Odontoceti. These results are also supported by a recent analysis using the supertree approach of matrix representation with parsimony (Price, Bininda-Emonds & Gittleman, 2005).

Although the position of the physeteroids within the cetacean clade has been investigated in depth by these and other published studies, little attention has been given to the relationships within this superfamily. The few studies on this topic have mainly focused on the

position of the two extant species of *Kogia* and other related fossil taxa with the other sperm whales (Muizon, 1991; Luo & Marsh, 1996; Bianucci & Landini, 1999). The only analysis to consider a large number of physeteroid taxa is that of Kazár (2002), but hers is not a cladistic analysis This gap is partially due to the scarcity of fossils belonging to this odontocete group examined and published in recent years. In fact, apart from the recent publications by Hirota & Barnes (1995) and Kazár (2002), the last significant studies on fossil physeteroids are those by Kellogg (1925, 1927, 1965).

The aim of our cladistic analysis is to propose a first phylogeny for the physeteroids, with particular attention to the position of *Zygophyseter* within this clade.

The 23 characters considered, coded in a matrix as either binary or multistate (Table 2), are detailed in Appendix 2.

The result of the PAUP analysis was a unique minimal cladogram of 39 steps, consistency index (CI) = 0.897 (reduced to 0.882 after excluding uninformative characters) and retention index (RI) = 0.907. This cladogram is presented in Figure 16 and discussed below:

1. *Zygophyseter* is placed clearly within the Physeteroidea. The position of *Zygophyseter* is supported by 14 apomorphies, seven of which are unique to this superfamily (autoapomorphies): the presence of a supracranial basin; the transverse widening of the posterior portion of the right premaxilla; the reduction of the left premaxillary foramen; the lack of at least one nasal; the triangular shape of the zygomatic process in lateral view; the concavity of the involucrum; the ventral location of the mandibular condyle.

2. *Zygophyseter* is sister group of *Naganocetus*, as indicated by the similar large size of skull and teeth. The presence of these derived characters and of the plesiomorphic anteroposterior elongation of the temporal fossa favoured a feeding adaptation directed toward large prey.

3. *Diaphorocetus* appears as the more basal physeteroid in its small size, the small angle formed by the frontal–maxillary suture with the horizontal plane and the more inclined occipital shield.

4. The other physeteroids considered form a distinct clade characterized by the anteroposterior compression of the temporal fossa and by the trend toward upper tooth reduction.

5. Inside this last clade, *Aulophyseter* is the sister group of all other physeteroids and is characterized by a large angle formed by the frontal–maxillary suture with the horizontal plane and by other peculiar derived characters, pointed out by Kazár (2002) but not considered in this analysis. The last cited author referred this taxon to the monogeneric subfamily Aulophyseterinae.

6. [*]

7. The clade formed by the other physeteroids is defined by the decrease in size of the skull (character lost in *Physeter* and *Physeterula*) and the autoapomorphic loss of dental enamel. This crown-group Physeteroidea is divided in two clades: the Kogiidae (*Kogia* and *Scaphokogia*) and Physeteridae (the remaining taxa).

8. The Kogiidae are defined by some derived characters already emphasized by Barnes (1973), Muizon (1991) and Bianucci & Landini (1999). The lack of the transverse widening of the posterior portion of right premaxilla is here interpreted as a reversion. *Praekogia* from the early Pliocene of Baja California (Barnes, 1973) and probably *Thalassocetus antwerpiensis* ('crane I' of Abel, 1905) from the Miocene of Antwerp, even if not included in this analysis, must also be referred to this family.

9. The Physeteridae, here restricted to the subfamily Physeterinae, are characterized by a relatively high and vertical or concave occipital crest. Even if the relationships of the genera within this taxon need a subsequent investigation, the extant *Physeter* appears to belong to a specialized lineage characterized by the increase in size of the skull and by the extension of the cranial basin in the rostrum.

