Zoological Journal of the Linnean Society, 2013, **167**, 569–598. With 16 figures

The most basal beaked whale *Ninoziphius platyrostris* Muizon, 1983: clues on the evolutionary history of the family Ziphiidae (Cetacea: Odontoceti)

OLIVIER LAMBERT[1,2]*, CHRISTIAN DE MUIZON[2] and GIOVANNI BIANUCCI[3]

[1]*Département de Paléontologie, Institut royal des Sciences naturelles de Belgique, 1000 Brussels, Belgium*
[2]*Département Histoire de la Terre, Muséum national d'Histoire naturelle, 75005 Paris, France*
[3]*Dipartimento di Scienze della Terra, Università di Pisa, 56126 Pisa, Italy*

Received 19 September 2012; revised 4 January 2013; accepted for publication 11 January 2013

Ninoziphius platyrostris, from the late Neogene of Peru, is one of the best-known fossil beaked whales (Odontoceti: Ziphiidae), with a holotype including the skull with ear bones, mandibles, teeth, and postcranial elements. Furthermore, based on several characters, including a complete functional upper and lower dentition, it is usually considered as one of the most archaic ziphiids. However, the poorly preserved dorsal portion of the holotype skull has led to unresolved phylogenetic relationships. With the addition of two newly prepared skulls from the same Peruvian locality we redescribed *N. platyrostris*. In the light of recent ziphiid discoveries, an emended diagnosis of the species is proposed here. In our cladistic analysis *Ninoziphius* is the most basal stem ziphiid. Newly observed or reassessed morphological traits allow functional and ecological considerations. The morphology of the oral apparatus suggests that *Ninoziphius* was less specialized for suction feeding than most extant ziphiids. Tooth wear in the holotype may indicate benthic feeding. Although the vertebral column of *Ninoziphius* corresponds to less developed locomotor abilities for deep dives, its cranial morphology does not provide definitive arguments for an echolocation system less efficient than in deep diving extant ziphiids. Finally, the phylogenetic tree produced was used to detail the evolutionary history of several major ziphiid features (dental reduction, development of mandibular tusks, and increased body size).

doi: 10.1111/zoj.12018

ADDITIONAL KEYWORDS: body size – deep diving – echolocation – feeding strategy – late Neogene – Peru – phylogeny.

INTRODUCTION

Beaked whales (Ziphiidae) are a fascinating family of medium to large size toothed whales (Odontoceti), including at least 21 species in six genera (Dalebout *et al.*, 2002; Mead, 2008). Extant members display a series of morphological, physiological, and behavioural adaptations to deep diving and suction feeding; several species have been recorded at depths beyond 1000 m, searching for cephalopods or fish with their sonar (echolocation) and catching them without tooth prehension (Heyning & Mead, 1996; Johnson *et al.*, 2004; Tyack *et al.*, 2006; Werth, 2006; Minamikawa, Iwasaki & Kishiro, 2007). Indeed, most extant ziphiids lack a functional dentition; only one or two pairs of mandibular tusks erupt in adult males, most likely involved, at least in some species, in intraspecific fights, in addition to the occasional occurrence of vestigial teeth in the gum (Boschma, 1951; Heyning, 1984; MacLeod, 2002; MacLeod & Herman, 2004).

The oldest fossil ziphiids date from the late early–middle Miocene (Bianucci *et al.*, 2005; Lambert & Louwye, 2006) and the fossil record of the family

---

*Corresponding author. E-mail: olivier.lambert@naturalsciences.be

has improved greatly in recent years (Bianucci & Post, 2005; Lambert, 2005c; Bianucci, Lambert & Post, 2007, 2010; Post, Lambert & Bianucci, 2008; Lambert, Bianucci & Post, 2009; Bianucci *et al.*, 2013), with the number of known fossil species now higher than the number of extant species as a consequence. The fossil beaked whale *Ninoziphius platyrostris* de Muizon, 1983, known from material from the latest Miocene–Pliocene of Peru (Pisco Formation), is an important species for several reasons. First it is one of the best-known fossil ziphiids, with a holotype including a partial skull with ear bones, mandibles, teeth, vertebrae, ribs, sternum, and distal flipper elements. Secondly, a complete set of upper and lower teeth is observed, as in the extant *Tasmacetus shepherdi* and the extinct *Messapicetus* spp. Furthermore, *Ninoziphius* displays several additional characters in the vertex, the palate, and the periotic that are usually interpreted as primitive for a ziphiid (de Muizon, 1984; Bianucci *et al.*, 2010). Unfortunately, the facial area and the dorsal part of the rostrum are poorly preserved in the holotype, diagnostic ziphiid characters remaining therefore unknown in *Ninoziphius*. For this reason, this taxon was not included in recent ziphiid phylogenies (Bianucci, Post & Lambert, 2008; Lambert *et al.*, 2009; Bianucci *et al.*, 2010, 2013); it only appeared in a more general cetacean cladistic analysis, where it falls as a stem or crown-ziphiid depending on the character set (Geisler *et al.*, 2011). More fragmentary ziphiid remains from other late Neogene localities (Florida and North Carolina, USA) have been tentatively referred to *Ninoziphius* (de Muizon, 1984; de Muizon & DeVries, 1985; Morgan, 1994; Whitmore & Kaltenbach, 2008), but none of these have provided additional information on the most informative parts of the skull.

Two undescribed specimens of *N. platyrostris*, originating from the same Peruvian latest Miocene–Pliocene locality as the holotype, were discovered by one of us (C. M.) in the early eighties and have been recently prepared. These partial skulls provide data on previously unknown parts of *N. platyrostris*. In the light of recent fossil ziphiid discoveries, we propose a description of these two new specimens and further description of relevant parts of the holotype in order to comprehend better the anatomy and phylogenetic relationships of this important archaic ziphiid, and to eventually provide comments about the evolution of the main morphological and ecological features of members of the family.

MATERIAL AND METHODS

INSTITUTIONAL ABBREVIATIONS

IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHN, Muséum National d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; ZMA, Zoölogisch Museum Amsterdam, Amsterdam, The Netherlands.

FOSSIL PREPARATION

Enclosed in a fine-grained sand cemented with carbonatic matrix, referred specimen MNHN SAS 1628a-e was prepared using acid etching (bath of formic acid diluted in water, concentration about 10%, with tricalcium phosphate buffer); this technique, which was also used for the preparation of the holotype, allowed the preservation of fragile bone elements, including the delicate, in some places translucent, lateral lamina of the pterygoid, as well as the peculiar inner surface of the hamular fossa.

CLADISTIC ANALYSIS

The phylogenetic relationships of *Ninoziphius* with the other 22 ziphiid genera (including the six Recent genera) were investigated by means of a matrix of 46 characters (see Appendices S1–S2) partly taken from previous analyses (Lambert, 2005a, b, c; Bianucci *et al.*, 2007, 2010, 2013; Lambert *et al.*, 2009;). We also included in the analysis *Squaloziphius*, a fossil odontocete genus whose relationships with ziphiids (de Muizon, 1991; Fordyce & Muizon, 2001) are still debated (Fordyce & Barnes, 1994; Geisler & Sanders, 2003; Lambert & Louwye, 2006). *Squalodon*, *Waipatia*, and the eurhinodelphinids *Eurhinodelphis*, *Schizodelphis*, and *Ziphiodelphis* were used as outgroups. The genus *Mesoplodon*, possibly paraphyletic (Bianucci *et al.*, 2007), is represented by the type species *Mesoplodon bidens*. We preferred not to include in our analysis the fossil ziphiid genera based on very fragmentary material (e.g. *Caviziphius* and *Khoikhoicetus*) because it can be difficult for taxa for which very few characters have been scored to be placed accurately on the tree, with a consequent decrease in the phylogenetic accuracy (Wiens, 2003). Character states were designed to be plesiomorphic (0) or derived (1 – n) according to the outgroup comparison method of Maddison, Donoghue & Maddison (1984). The matrix includes 46 morphological characters; 26 binary (5, 6, 12, 17, 18, 19, 20, 21, 24, 25, 26, 27, 29, 30, 31, 32, 33, 35, 37, 38, 40, 41, 42, 43, 44, 46), 14 multistate ordered (1, 3, 7, 8, 9, 11, 13, 14, 15, 16, 22, 23, 36, 45), and six multistate unordered (2, 4, 10, 28, 34, 39). One character (26) was parsimony-uninformative in this analysis. Multistate characters were treated as ordered when character states could be arranged so that each state was most similar to the states adjacent to it (e.g. state 1 is most similar to states 0 and 2) (Geisler & Sanders, 2003). As neither the number of fossil specimens available nor the number of individuals of the living taxa measured were sufficient to lend statistical significance to the standard deviations of the variations within each taxon observed, the continuous multistate characters were transformed into discrete states by placing the divisions between states in correspondence with the largest gaps, following the gap-coding method of Mickevich & Johnson (1976) as modified by Geisler & Sanders (2003) to suit the case of taxa represented by just a few specimens. The analysis was executed with the software PAUP (v. 4.0b10, Swofford, 2001), using the branch-and-bound algorithm. As preliminary analyses led to less-resolved trees, we downweighted the homoplastic characters using the default value of 3 for the constant *k* of the method of Goloboff (1993).

Several characters discussed in the text were optimized using the software MacClade 4 (Maddison & Maddison, 2005).

SYSTEMATIC PALAEONTOLOGY

CETACEA BRISSON, 1762

ODONTOCETI FLOWER, 1867

ZIPHIIDAE GRAY, 1850

Remark: As stated below in the diagnosis of *Ninoziphius*, we define the family Ziphiidae as an apomorphy-based clade, including both crown-Ziphiidae (a clade containing the last common ancestor of *Tasmacetus* and *Ziphius* and all its descendants) and stem-Ziphiidae (a paraphyletic group, with, amongst others, *Ninoziphius*).

NINOZIPHIUS DE MUIZON, 1983

Emended diagnosis: Same as for the only referred species, *N. platyrostris*.

NINOZIPHIUS PLATYROSTRIS DE MUIZON, 1983

Holotype: MNHN SAS 941, incomplete skeleton including: partial skull with two periotics, right tympanic bulla, and teeth, mandibles with teeth, five cervical vertebrae, five thoracics, one lumbar, five caudals, chevrons, six ribs and rib fragments, two sternum elements, and two distal forelimb elements (probably partial metacarpals).

Referred specimens: MNHN SAS 1628a–e, partial skull including rostrum base, part of the facial area with elements of vertex, and finely preserved palate and basicranium; MNHN SAS 1629a–b, partial skull including part of rostrum base and moderately dislocated facial area with vertex. Both specimens were found in the same Sud-Sacaco locality as the holotype, in the Sud-Sacaco level.

Remarks: Based on our own observations, none of the specimens from Lee Creek Mine, North Carolina, curated at the USNM and previously tentatively referred to *N. platyrostris* (mostly jaw fragments, teeth, periotics, and humeri), can be definitively assigned to the species, being either too fragmentary and/or differing somewhat from the Peruvian specimens. Some of them, especially the partial dentaries USNM 314753 and USNM 475494, are possibly Ziphiidae aff. *Ninoziphius*. Pending more complete material, the presence of the species *N. platyrostris* on the eastern coast of North America remains hypothetical. At least a closely related taxon was probably present there, and rather common, during the early Pliocene.

The assignation of the isolated ziphiid humerus MNHN SAS 943 (see de Muizon, 1984: 162–164), from the type locality, to *N. platyrostris* is only tentative.