CONCLUSIONS

Zygophyseter varolai exhibits two distinctive and bizarre features: the presence of a peculiar anterior projection of the supraorbital process of the right maxilla and a very anteroposteriorly elongated zygomatic process of the squamosal. The first character is a consequence of the marked dorsal modification of the cranium, probably for housing the spermaceti organ. The second character, related to the wide mouth opening and to the strong musculature, is an apparently plesiomorphic condition that may suggest a relationship between *Z. varolai* and primitive archaeocetes. *Z. varolai*, together with *Naganocetus shigensis*, belongs to a Middle–Late Miocene lineage of basal sperm whales adapted for feeding on large prey, similarly to the extant killer whale (*Orcinus orca*). These cetaceans were rather large; the body length of *Z. varolai* and *N. shigensis* was near 7 m. The large size of the body, large teeth and anteroposteriorly elongated temporal fossa are characters related to this trophic adaptation. *Z. varolai* and *N. shigensis* are only one lineage of the wide Miocene radiation of sperm whales. Appearing as early as in the Late Oligocene, the physeteroids radiated widely during the Miocene, as judged from the fossil record (Table 1). Even if most of the early material studied now needs revision, the wide diversification of this superfamily

during the Miocene is evident. Our cladistic analysis of some selected genera reveals the presence during the Miocene of five distinct lineages, which may reflect different ecological adaptations: (1) *Diaphorocetus*, (2) *Zygophyseter + Naganocetus*, (3) *Aulophyseter*, (4) Kogiidae and (5) Physeteridae. Lineages 1, 2 and 3 represent the stem group of Physeteroidea; lineages 4 and 5 form a clade representing the crown-group Physeteroidea. The extant *Physeter macrocephalus*, *Kogia breviceps* and *K. sima* are the only surviving species of one of the greatest cetacean radiations of the past.

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APPENDIX 1

SPECIMENS EXAMINED

The specimens directly examined for comparisons and cladistic analysis are as follows (excluding comparative material not belonging to physeteroids or to the two outgroup genera): *Eudelphis mortselensis* (IRSNB 523, holotype); *Kogia breviceps* (MNHNP 1877-277; MNHNP 1976-37; MNHNP 1883-483; MBMS 4000; ZMA 5068); *Kogia pusilla* (MGPUF 1540V, holotype); *Kogia sima* (MZAFS, not catalogued); *Kogia* sp. (MSN-TUP I13798, isolated ear bones); *Orycterocetus* sp. (MAUL 29/1); *Physeter macrocephalus* (MNHNP 1831; MSNTUP M265; MSNTUP M266; MSNTUP M267); *Physeterula dubusii* (IRSNB 528, holotype) (h); *Placoziphius duboisii* (IRSNB 530, holotype); *Scaldicetus caretti* (IRSNB 512, holotype) 'Scaldicetus' degiorgii (ITCL, not catalogued, holotype); 'Scaldicetus' grandis (IRSNB 422, holotype); *Squalodon bariensis* (MPUP 26084, MPUP 20196); *Squalodon bellunensis* (MPUP 26131 holotype); *Squalodon* sp. (MAUL 8; MAUL8/1); *Thalassocetus antwerpiensis* (IRSNB 525, syntype 1; IRSNB 526, syntype 2); *Zygorhiza kochii* (cast of USNM 11962).

APPENDIX 2

CHARACTER ANALYSIS

1. *Size of skull (expressed as condylobasal length)*: 0, 50–90 cm; 1, 90–120 cm; 2, >120 cm; 3, < 50 cm. A

skull length between 50 and 90 cm (observed in the outgroups *Zygorhiza* and *Squalodon* and in the presumed archaic physeteroid *Diaphorocetus*) is considered as the plesiomorphic condition. The increase in relative size of the skull (and probably also of the body) seems to be a general trend of the physeteroid evolution (except in the kogiids), culminating in *Zygophyseter* and in *Naganocetus*, *Physeterula* and particularly in *Physeter*.

2. *Supracranial basin of the skull*: 0, absent; 1, present; 2, extended onto the whole dorsal surface of the rostrum (modified by Heyning, 1989; Muizon, 1991). The deep dorsal concavity of the skull (termed scaphidiomorphy by Abel, 1905) is a peculiar apomorphy that characterizes all the physeteroids and that in the two extant genera (*Physeter* and *Kogia*), and probably also in the fossil taxa, is related to the presence of the spermaceti organ. The supracranial basin is present in the skull of *Zygophyseter*, where it extends onto the dorsal surface of the cranium and onto only the posterior portion of the rostrum. In *Physeterula*, *Idiophyseter* and particularly in *Physeter* the dorsal concavity extends 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 (modified by Messenger & McGuire, 1998 and Muizon, 1991). *Zygophyseter* shows both 2 (left antorbital notch) than 3 (right antorbital notch) states. Even if Geisler & Sanders (2003) reported that the shape of the antorbital notch is derived from two independent characters (the convexity of the rostrum lateral margin and the direction of the anterior margin of the supraorbital process), we prefer to maintain the original definition of Muizon (1991), also because *Zygophyseter* and *Scaphokogia* have both margins parallel to the sagittal plane, a peculiar condition not considered in the analysis of Geisler & Sanders (2003).