Emended diagnosis: Ninoziphius platyrostris is a member of the family Ziphiidae because of the following apomorphies (see phylogeny below): elevated vertex bearing outwardly projecting crest of premaxilla; enlarged fossa for hamular lobe of pterygoid sinus, extended anteriorly on palatal surface of rostrum and ventrally close to ventral limit of basicranium; ventral margin of postglenoid process of squamosal clearly more dorsal than ventral margin of paroccipital process of exoccipital in lateral view (also present for example in some delphinoids); absence of a dorsal keel on posterior process of periotic; enlarged posterior process of tympanic attached to elements of squamosal/exoccipital (character possibly absent in *Messapicetus* and *Nazcacetus*, even though we acknowledge that its detection on fossil skulls is not easy, and also present in physeteroids); presence of a posteroventral corner on sigmoid process of tympanic; enlarged pair of mandibular alveoli (probably corresponding to tusks); presence of a precoronoid crest on dorsal margin of mandible (also present in the ziphiid-like dolphin *Australodelphis* and some other delphinoids).

Compared to other known ziphiids, *N. platyrostris* retains a series of plesiomorphies (see phylogeny below): unexcavated apex of hamular process of pterygoid; higher and thinner lateral lamina of pterygoid; posterior margin of sigmoid process of tympanic rectilinear and transversely directed; transversely narrow anterior process of periotic in ventral view, laterally short lateral tuberosity of periotic, and posterior process of periotic narrow, not fan-shaped (three last characters shared with *Messapicetus*); retention of a full series of functional upper and lower postapical teeth (shared with *Messapicetus* and *Tasmacetus*); proportionally longer cervical region (ratio of centrum length/posterior centrum width for each of the vertebrae c3-c6 > 0.35; unknown in most extinct ziphiids; number of fused cervicals varies amongst ziphiids).

Ninoziphius differs from all other ziphiids in: extension of pterygoid sinus in orbit region; possibly development of two pairs of subapical mandibular tusks set on a bony pad, in addition to apical tusks.

Ninoziphius shares with members of the *Messapicetus* clade and with ziphiines the anterolateral direction of premaxillary crest, with members of the *Messapicetus* clade and some of the ziphiines (*Choneziphis*, *Izikoziphius*, and *Ziphius*) the reduced contact between nasal and premaxillary crest. It differs from members of the *Messapicetus* clade and some of the ziphiines (*Choneziphis*, *Globicetus*, *Imocetus*, and *Tusciziphius*) by the absence of a dorsoventral closure of mesorostral groove by thickened premaxillae, and from members of the *Messapicetus* clade, *Imocetus*, and *Ziphius* by the absence of a distinct prenarial basin. It also shares with *Messapicetus* the extreme elongation of the rostrum, making up more than 70% of condylobasal length and the elongated symphyseal portion of mandibles. It further differs from *Messapicetus* in having a greater vertex elevation, but without vertical posterodorsal portion of the ascending process of the premaxillae, nasal more anteroposteriorly elongated and without anteromedial excavation, and tympanic bulla without anterior spine.

It shares with *Berardius* the presence of a tall cochlear spine in periotic (taller than in eurhinodelphinids), with *Berardius* and *Messapicetus* the semicircle-shaped section of symphyseal portion of mandibles. It differs from *Berardius* and related fossil genera in: supraoccipital reaching a level as high as the frontal and nasal in vertex; absence of a rounded protuberance on posterior part of vertex.

Type locality: Sud-Sacaco, southern coast of Peru, 550 km south of Lima, approximately km 543 of the Pan-American Highway (de Muizon, 1981). Geographical coordinates: 15°34′51″S, 74°43′11″W. The two referred specimens were discovered a few metres away from the site of the holotype.

Type horizon and age: Sud-Sacaco vertebrate level of the Pisco Formation (de Muizon & DeVries, 1985; de Muizon, 1988a; SAS). This level is just above the Mio-Pliocene unconformity and has been dated to Zanclean (early Pliocene) by means of molluscans and shark teeth (presence of *Carcharodon carcharias* and absence of *Carcharodon hastalis*) (de Muizon & DeVries, 1985). A tuff layer from the Sacaco level, above the Sud-Sacaco level, has been dated radiometrically (K/Ar) to 3.9 Myr (de Muizon & Bellon, 1980, 1986). It should be noted that in a recently published work (Ehret *et al.*, 2012), strontium-ratio isotopic analyses gave a somewhat older age estimate for molluscan shells from the Sud-Sacaco level (latest Miocene, 5.93 Mya, 95% confidence interval = 6.35–5.47 Mya). However, the relative position of the sampled shells and the holotype of *N. platyrostris* in the Sud-Sacaco section is unknown. The associated SAS marine mammal fauna includes the phocids *Acrophoca longirostris* and *Piscophoca pacifica*, two unnamed monachines, the aquatic sloth *Thalassocnus littoralis*, the pontoporiid *Pliopontos littoralis*, the phocoenid *Piscolithax longirostris*, the 'walrus-like' dolphin *Odobenocetops peruvianus*, a new globicephaline delphinid, the cetotheriid *Piscobalaena nana*, and a balaenopterid (*Balaenoptera* sp.) (de Muizon & DeVries, 1985; Bouetel & Muizon, 2006).

MORPHOLOGICAL DESCRIPTION AND COMPARISON

The skeleton of the holotype MNHN SAS 941 has been described and illustrated in detail (de Muizon, 1984). The present description mostly focuses on cranial parts of the referred specimens that are unknown or less well preserved in the holotype, for example the vertex and the facial area, and new interpretations of anatomical features of the holotype in the light of recent fossil ziphiid studies and new observations on extant species (Figs 1–4, 6–13).

Skull

Skull general features: The condylobasal length (cbl) of the holotype was estimated at 960 mm and the bizygomatic is 330 mm (de Muizon, 1984). The basicranium of MNHN SAS 1628 is slightly smaller, as is the facial area of MNHN SAS 1629 (see Table 1). Based on the position of the base of the jugal in MNHN SAS 1628 and the length of the mandible in the holotype, the rostrum length is estimated at 690 mm, about 72% of the cbl, only slightly shorter than in *Messapicetus* spp., the ziphiid with the longest snout (Bianucci *et al.*, 2010). The rostrum is dorsoventrally flattened (Figs 1, 2); the transverse section is 37 mm high and 101 mm wide, 180 mm anterior to the antorbital notch in MNHN SAS 1628. This condition is close to that in *Berardius* or *Tasmacetus*, wider than in *Messapicetus*.

Premaxilla: In MNHN SAS 1628 the left premaxilla is nearly complete above the mesorostral groove

Table 1. Skull measurements (in mm) for the three specimens of *Ninoziphius platyrostris*, MNHN SAS 941 (holotype), MNHN SAS 1628, and MNHN SAS 1629. Additional measurements of the mandibles and vertebrae of the holotype are provided in de Muizon (1984)

Feature	MNHN SAS 941	MNHN SAS 1628	MNHN SAS 1629
Width of rostrum at base	-	e186	-
Longitudinal distance between anterior margin of bony nares and premaxillary foramen (left/right)	e81/e93	80/e86	- /-
Maximum width of premaxillary sac fossae	96	99.5	-
Maximum width of right premaxillary sac fossa	+38	e42	48
Maximum width of left premaxillary sac fossa	+34.5	e35	43
Ratio between left and right premaxillary sac fossa width	-	0.83	0.90
Width of bony nares at level of dorsal margin of mesethmoid	-	e64	51.5
Maximum width of choanae between medial laminae of pterygoids	e85	83	-
Maximum width of nasals	e68	56.5	50
Oblique (anteroventral to posterodorsal) length of suture between nasals	e64	61	e55
Maximum length of suture between frontals on vertex	29	25	22
Minimum distance between maxillae posterior to nasals	e48	-	e47
Bizygomatic width of the skull	e330	e316	-
Maximum distance between lateral margins of basioccipital crests	158	164	-
Maximum distance between lateral margins of exoccipitals	290	-	-
Maximum transverse width of mandibular fossa on the squamosal	38	39	-
Distance between spiny process and anterior end of zygomatic process of squamosal	128	127	-

e, estimate; +, nearly complete; -, missing data.

190 mm anterior to the antorbital notch (Fig. 3). It forms a thin plate that does not reach the sagittal plane of the rostrum. As a consequence, the premaxilla is not thickened above the groove and does not close it mediodorsally, differing from the condition in the *Messapicetus* clade sensu Bianucci *et al.* (2010) and some ziphiines. The small premaxillary foramen is anterior (more than 20 mm) to the antorbital notch, a condition also found in ziphiids possessing a prenarial basin (*Aporotus*, *Beneziphius*, *Messapicetus*, *Ziphirostrum*, and *Ziphius*), in *Pterocetus*, and in some skulls of *Indopacetus*. In addition the posteromedial sulcus is long and deep (Fig. 4); together with the anterior position of the premaxillary foramen this may indicate a preliminary step towards the formation of a prenarial basin. However, the premaxilla is higher than the maxilla from the rostrum base onwards. The premaxillary sac fossae are relatively narrow and elongated, with only a moderate asymmetry (ratio between maximum widths of left and right fossae between 0.83 and 0.91), much lower than in *Hyperoodon*, *Ziphius*, and three extinct taxa (*Choneziphius*, *Globicetus*, and *Tusciziphius*). The anteromedial part of the premaxillary sac fossa, along the posteromedial suclus, is convex, whereas posterolaterally the surface becomes slightly concave, but to a smaller extent than in *Choneziphius*, related extinct taxa (*Globicetus*, *Imocetus*, and *Tusciziphius*), and adult males of *Ziphius*. The elevation of the premaxilla towards the vertex is progressive, with the ascending process not vertical. Fragments of the premaxilla are preserved along the nasal of each specimen. In MNHN SAS 1629, the surface of the premaxilla just lateral to the nasal faces anteromedially on both the right and left sides (Fig. 4). Additionally the crest is anteroposteriorly thin in its medial portion. These observations strongly suggest that the unswollen premaxillary crest was originally directed anterolaterally (Fig. 1B), as in members of the *Messapicetus* clade and in ziphiines, differing from the transversely directed crest of *Berardius* and *Tasmacetus* and from the posterolaterally directed crest of *Hyperoodon*, *Indopacetus*, and *Mesoplodon*. The premaxillary crest contacts the nasal in its posterolateral corner, a condition only seen in members of the *Messapicetus* clade and in ziphiines (linked to the shape of the nasal, see below).

Maxilla: At least on the proximal half of the rostrum the maxilla is wider than the premaxilla in dorsal view (Fig. 2A), as in *Tasmacetus*. The widening of the rostrum towards the antorbital notch is progressive, less abrupt than in *Berardius* and *Tasmacetus*. One major dorsal infraorbital foramen is present along the

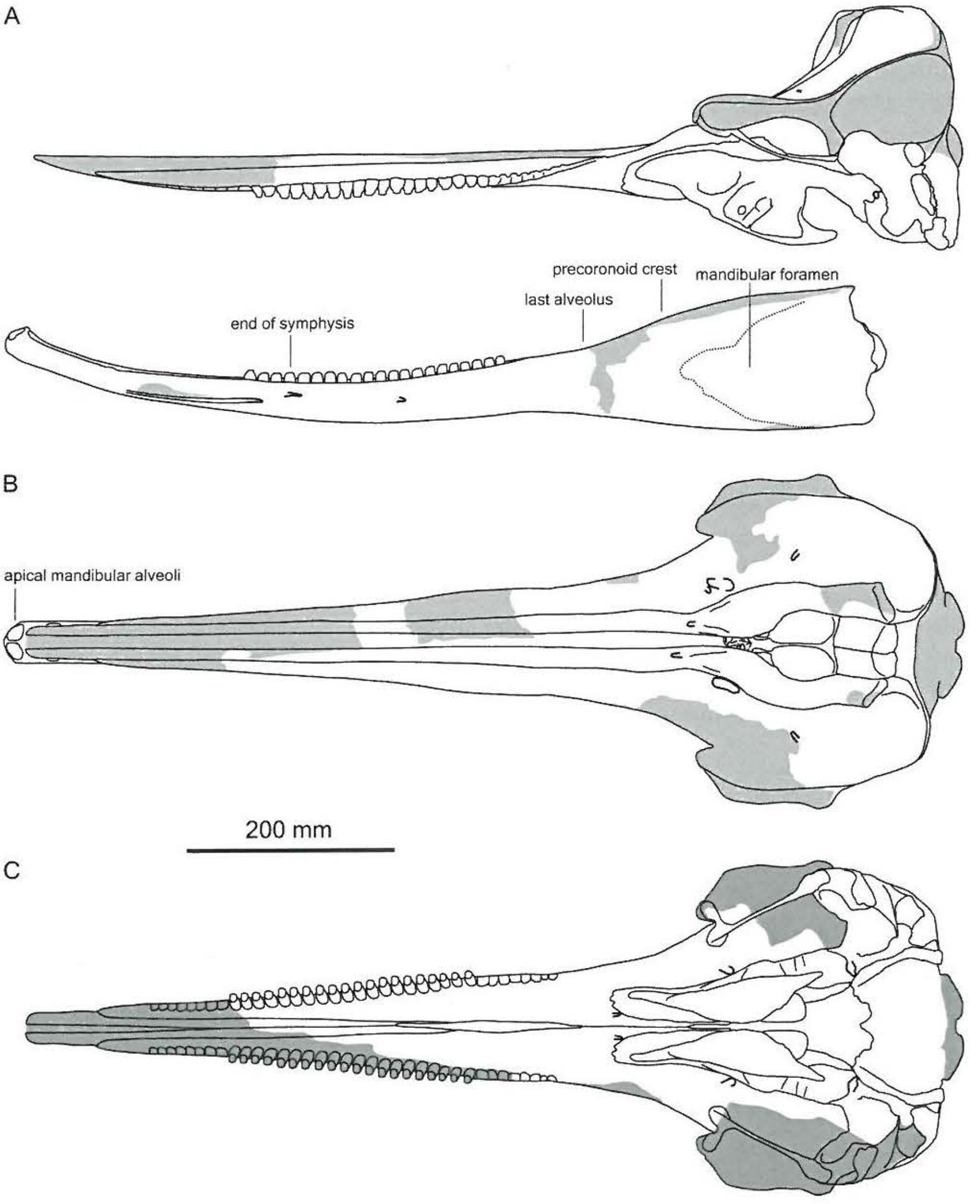


Figure 1. Reconstruction of the skull and mandibles of *Ninoziphius platyrostris* based on the three specimens MNHN SAS 941 (holotype), MNHN SAS 1628 (N3), and MNHN SAS 1629 (N2): A, left lateral view of skull and mandible; B, dorsal view of skull and mandibles; C, ventral view of skull. Shaded areas indicate missing parts. The outline of the mandibular foramen (dotted line) is only visible in medial view.

maxilla–premaxilla suture, as in many extant ziphiids, possibly with a smaller secondary foramen. The large foramen is posterior to the premaxillary foramen. The supraorbital area, partly preserved in MNHN SAS 1628, reveals a roughly flat dorsal surface, with no clue as to the presence of a maxillary crest or rostral maxillary crest; the area around the antorbital notch is more elevated in *Berardius*, *Hyperoodon*, *Tasmacetus*, and several fossil ziphiids (e.g. *Africanacetus* and *Imocetus*).

The presence of deep maxillary alveoli for a complete set of upper teeth is confirmed in MNHN SAS 1628 (Fig. 6), a condition only observed in *Messapicetus* and *Tasmacetus*; remains of upper alveoli occasionally occur in other fossil taxa, for example *Choneziphius* spp. or *Ziphirostrum marginatum*, but they are always shallower (Lambert, 2005c). The alveoli are distinctly shorter anteroposteriorly than in *Messapicetus* and are instead more similar to those in *Tasmacetus*. The upper tooth count is estimated

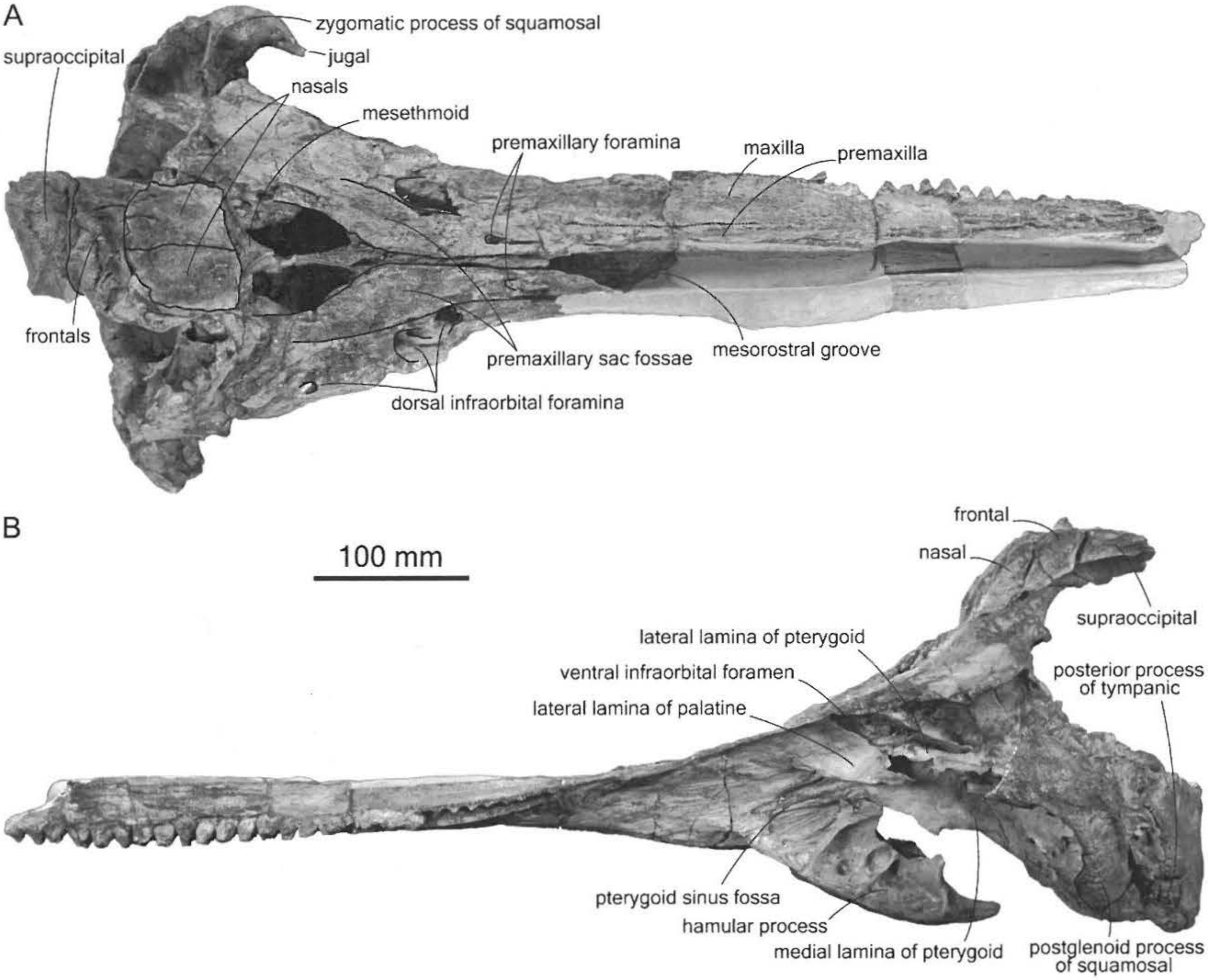


Figure 2. Skull of *Ninoziphius platyrostris* MNHN SAS 941 (holotype): A, dorsal view; B, left lateral view.

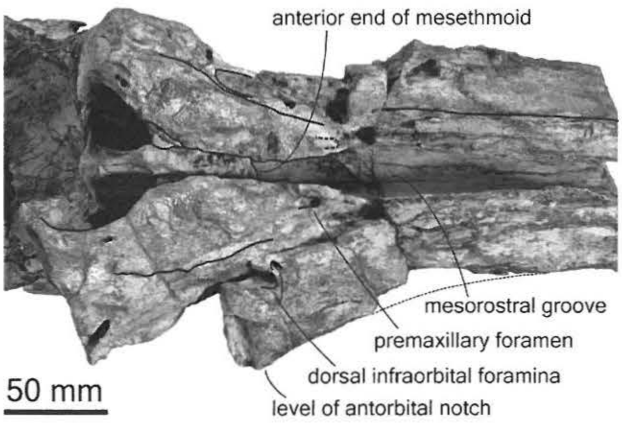


Figure 3. Facial area and rostrum base of *Ninoziphius platyrostris* MNHN SAS 1628 in dorsal view.

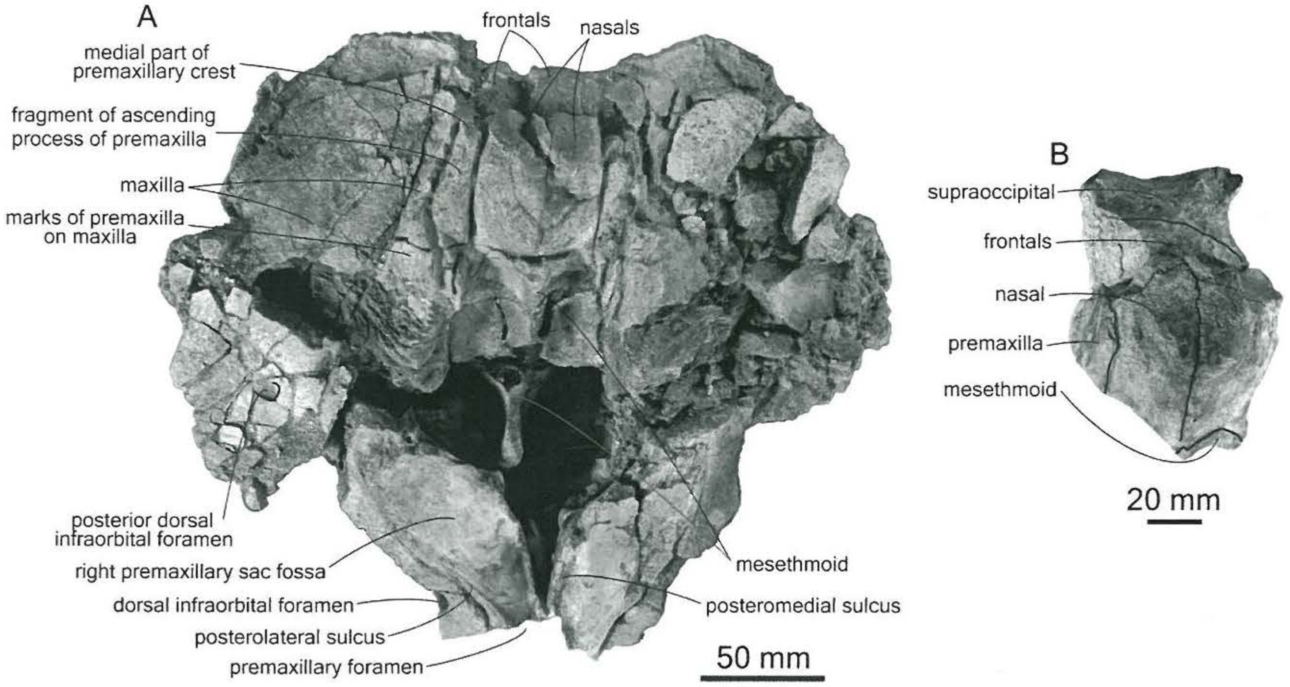


Figure 4. A, facial area and vertex of *Ninoziphius platyrostris* MNHN SAS 1629 in dorsal view. B, vertex of *N. platyrostris* MNHN SAS 1628 in dorsal view.

at 40 in *Ninoziphius* (de Muizon, 1984), higher than in *Tasmacetus* (17–21; Mead & Payne, 1975) and *Messapicetus* (26–27 in *Messapicetus longirostris*; Bianucci, Landini & Varola, 1994). The last posterior alveolus is 95 mm anterior to the level of the antorbital notch in MNHN SAS 1628; in the less complete holotype the distance may be greater, possibly indicating a shorter alveolar groove. The alveolar groove is considerably shorter posteriorly in *Tasmacetus*; the lateral margin of the rostrum rises at a more anterior level towards the height of the antorbital notch in the latter, leaving a higher space for the elevated dorsal margin of the mandible (see comparison below, precoronoid crest sensu Fordyce, Quilty & Daniels, 2002).