4. *Maxillae, premaxillae and vomer, all reaching the tip of the rostrum which is not formed only by the premaxillae*: 0, no; 1, yes (Muizon, 1991). This derived condition is observed in *Kogia* and *Scaphokogia* but not in the other physeteroids. In particular the tip of the rostrum of *Zygophyseter* is formed only by the premaxillae.

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° (modified by Geisler & Sanders, 2003). We observed a different degree of inclination of the frontal–maxillary suture within the physeteroids. This value is lower in

Diaphorocetus (about 17°), intermediate (20–40°) in *Zygophyseter* and most other physeteroids, and relatively large in *Aulophyseter* (40°) and in *Physeter (*40–50°). This character cannot be considered for *Zygorhiza*, which lacks an overlap of the maxilla onto the frontal.

6. *Right premaxilla*: 0, posteriorly extended as the left premaxilla; 1, more posteriorly extended than the left premaxilla (modified from Barnes, 1990; Messenger & McGuire, 1998; Geisler & Sanders, 2003). Even if the dorsal surface of the cranium of *Zygophyseter* is not well preserved, it seems that, as in all physeteroids, its right premaxilla extends more posteriorly than the external nares while the left premaxilla terminates posteriorly at level of the external nares.

7. *Right premaxilla*: 0, not posteriorly widened; 1, posteriorly widened transversely and passed to the left side of the skull (Muizon, 1991). The derived condition is observed in *Zygophyseter* and in all other physeteroids except the kogiids (Muizon, 1991; Bianucci & Landini, 1999).

8. *Left premaxillary foramen very small or absent*: 0, no; 1, yes. We observed an apparent lack of the left premaxillary foramen in *Zygophyseter* and either a similar condition or a very small foramen in all other physeteroids. Messenger & McGuire (1998) and Geisler & Sanders (2003) erroneously reported a larger left premaxillary foramen for the physeteroids.

9. *Increase in size of the right premaxillary foramen*: 0, no; 1, yes. *Zygophyseter*, as all physeteroids except the kogiids, exhibits a very large right premaxillary foramen.

10. *Lack of nasals*: 0, both nasals present; 1, one nasal absent; 2, both nasals absent (Heyning, 1989; Muizon, 1991; Geisler & Sanders, 2003). The absence of at least one nasal is a derived condition shared by *Zygophyseter* and all physeteroids. The kogiids have lost both nasals.

11. *Presence of a sagittal crest* (*sensu* Wall, 1851; = facial crest of Muizon, 1991): 0, absent; 1, present (Muizon, 1991). *Zygophyseter* lacks the peculiar sagittal crest of the kogiids between the external nares and the occipital. A sagittal crest is also present in *Thalassocetus* ('crane I' of Abel, 1905), a sperm whale genus not included in this cladistic analysis.

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°. The occipital crest of the *Zygophyseter* skull is not preserved and consequently the state of this character for this new genus cannot be evaluated. As observed by Kazár (2002: Fig. 2) a vertical and concave occipital crest is a derived condition of the Physeterinae (= Physeteridae).

13. *Fusion of lacrimal and jugal*: 0, no; 1, yes (Miller, 1923; Heyning, 1989; Muizon, 1991; Geisler & Sand-

ers, 2003). The lacrimal and the jugal are fused in *Zygophyseter* as in all physeteroids. This derived condition was also observed in other odontocetes as in the delphinoids and in *Eurhinodelphis* (Geisler & Sanders, 2003).

14. *Temporal fossa*: 0, anteroposteriorly elongated (width/height > 1); 1, not anteroposteriorly elongated (width/height = 1); 2, anteroposteriorly compressed (width/height < 1). The temporal fossa of *Zygophyseter* is anteroposteriorly elongated as in *Naganocetus*. This is apparently a plesiomorphic condition that links *Zygophyseter* to the archaeocetes. The more derived state (anteroposterior constriction of the temporal fossa) was observed in the physeterines by Kazár (2002).