Vomer: The thin vomer covers the walls of the mesorostral groove in the holotype and MNHN SAS 1628 (Figs 2A, 3); it is also not thickened at the rostrum base in MNHN SAS 1629. Therefore, even though the possibility that the three specimens are females cannot be ruled out, we consider that the mesorostral groove was not filled by the pachyosteosclerotic vomer in *Ninoziphius* (de Muizon, 1984; Lambert, de Buffrénil & de Muizon, 2011), differing from adult males of *Mesoplodon*, *Ziphius*, and extinct related taxa.

Mesethmoid: The mesethmoid is ossified from the level of the antorbital notch in MNHN SAS 1628 (Fig. 3) and probably the holotype (not fully prepared). In many specimens of *Berardius*, the ossified but spongy mesethmoid partly fills the mesorostral groove (Bianucci *et al.*, 2007; Lambert, de Buffrénil & de Muizon, 2011).

Nasal: The dorsal exposure of the nasals on the vertex is made up of a posterior triangular, flat, and subhorizontal surface, separated by a distinct angle from the roughly rectangular anterodorsally facing anterior surface. The latter makes up two thirds of the bone in dorsal view (Figs 2, 4). The posterior triangle lacks any medial or anteromedial depression; it is much shorter than in *Berardius*, *Tasmacetus*, and *Ziphius*, and more similar to members of the *Messapicetus* clade (e.g. *Beneziphius*, *Messapicetus*, and the possibly related *Aporotus dicyrtus*; Fig. 5). As mentioned above this similarity is further supported by the posterolaterally located contact with the premaxillary crest, also observed in *Choneziphius*. The anterodorsal surface is high and slopes steeply anteroventrally. The medial suture between the nasals is distinctly shifted posterolaterally to the left side compared to the sagittal plane.

Frontal: A strip of frontals, nearly as long as the posterodorsal triangular surface of the nasals, separates the nasals from the supraoccipital (Figs 2A, 4). No rounded protuberance made up of the frontals or

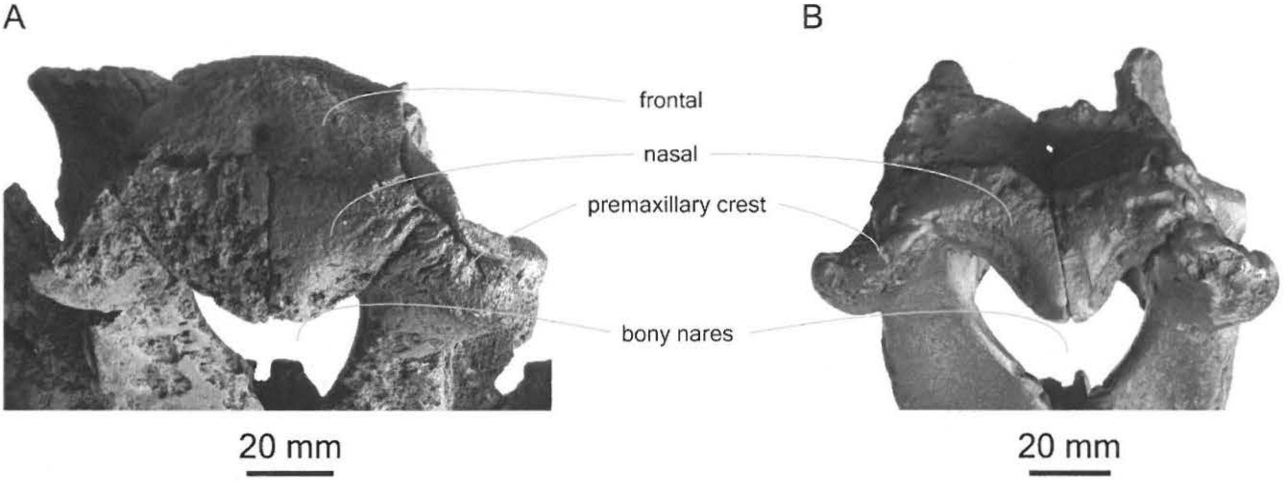


Figure 5. Vertex of the skull of two fossil ziphiids from the Neogene of the North Sea in dorsal view: A, *Aporotus dicyrtus* IRSNB M.541; B, *Beneziphius brevirostris* IRSNB M.1885, displaying the contact of the premaxillary crest with the posterolateral corner of the short nasal.

the interparietal is observed in this area, differing from *Berardius* and related extinct taxa. This posterior part of the vertex is less transversely compressed than in *Tasmacetus* (the condition in *Berardius* is variable). No informative frontal element of the orbit roof was preserved in any specimen and the preservation state of the roof of the temporal fossa in MNHN SAS 1629 does not provide precise information about its outline. The fossa is completely covered dorsally by the frontal and the maxilla, as in all other ziphiids.

Supraoccipital: The supraoccipital sends a wide and 25–30 mm long projection between the maxillae until the vertex (Fig. 4), reaching the same vertical level as the frontals and nasals on the vertex. This condition contrasts with the lower supraoccipital in *Berardius* and related extinct taxa.

Palatine: In MNHN SAS 1628 the anterior end of the palatine is 81 mm anterior to the antorbital notch (Figs 6, 9). As in the holotype the medial suture with the maxilla is more easily distinguished than the lateral limit of the much thinner lateral part of the palatine. The palatine is 25–30 mm longer than the pterygoid, which does not contact the maxilla anteriorly. Such a pterygoid–maxilla contact is occasionally observed in most extant ziphiids, including *Berardius*, *Indopacetus*, and *Tasmacetus*. The fossa for the hamular lobe of the pterygoid sinus is limited laterally by a thin lamina rising posteriorly to a maximum height slightly posterior to the level of the antorbital notch (Figs 6, 7, 9). This anterior part of the lateral lamina, somewhat higher than in most other ziphiids, is interpreted here as made up by the sole palatine. A similar condition is for example observed in *Berardius*, with the pterygoid barely involved in the anterior part of the lateral lamina. Similar to other ziphiids this lateral lamina of the palatine ends before the level of the frontal groove. The palatine is extremely thin in the fossa for the hamular lobe, and in some parts of the fossa the maxilla is possibly exposed. In the bony nares, two main foramina presumably pierce each palatine (limits of bones are difficult to identify in this area). The foramen on the anterior wall of the naris may be the posterior palatine foramen, located on the ethmoidal crest of the palatine sensu Mead & Fordyce (2009). In MNHN SAS 1628, this foramen exits on the medial wall of the large dorsal infraorbital foramen. The second foramen, located on the lateral wall of the naris and exiting on the medial wall of the ventral infraorbital foramen, is likely to be the sphenopalatine foramen (see Mead & Fordyce, 2009; additional dorsal exit for infraorbital complex mentioned by Rommel, 1990 for *Tursiops*; possibly homologous to the 'blind pit' identified in the vomer of *Berardius arnuxii* by MacCann, 1975).

Pterygoid: As observed in all the known ziphiids, the fossa for the hamular lobe of the pterygoid sinus is wide, extending anteriorly on the palatal surface of the rostrum and ventrally close to the ventral limit of the basicranium (Figs 2, 7). Considering the extent of the preserved portion of the pterygoid on the floor of the wide and long fossa for the hamular lobe of the pterygoid sinus and the marks of the pterygoid sutures in the fossa of both the holotype and MNHN SAS 1628 (Figs 2B, 6, 7), it is likely that the pterygoid did not completely cover the fossa in *Ninoziphius*. Large parts of the palatine or maxilla were probably

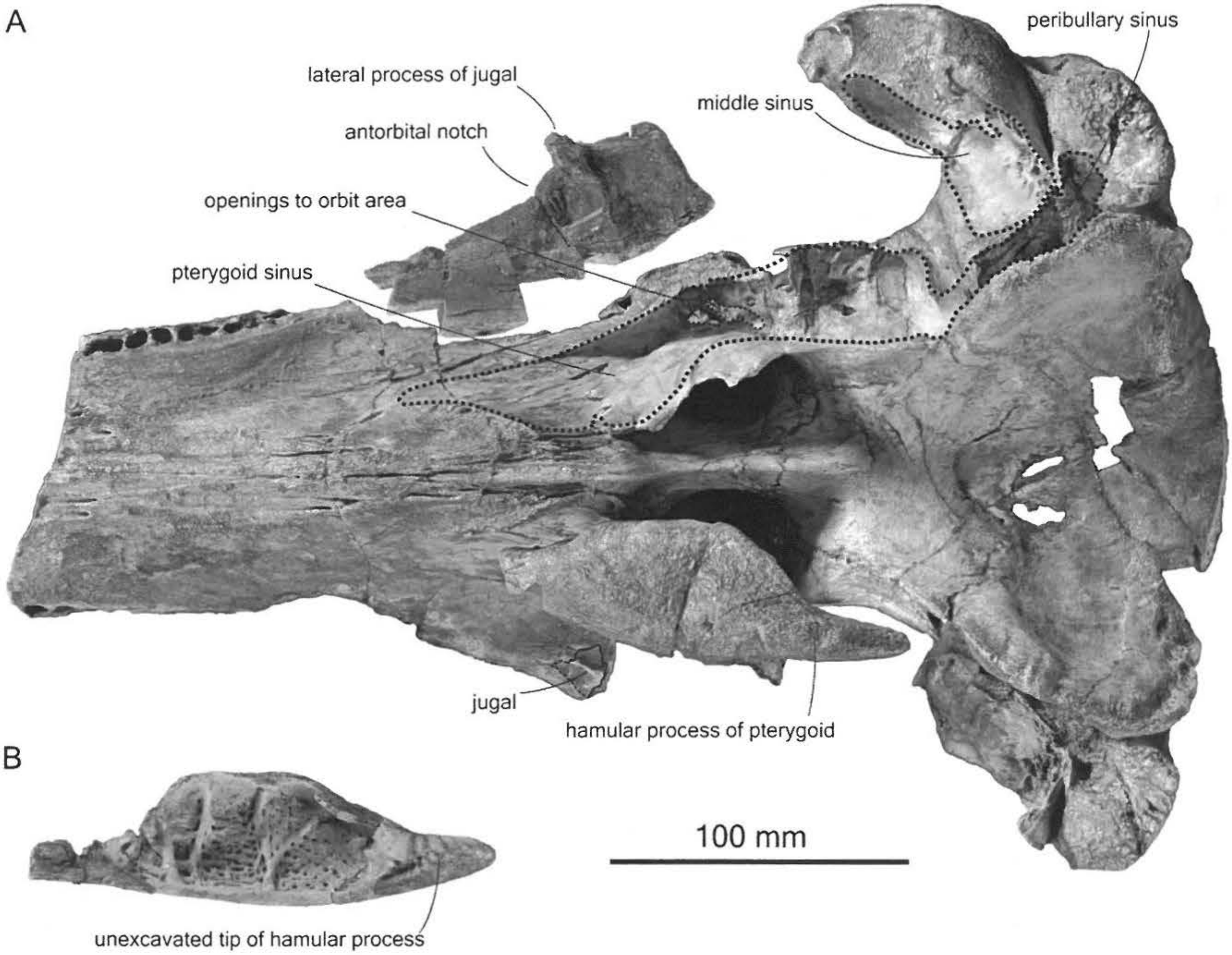


Figure 6. A, skull of *Ninoziphius platyrostris* MNHN SAS 1628 in ventral view; B, detached left hamular process of the pterygoid of MNHN SAS 1628 in dorsolateral view.

exposed (see above). Small fenestrae occur in the fossa in many extant ziphiids, but the condition in *Ninoziphius* is especially similar to some specimens of *Berardius bairdii* (e.g. USNM 49725) and to the archaic odontocete *Squaloziphius*, in which most of the anterior part of the fossa is not covered by the pterygoid.