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. *Zygophyseter* exhibits a zygomatic process of the squamosal that is triangular in lateral view owing to the dorsal bending in its posterior portion, a derived condition that we observed in all physeteroids and that differs from that of all other cetaceans that have an 'L'-shaped zygomatic process, with the dorsal margin ventrally bending or parallel to the horizontal plane in its posterior portion (Fig. 12).

16. *Anterior bullar facet*: 0, very anteroposteriorly elongated; 1, reduced; 2, absent or very small (modified from Luo & Marsh, 1996). The anterior process of the periotic of *Zygophyseter* has a very small anterior bullar facet near the apex also observed in the other physeteroids (Fig. 11).

17. *Accessory ossicle*: 0, absent; 1, present; 2 present and partially fused with the anterior process (Luo & Marsh, 1996). The tympanic bulla of *Zygophyseter* has a large accessory ossicle partially fused with the anterior process of the periotic, a derived condition observed in all physteroids (Luo & Marsh, 1996) (Fig. 11). Consequently, the fovea epitubaria of the periotic of *Zygophyseter* is large and rectangular (owing to the large accessory ossicle), as observed by us in all other periotics of physeteroids. This shape differs from the elliptical shape of most other odontocetes and from the anteroposteriorly compressed form of the ziphiids (Fig. 11).

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 (Muizon, 1991; Luo & Marsh, 1996). The only preserved incomplete periotic of *Zygophyseter* lacks the posterior process so it is not possible to evaluate the state of this character. Probably, as suggested by Muizon (1991), the derived condition of this character is an autoapomorphy of the kogiids, even if the fossil material is too poorlt preserved to support this hypothesis strongly.

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 (modified by Muizon, 1991). We observed this peculiar morphology of the involucrum (and particularly the concavity of the medial margin in ventral view) in *Zygophyseter* and only in tympanic bullae of the other physeteroids.

20. *Loss of dental enamel*: 0, no; 1, yes. The crown of the teeth of *Zygophyseter* is covered with enamel as in *Aulophyseter*, *Naganocetus* and *Eudelphis*, whereas the teeth of *Physeter*, *Orycterocetus*, *Physeterula*, *Placoziphius* and *Kogia* lost the enamel. The teeth of *Diaphorocetus*, *Idiophyseter* and *Scaphokogia* are unknown.

21. *Size of teeth (greatest diameter of root expressed as percentage of the condylobasal length of skull)*: 0, < 3%; 1, > 3%. *Zygophyseter* and *Naganocetus* have larger teeth, proportionally to the skull, with respect to the other physeteroids. In fact, the greatest diameter of the root in *Zygophyseter* is about 3.7% of the condylobasal length of the skull, a value probably similar to that of *Naganocetus* and larger than that of all other physeteroids (ranging approximately between 1 and 2.5%). The extant *Physeter* has large teeth but the diameter of which represents only about 1% of the condylobasal length of the skull.

22. *Upper tooth row*: 0, deep alveoli; 1 alveoli shallow or absent. *Zygophyseter* has a complete upper dentition and deep alveoli as in *Naganocetus* and *Diaphorocetus* but unlike *Aulophyseter*, *Physeter*, *Orycterocetus*, *Placoziphius*, *Kogia* and *Scaphokogia*, which have a more or less accentuated reduction of upper dentition. This character is not of value in *Physeterula*, the rostrum of which is not preserved, nor in *Idiophyseter*, the rostrum of which is preserved only with a small posterior portion bearing two alveoli (Kellogg, 1925).

23. *Ventral position of the mandibular condyle*: 0, no; 1, yes. The mandibular condyle of *Zygophyseter* is located near the ventral margin of the mandible as in *Physeter*. Among the fossil physeteroids, only *Naganocetus shigensis* and 'Aulophyseter' rionegrensis (this latter species is not considered in our cladistic analysis) have a well-preserved posterior margin of the mandible. Both species exhibit a ventral location of the condyle. A similar (but more dorsal) position of the condyle has also been observed in some (but not in all) examined mandibles of *Kogia* spp. (Fig. 14).