As described for the holotype by de Muizon (1984), the hamular process of the pterygoid is robust in MNHN SAS 1628 (Fig. 6). It is even slightly thicker and longer than in the holotype. The inner surface of the bone is similarly buttressed by a series of transverse crests (Figs 7, 8B), a feature rarely seen in extant ziphiids (e.g. *Indopacetus pacificus*, see USNM 593534 and Dalebout *et al.*, 2003; a few specimens of *Ziphius cavirostris*, see Omura, 1972>). It is interesting to note that very similar transverse crests were observed in the fossa for the hamular lobe of the pterygoid sinus during a dissection of a skull of *Z. cavirostris* (Cranford *et al.*, 2008: fig. 12; Fig. 8A); in this case the crests proved to be made up of soft, connective tissue, not bone (T. W. Cranford, pers. comm., 2012). Transverse bony crests are also observed in some delphinids (e.g. *Delphinus* and *Tursiops*). In MNHN SAS 1628, the surface between the crests is made of a peculiar type of bone, a network of intermingled fibres forming a lot of small cavities (Fig. 8B), more conspicuous than in the holotype. This unusual organization of the bone is reminiscent of the soft tissue fibrous venous plexus described lateral to the pterygoid sinus in the same region in *Z. cavirostris* (Cranford *et al.*, 2008: fig. 12; Fig. 8A). The apex of the hamular process is more posteriorly extended in ventral view than in extant ziphiids and *Messapicetus*. It is not completely excavated by the fossa for the hamular lobe of the pterygoid sinus, a presumably primitive feature (see phylogeny below), differing from all ziphiids for which this area is preserved,

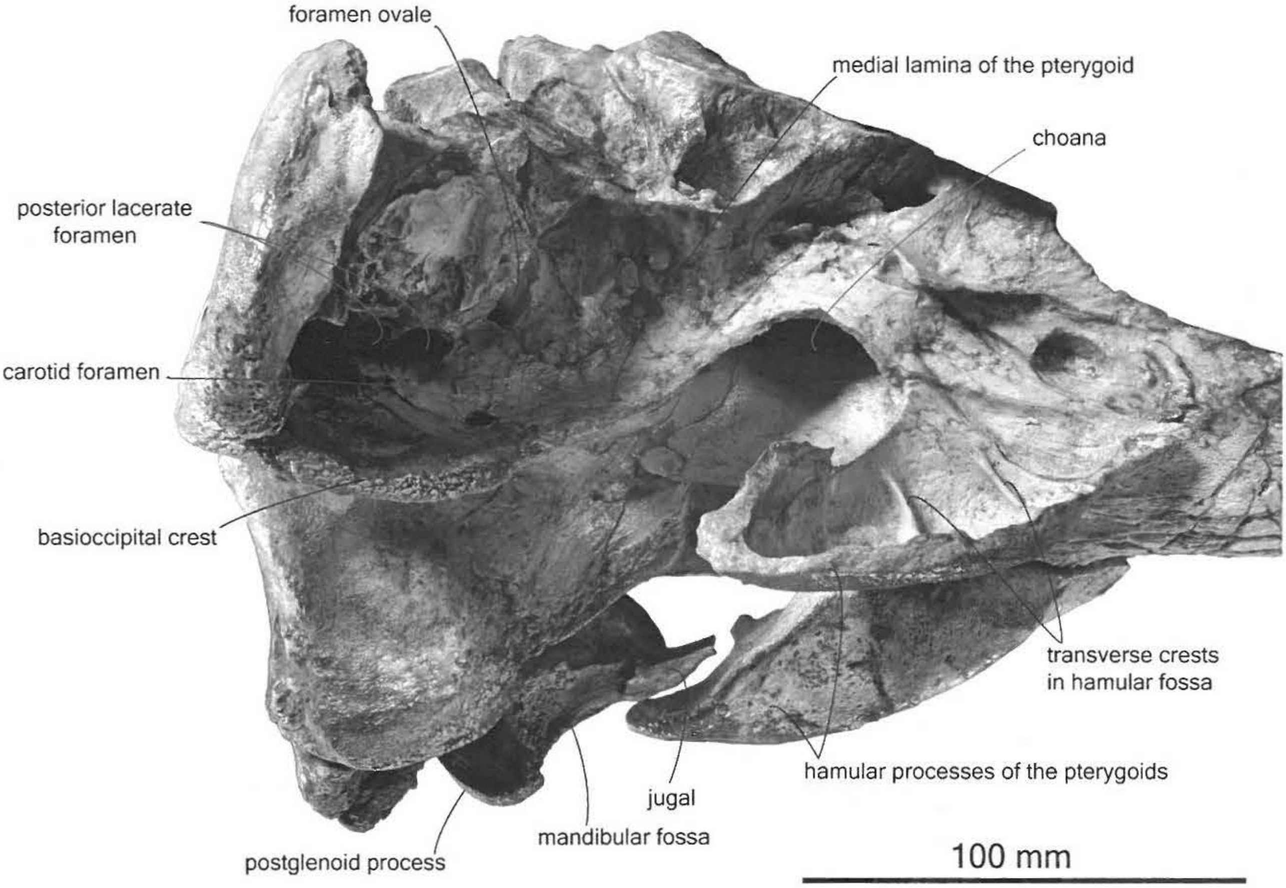


Figure 7. Cranium of *Ninoziphius platyrostris* MNHN SAS 941 (holotype) in right ventrolateral view. The right squamosal, most of the right supraorbital region, and the apex of the right hamular process are missing.

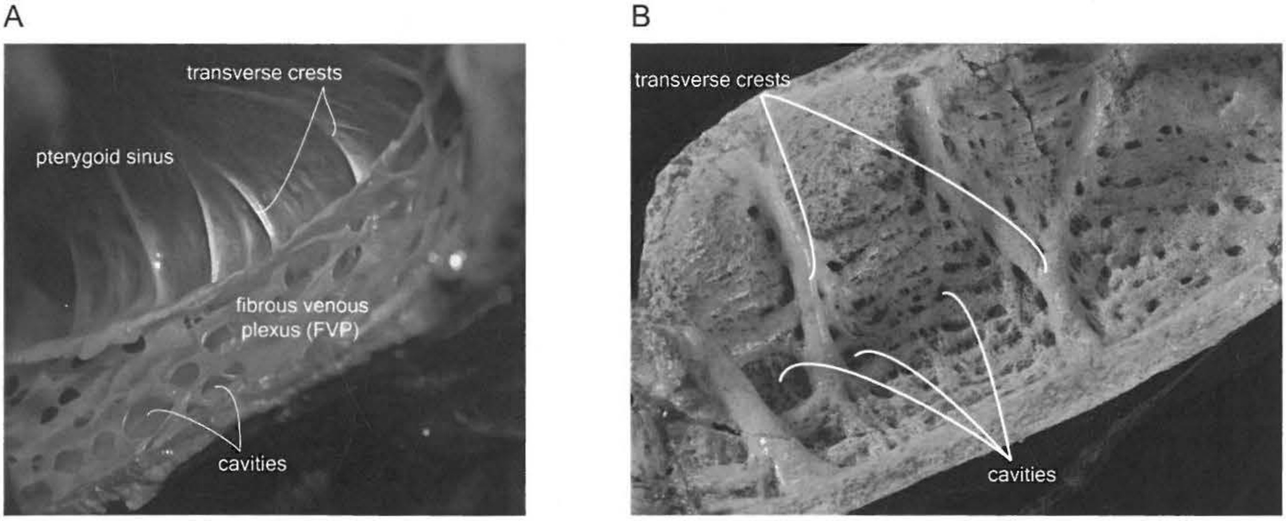


Figure 8. Comparison of the hamular region in *Ziphius cavirostris* and *Ninoziphius platyrostris*: A, gossamer-like trabeculae in the fibrous venous plexus of the hamular region of *Z. cavirostris*, with soft tissue transverse crests on the medial wall of the pterygoid sinus fossa, modified from Cranford *et al.* (2008; courtesy of T. W. Cranford); B, detail of the surface of the left pterygoid of *N. platyrostris* MNHN SAS 1628 on the medial wall of the fossa for the hamular lobe of the pterygoid sinus, with bony transverse crests and numerous small cavities.

including *Messapicetus*, *Nazcacetus*, and possibly *Archaeoziphius*. The unexcavated part of the process is even somewhat longer in MNHN SAS 1628 than in the holotype; it is somewhat reminiscent of the morphology of the process in some delphinids (e.g. *Globicephala*, see Fraser & Purves, 1960: pl. 34). The apex is similarly unexcavated and finger-like in some eurhinodelphinids, *Argyrocetus joaquinensis*, *Simocetus*, and *Squaloziphius* (Kellogg, 1932; de Muizon, 1991; Fordyce, 2002), but in these taxa left and right apices are near each other, instead of divergent as in *Ninoziphius* and other ziphiids. Consequently the posterior margin formed by the joined right and left apices is concave in *Ninoziphius*. As in *Messapicetus* and *Tasmacetus*, it is V-shaped, whereas it is U-shaped in all other extant ziphiids.

Posterior to the lateral lamina of the palatine, the outer margin of the pterygoid sinus fossa is made up of the low and thin lateral lamina of the pterygoid. Here again the bone is buttressed by transverse crests (Fig. 9), a feature also observed in *Indopacetus* USNM 593534, separating areas where the fossa deepens dorsally. The reduced lateral lamina of the pterygoid does not contact the short falciform process of the squamosal, a condition also observed in other ziphiids, physeteroids, *Squaloziphius*, and *Simocetus*. *Ninoziphius* differs in this respect from the platanistoids, *Pontoporia*, and at least some eurhinodelphinids, in which the lateral lamina of the pterygoid is continuous with the falciform process of the squamosal. Posteromedial to the ventral infraorbital foramen, the dorsolateral surface of the pterygoid is pierced by a series of small fenestrae (three on the left side of MNHN SAS 1628 and at least three on the partly prepared left side of the holotype), connecting the pterygoid sinus fossa with the orbit just anterior to the frontal groove (Figs 6, 9). These fenestrae probably correspond to extensions of the pterygoid sinus in the orbit region, a feature previously unknown in ziphiids (see Fraser & Purves, 1960). The invasion of the orbit by the pterygoid sinus has been detected in *Inia*, *Pontoporia*, delphinids, phocoenids, and eurhinodelphinids (Fraser & Purves, 1960; de Muizon, 1988, 1991; Lambert, 2005a). The condition in *Ninoziphius* may correspond to a preliminary step towards the development of a fossa for the preorbital lobe of the pterygoid sinus as observed in many delphinidans and later lost in other ziphiids. Alternatively, this condition may have evolved independently from other odontocete lineages.

Posteriorly the dorsal lamina of the pterygoid partly covers the alisphenoid (Fig. 9). In most extant ziphiids, except *Tasmacetus* and some specimens from other taxa, the alisphenoid is more extensively covered, sometimes completely hidden in ventral view, and the pterygoid in *Ninoziphius* probably represents the primitive condition, as observed in *Simocetus* and possibly in *Archaeoziphius*.

Jugal–lacrimal: In addition to the well-preserved and slender styliform part of the jugal in the holotype, the anterior part of the bone is partly preserved in MNHN SAS 1628 (Fig. 6). It displays a long, lateral projection that corresponds either to a part of the wide lateral process of the jugal seen in other ziphiids, *Squaloziphius*, and *Eurhinodelphis* ('ventroposterior projection of the jugal', Lambert, 2005b; preferred hypothesis), or to a part of the lacrimal partly fused to the jugal, as proposed for the delphinid *Tursiops* by Mead & Fordyce (2009). Obviously, in taxa in which the lacrimal and jugal are fused, it is difficult to distinguish the contribution of each bone to the general shape of the complex.

Alisphenoid: Ventrally the exposed surface of the alisphenoid displays a distinct concavity directed anteroventrally, corresponding to the pterygoid sinus fossa (Figs 6, 9). A thin and high crest separates this concave area from the large foramen ovale posteriorly. The latter is completely included in the alisphenoid. The foramen ovale opens anterolaterally, but another large foramen, dorsally joined to the foramen ovale as seen in the cerebral cavity (Fig. 10), exits posteroventrally. In extant ziphiids the posteroventral foramen is sometimes smaller and/or not completely separated from the foramen ovale (e.g. *Mesoplodon stejnegeri* USNM 504330). It might correspond to a part of the posterior lacerate foramen, the path for some of the cranial nerves and vessels. More generally, the topology of the foramina of the basicranium differs in larger ziphiid species, probably because of differences in proportions (larger bones and relatively smaller foramina in *Berardius* or *Hyperoodon*). The path for the mandibular nerve V3 is a wider sulcus than in *Archaeoziphius*. The carotid foramen is located in the alisphenoid or the basisphenoid, along the suture with the medial lamina of the pterygoid.

Squamosal: As in all other ziphiids, the zygomatic process of the squamosal is elevated, anteriorly short, and robust (Figs 1A, 2B). The surface of articulation for the jugal is a well-marked oval depression. The mandibular fossa (= glenoid cavity) is wide (Fig. 9), more so than in *Archaeoziphius*; its medial part overhangs the deep tympanosquamosal recess, with a slender, spine-shaped posteromedial projection only observed in MNHN SAS 1628. The tympanosquamosal recess (for the middle sinus) extends anteriorly near the end of the zygomatic process and deeply excavates the medial surface of the postglenoid process. The latter is therefore transversely narrow in ventral view, as in other ziphiids, but narrower than

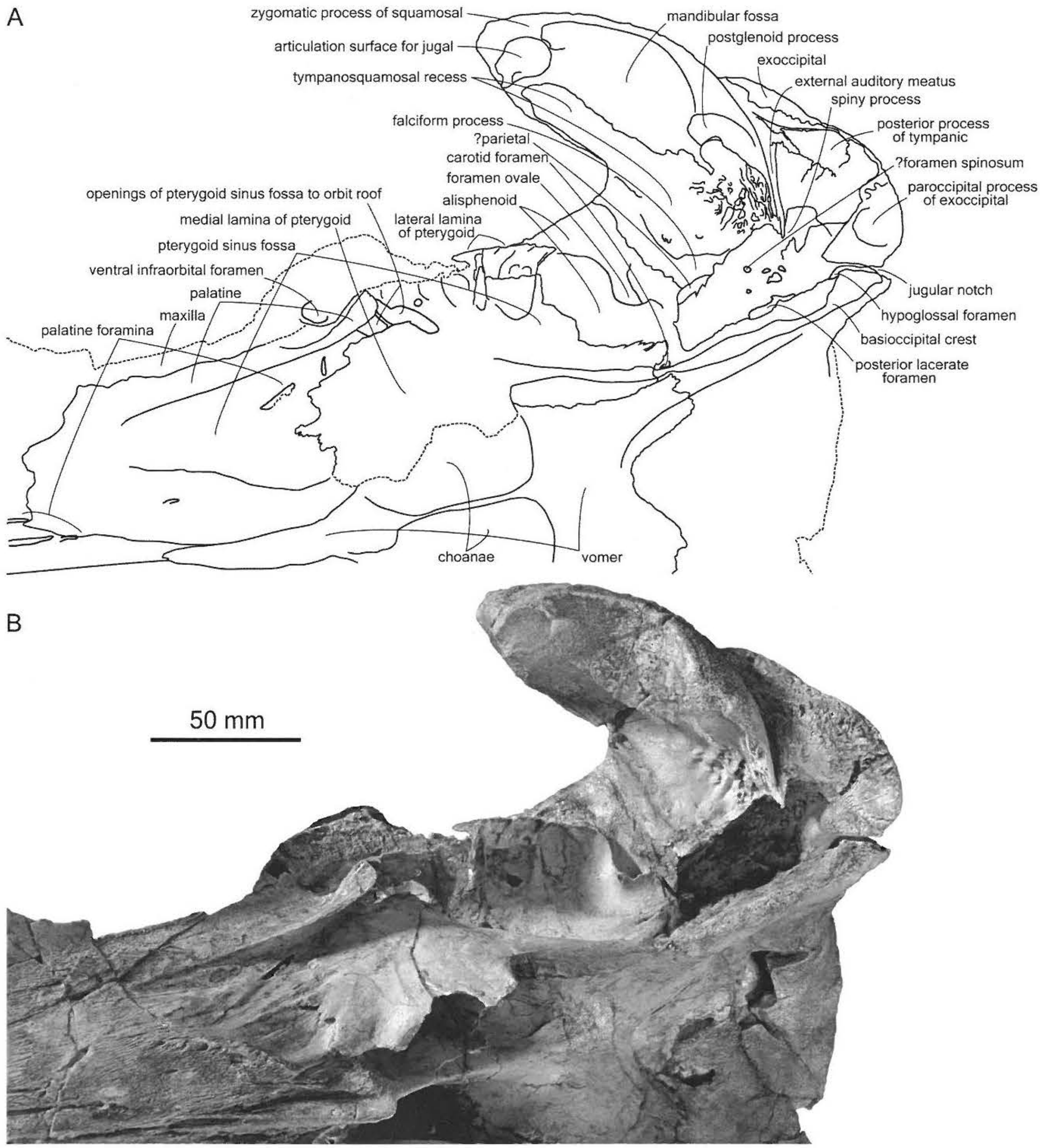


Figure 9. Basicranium of *Ninoziphius platyrostris* MNHN SAS 1628 in ventral to slightly ventrolateral view: A, line drawing; B, corresponding photograph.

the large, bulging process in *Squaloziphius*, and, to a lesser extent, in eurhinodelphinids, despite the similarities with the latter in lateral view. Furthermore, as in all other ziphiids, and differing from *Squaloziphius*, the ventral margin of the postglenoid process is clearly more dorsal than the ventral margin of the paroccipital process of the exoccipital (Fig. 2B). The surface of the posterior part of the tympanosquamosal recess has numerous pits and crests. These are common but variable in other ziphiids and various odontocetes. Medial to the recess is the short and thin remainder of the falciform process. This is under

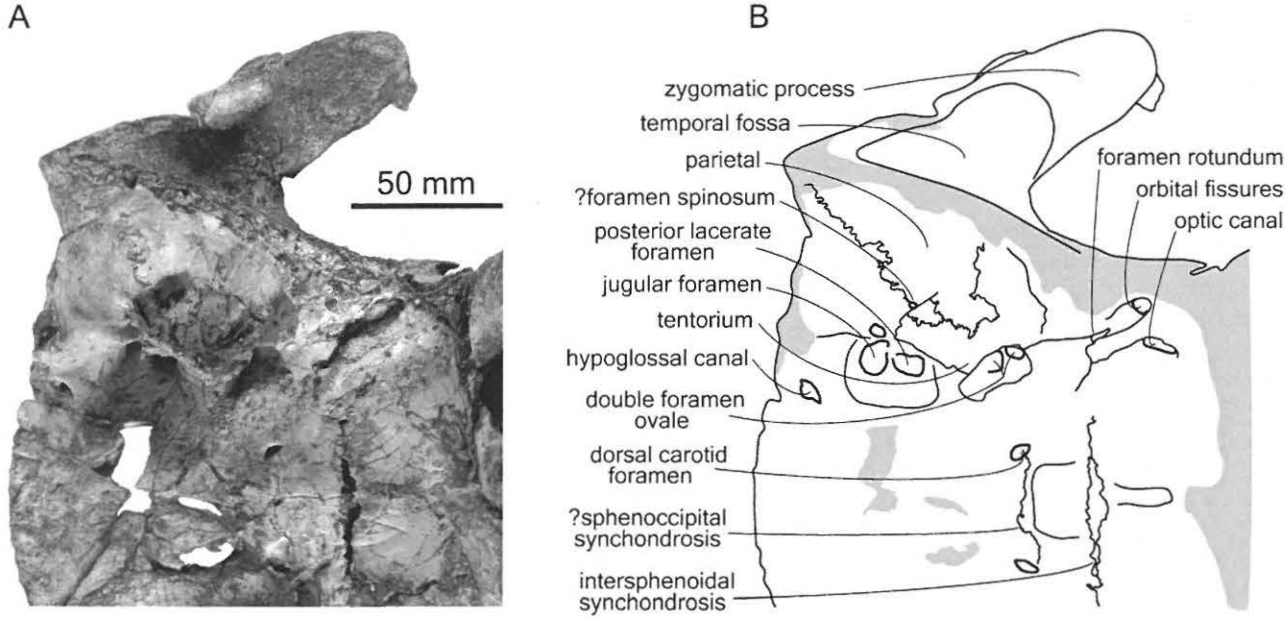


Figure 10. Cerebral cavity of *Ninoziphius platyrostris* MNHN SAS 1628: A, dorsal view (supraoccipital and vertex detached); B, corresponding line drawing. Shaded areas indicate missing parts.

10 mm long (Fig. 9) and not as developed as the long, rod-like process displayed by various extant ziphiids and *Nazcacetus*. Anteromedial to the spiny process is a small foramen probably corresponding to the foramen spinosum sensu Fordyce (1994).

Exoccipital: As in other ziphiids (Fraser & Purves, 1960), the anterior surface of the paroccipital process of the exoccipital does not bear any fossa for the posterior sinus. The large hypoglossal foramen is located in the jugular notch. The jugular foramen is not completely separated from the posterior lacerate foramen, and at least two to three smaller foramina are lateral to these two foramina in both the holotype and MNHN SAS 1628 (Fig. 9).

Tympanic bulla: In ventral view the inner posterior prominence is much narrower than the outer prominence, and slightly shorter posteriorly (Fig. 11B). The inner prominence is proportionally wider in *Berardius*, *Tasmacetus*, the eurhinodelphinid *Eurhinodelphis cocheteuxi*, and archaic odontocetes like *Albertocetus* (see Uhen, 2008), whereas other eurhinodelphinids (e.g. *Schizodelphis*, *Xiphiacetus*) and ziphiids, including *Indopacetus* and *Messapicetus*, display a narrow inner prominence. In *Hyperoodon* and *Ziphius* the inner prominence is even more reduced, being much shorter posteriorly. The ventral groove is deep and narrow, ending roughly at the mid-length of the bone; it is deeper than in *Hyperoodon* and *Tasmacetus*, being instead more similar to *Messapicetus* and eurhinodelphinids like *Xiphiacetus*. The ventral groove is virtually absent in the related eoplatanistids (de Muizon, 1988c). In ventral view the anterior margin of the bone is nearly rectilinear, and no individualized anterior spine can be detected, contrary to what the medial view suggests. The dorsal margin of the involucrum is cut by an indentation at about one third of its length (Fig. 11C). As in most ziphiids this indentation is better seen in dorsal view, whereas in eurhinodelphinids and some other archaic odontocetes it is more distinct in medial view. The anterior part of the involucrum is higher in *Hyperoodon* and *Tasmacetus*. Here again, the closest form is *Messapicetus*. In lateral view, the posterior margin of the sigmoid process is rectilinear and roughly perpendicular to the long axis of the bone (Fig. 11A). In other ziphiids, including *Messapicetus* and *Nazcacetus*, the posteroventral margin of the process is posteriorly projecting. In eurhinodelphinids and eoplatanistids this posterior margin is also perpendicular to the long axis of the tympanic, as in *Ninoziphius*, but the sigmoid process is ventrally shorter than in the latter and in other ziphiids.

Between the posterior meatal crest of the squamosal and the paroccipital process of the exoccipital, a prominent and rounded bony part (Fig. 9) is interpreted, following de Muizon (1984) and contrary to a comment in Bianucci *et al.* (2010), as the enlarged posterior process of the tympanic bulla, partly fused with elements of the post-tympanic process of the squamosal, and possibly parts of the exoccipital

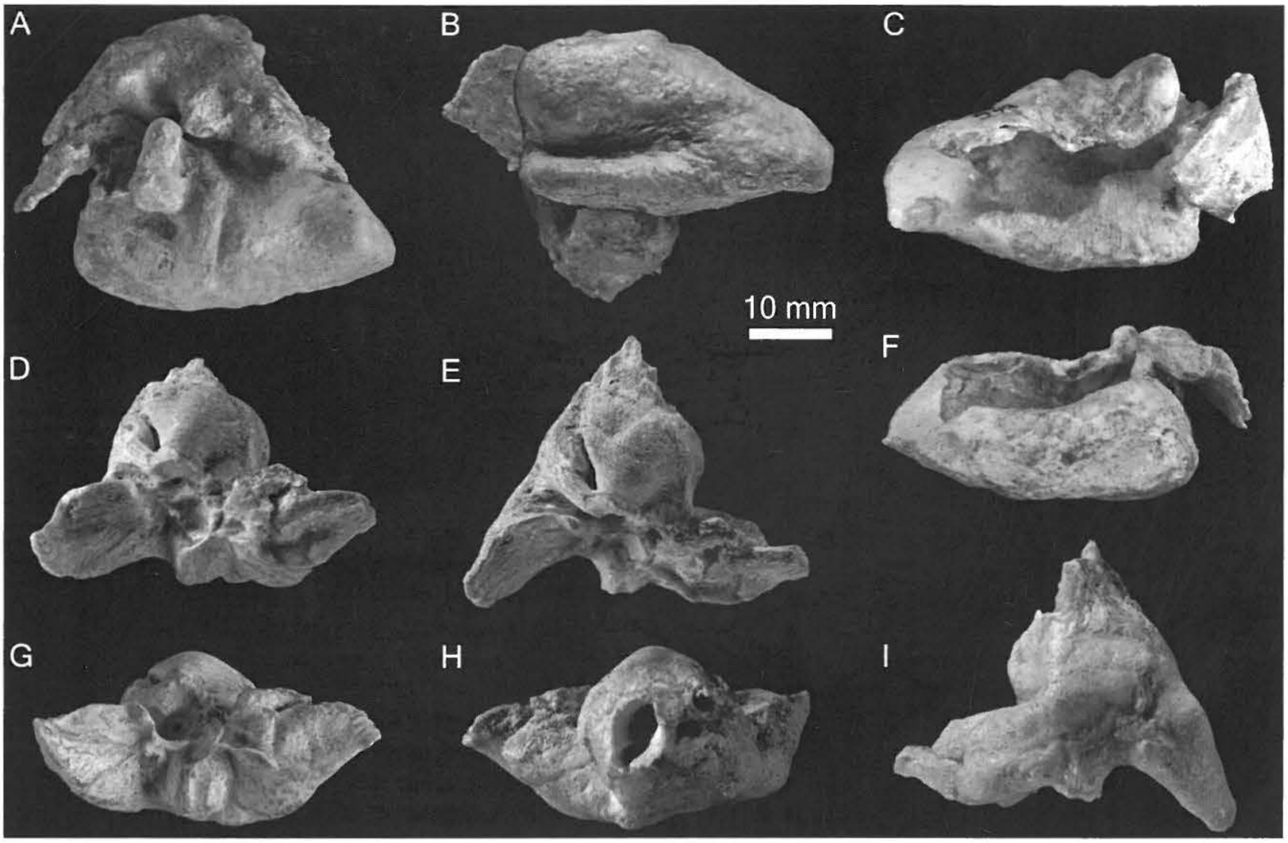


Figure 11. Right ear bones of *Ninoziphius platyrostris* MNHN SAS 941 (holotype). Periotic and tympanic in lateral (A) and ventral (B) view; tympanic in dorsal (C) and medial (F) views; periotic in ventral (D), medioventral (E), lateral (G), medial (H), and dorsal (I) views.

(= mastoid process, see Fraser & Purves, 1960). Even though, as in other ziphiids, the limits of this process are difficult to define, its size is not distinctly smaller than in similarly sized extant ziphiids. Such an enlarged posterior process could not be detected in *Squaloziphius*. It is also important to note that the proximal part of the posterior process (which bears the facet for the articulation with the periotic) in the holotype of *Ninoziphius* does not differ significantly from the process in odontocetes that lack the enlarged distal portion: the facet for the posterior process of the periotic is smooth and the posteroventral margin is thin and regular, displaying no clue as to the presence of a large distal part. In fact, in Recent ziphiids, the transition between the articular proximal portion of the posterior process and the distal spongy portion is a thin bridge of bone that breaks easily; thus, there is little chance of discovering an isolated tympanic of a fossil ziphiid that still bears the distal portion of the posterior process. Therefore, isolated tympanics are unlikely to be of use in proving the absence of an enlarged posterior process, and the contribution of the tympanic to this 'mastoid process' (versus the contribution of the squamosal and the exoccipital) should be further investigated, for example with ontogenetic series of extant ziphiids.

Periotic: As in *Messapicetus*, and differing from all other ziphiids including *Berardius*, *Nazcacetus*, and *Tasmacetus*, in ventral view the anterior process of the periotic is barely wider (Fig. 11D) than in eurhinodelphinids, eoplatanistids, *Waipatia*, and other archaic odontocetes. In medial view, the anterior process of *Messapicetus* and *Ninoziphius* is also distinctly more slender (Fig. 11H) than in other ziphids; the anterodorsal angle is less bulging. The size and shape of the accessory ossicle are similar to those of large eurhinodelphinids (e.g. *E. cocheteuxi*), *Messapicetus*, and *Mesoplodon* spp., and smaller and less spherical than in *Berardius*, *Nazcacetus*, *Hyperoodon*, *Tasmacetus*, and *Ziphius*. In ventral view the lateral tuberosity is distinctly transversely shorter than in all other ziphiids, apart from *Messapicetus* (Bianucci *et al.*, 2010). Here again, the condition is considered as primitive (see phylogeny below), shared with many other odontocete groups including eurhinodelphinids, eoplatanistids, and *Waipatia*. As described by de Muizon (1984), a large cochlear spine posterodorsal to the internal auditory meatus is one of the main features of the periotic of *Ninoziphius* (Fig. 11E). A spine has been observed in specimens of *Berardius* (de Muizon, 1984; *Berardius arnuxii* ZMA 21007), and, even though shorter, in some eurhinodelphinids (see *E. cocheteuxi*; Lambert, 2005b) and in *Monodon*. It is absent in known specimens of *Messapicetus* and *Nazcacetus*. The outline of the posterior bullar facet of *Messapicetus* and *Ninoziphius* in ventral view is clearly less rounded and less fan-shaped than in other ziphiids, including *Nazcacetus*, and is instead more similar to eurhinodelphinids and eoplatanistids because of the longer posteroventral tip of the posterior process. However, the posterior bullar facet is more regularly posteroventrally curved (= longitudinally concave) in *Messapicetus* and *Ninoziphius* than in eurhinodelphinids. Furthermore, as in most other ziphiids, the posterior process of *Messapicetus* and *Ninoziphius* lacks a distinct and complete dorsal keel, a feature observed in many eurhinodelphinids and eoplatanistids. Finally, the dorsal and dorsolateral surfaces of the process are smooth in these two fossil ziphiids, as in all other ziphiids, whereas they are rough and pitted in eurhinodelphinids and eoplatanistids, for which a more extensive bony contact with the squamosal and possibly the exoccipital is suggested.

Basioccipital: In ventral view the basioccipital crests are more posteriorly diverged in MNHN SAS 1628 (Fig. 6) than in the holotype (angle between the crests about 60 and 45°, respectively). The condition in *Ninoziphius* is therefore intermediary between taxa with a wide basioccipital basin (most ziphiids except *Messapicetus*, *Squaloziphius*, and *Waipatia*) and those with a narrower basin (eurhinodelphinids).

Cerebral cavity: Owing to the peculiar preservation state of the specimens, the floor and anterior wall of the cerebral cavity of the holotype and MNHN SAS 1628 could be observed (Fig. 10). However, the lack of comparative material prevented a complete analysis; for now this area is only compared to *Mesoplodon densirostris* USNM 550351, *Mesoplodon mirus* USNM 504724, and *Tursiops truncatus* (Mead & Fordyce, 2009; adult and neonate). The ventral and dorsal orbital fissures are wider in *Ninoziphius* than in *Mesoplodon*. The dorsal exit of the foramen ovale is proportionally smaller in *Mesoplodon* and *Tursiops*, not divided into two branches in dorsal view contrary to *Ninoziphius*. The dorsal carotid foramen is anterior to the foramen ovale in *Mesoplodon*, whereas it is medial in *Ninoziphius* and *Tursiops*. It is also more distant from the tentorium in *Ninoziphius*; the tentorium is more medially projected in *Mesoplodon*, with the part of the cerebral cavity between the tentoria distinctly narrower than in *Ninoziphius*, whereas the lateral parts of the cerebral cavity are wider, suggesting differences in the proportions of the brain.

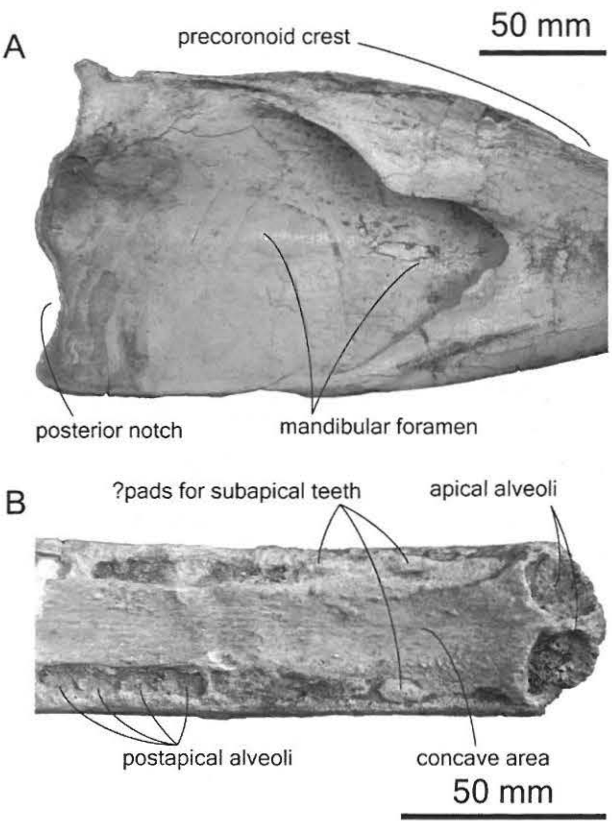


Figure 12. Mandibles of *Ninoziphius platyrostris* MNHN SAS 941 (holotype): A, posterior region of left dentary in medial view; B, anterior symphyseal region in dorsal view.

Mandible

Described in detail by de Muizon (1984) the mandibles are characterized by an elongated fused symphyseal portion (Figs 1A, 12B), about 36% of the total length, only slightly shorter than in *Messapicetus gregarius* (38–42% following Bianucci *et al.*, 2010). The degree of fusion of the two dentaries matches *Mess. gregarius* and *Tasmacetus*, and is more advanced than in any other ziphiid. The transverse section in the symphyseal region is much wider than high; it is also half-circled, a feature observed in specimens of *Berardius* and *Mess. gregarius*, whereas in other ziphiids, including *Nazcacetus*, the posteroventral region of the symphysis is more transversely pinched. However, it should be noted that the shape of the transverse section is related in several species (e.g. *Mess. gregarius* and *Ziphius*) to the development of the apical teeth and alveoli, a parameter known to be sexually dimorphic in most extant ziphiids (Moore, 1968; MacLeod & Herman, 2004; Lambert, Bianucci & Post, 2010a). The distal portion of the mandibles is distinctly curved upwards (Fig. 1A) to a greater extent than in *Messapicetus*. This feature is also especially pronounced in adult males of *Ziphius*. The large subcircular apical alveoli of the holotype of *Ninoziphius* (maximum diameter = 19 mm; Fig. 12B) differ from the transversely compressed apical alveoli of *Mess. gregarius*. Furthermore, they are not followed anteriorly by an anteromedian protuberance (sensu Lambert *et al.*, 2010a), differing from some, presumably adult male, specimens of *Mess. gregarius*. Nevertheless, the dorsal surface of the symphysis posteromedial to the alveoli is concave, suggesting a tight contact for the apex of the shorter rostrum, as in *Mess. gregarius*. In this region *Ninoziphius* differs from *Mess. gregarius* and *Tasmacetus* by the presence of two pairs of narrow and elongated exostoses in the alveolar grooves, between the apical alveoli and the first 'normal' postapical alveoli. Differing markedly from the deep second pair of alveoli in several isolated fossil ziphiid mandibles and *Berardius*, the only extant ziphiid with two pairs of tusks, these exostoses might correspond to pads for additional subapical teeth, as proposed by de Muizon (1984), with a diameter not exceeding the diameter of non-enlarged postapical teeth. In that case these teeth would have an intermediate status unknown in extant ziphiids: probably longer than more posterior teeth, they could be described as tusks, even though their diameter would have been much smaller than for apical teeth and they were mostly held in place by the gums. Another hypothesis would be simply that these exostoses did not bear teeth, corresponding instead to a differential filling of the alveolar groove in the diastema. A similar diastema is present in both the other ziphiids with a full set of postapical teeth, *Mess. gregarius* and *Tasmacetus*. In the former, secondary bone growth has also been noted in this area (Bianucci *et al.*, 2010). We estimate the number of large and deep postapical alveoli at 40 to 42 for each dentary (as proposed by de Muizon, 1984), again higher than in *Tasmacetus* (18–28; Mead & Payne, 1975) and *Mess. gregarius* (25–26; Bianucci *et al.*, 2010). Anterior alveoli are roughly as long as wide, whereas posterior alveoli are wider than long, a feature reflected in the section of the root of teeth (see below). Posterior alveoli of *Tasmacetus* are slightly proportionally longer, whereas all the alveoli of *Mess. gregarius* are longer and transversely flattened. Interalveolar septa are reduced.

Complete until the level of the anterior end of the mandibular foramen, the dorsal margin of the dentary displays a precoronoid crest (= dorsal margin convex, instead of rectilinear or concave, between the last alveolus and the coronoid process; Figs 1A, 12A) slightly lower than in *Berardius*, *Indopacetus*, *Nazcacetus*, and *Tasmacetus*, being instead more similar to *Mess. gregarius*. Absent or much lower in most other odontocetes (with the exception of some delphinoids), including eurhinodelphinids and eoplatanistids, the precoronoid crest of ziphiids and the strange ziphiid-like delphinid *Australodelphis* has been tentatively interpreted as an element constituting a rigid lateral wall for the oral cavity, probably useful during suction feeding (Fordyce *et al.*, 2002; Lambert *et al.*, 2009).

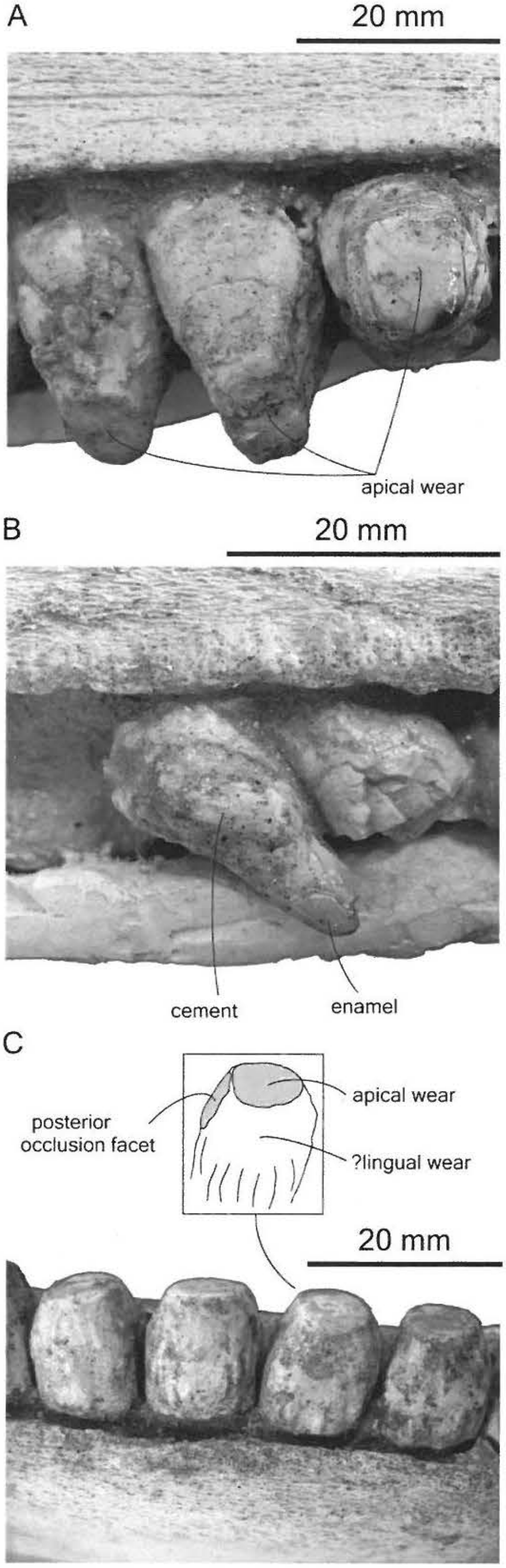
Compared to the total length of the mandible, the mandibular foramen of the long-snouted *Ninoziphius* is short (de Muizon, 1984; Fig. 12A). In the holotype, when the mandible is articulated to the skull, the mandibular foramen roughly reaches the anterior end of the pterygoid sinus fossa. In other ziphiids the foramen either ends at the same level (the condition in *Ninoziphius*), or is somewhat longer than the fossa. Considering the acoustic pathway recently proposed for the echolocation sounds towards the ear bones in *Ziphius* (see Cranford, Krysl & Hildebrand, 2008), entering below the head and between the lower jaws and passing through the opening created by the mandibular foramen, via the mandibular fat bodies until the ear bones ('gular pathway'), it is tempting to propose that the anterior extent of the pterygoid sinus fossa and the mandibular foramen are functionally related, forming a common low-density cavity for the propagation of sounds towards the ear.

A notch marks the posterior margin of the dentary between the mandibular condyle and the angular process (Fig. 12A; de Muizon, 1984), as in *Mess. gregarius* and some, but not all, specimens of *Tasmacetus* (de Muizon, 1984; Bianucci *et al.*, 2010: fig. 9). Absent in other ziphiids, such a notch might have helped to produce a larger gape in these ziphiids with a complete dentition, preventing any contact of the posterior margin of the mandible with the posteroventral part of the squamosal (postglenoid process, meatal crests). Direct observation of stranded specimens, as well as the shape and position of the tusks in adult males of *Mesoplodon layardii*, demonstrates that the gape is very limited at least in some extant ziphiids displaying a strong dental reduction, a feature probably related to suction feeding (Heyning & Mead, 1996).

Teeth

No apical lower teeth are preserved. Considering the circular alveoli, the root of these tusks is not transversely flattened, differing from *Berardius*, *Mesoplodon hectori*, *Mesoplodon perrini*, and *Mess. gregarius* (Bianucci *et al.*, 2010). Similarly, the section of the

Figure 13. Teeth of *Ninoziphius platyrostris* MNHN SAS 941 (holotype) and tooth wear: A, three anterior upper postapical teeth, slightly shifted from their original position; B, less worn posterior upper tooth, considerably shifted from its original position; C, four lower teeth, in situ.



root of the preserved functional postapical lower and upper teeth is subcircular to quadrate, more similar to *Tasmacetus* than to *Mess. gregarius*. The root is massive and covered with a thick layer of cement (Fig. 13), as in *Mess. gregarius*, *Tasmacetus*, and physeteroids. Successive teeth contact each other via the root, a feature probably related to ontogeny. Crowns are poorly preserved because of intense wear (see below). The crown base has a section slightly more anteroposteriorly compressed in the upper teeth, whereas it is subcircular in the lower teeth. The slender conical crown of one posterior left upper tooth is less worn; it bears a thin layer of smooth enamel and does not differ significantly from teeth of *Tasmacetus*.

The distal and/or mesial surfaces of the root and crown base often display wear corresponding to the occlusion surface for the opposite tooth (Fig. 13A, C); upper and lower teeth were therefore probably interlocking and part of this occlusion wear occurred before the complete apical wear. In some teeth of *Tasmacetus* and *Mess. gregarius* a similar wear type was detected (Oliver, 1937; Bianucci *et al.*, 2010), suggesting that, unsurprisingly, interlocking teeth is the primitive condition in ziphiids (as observed in most other odontocete clades).

Apical wear has removed most of the crown in lower teeth; in upper teeth a slightly longer part of the crown has been retained (Fig. 13A, C). The wear surface is very smooth and slightly convex. No macroscopic structure (grooves of ridge) could be observed on this uniform surface. For both the upper and lower dentition, successive teeth display the same degree of wear, and no difference between anterior and posterior preserved teeth could be detected. For example, teeth at the mid-length of the ramus are worn to the same degree as teeth from the posterior symphyseal region. However, teeth from the anterior-most part of the alveolar groove are unknown and one posterior upper tooth is significantly less worn. Even though some of the teeth were obviously tilted laterally post mortem, in their original position the apical wear surface was probably subhorizontal. Considering the equal degree of wear in one row and the proposed orientation of the wear surface, it is possible that the teeth were worn until the level of the gums, as in some offshore specimens of the killer whale *Orcinus orca* (see Ford *et al.*, 2011). In that case, the gums might have been slightly higher along the upper teeth. A similar apical wear, even if considerably less developed, is observed in the holotype of *Mess. gregarius* and in the holotype of *Tasmacetus shepherdi*, presumably an adult individual (Oliver, 1937; Bianucci *et al.*, 2010). Teeth of a sexually mature female of the latter display only weak apical wear (Mead & Payne, 1975; USNM 484878, O. Lambert, pers. observ.).

Finally, a subtly smoothed surface detected on the lingual surface of the root of some lower teeth (Fig. 13C) may indicate a slight degree of lingual wear, suggesting that at least the highest part of the root was not embedded in the gums on the lingual side; if proved, this interpretation would contradict the above hypothesis of apical wear reaching the level of the gums.

Vertebrae

The partial vertebral column of the holotype has been described and compared in detail by de Muizon (1984). As in *Mes. perrini* and *Nazcacetus*, only the atlas and the axis are fused, whereas in *Archaeoziphius* the atlas is free and in most extant ziphiids no more than four cervical vertebrae remain free. The atlas–axis complex of *Ninoziphius* is also longer than in *Nazcacetus* (Lambert *et al.*, 2009) and extant ziphiids (de Muizon, 1984). Together with more marked areas of insertion for neck muscles on the different cervical vertebrae, deeper and higher anterior articular facets on the atlas, and the development of the various apophyses, this suggests greater flexibility of the neck in *Ninoziphius* compared to extant ziphiids (de Muizon, 1984). The transverse process of the atlas is much longer than in the eurhinodelphinid *Xiphiacetus cristatus* and longer than in *Nazcacetus*. Cervicals c3, c4, and c6 are proportionally shorter than in *X. cristatus* (see Lambert, 2005a) and longer than in *Nazcacetus*.

The number of thoracic vertebrae is estimated to be at least 11, slightly higher than in extant ziphiids, even for species recently described or redescribed (Dalebout *et al.*, 2002, 2003). The morphology of the preserved thoracics suggests that nine pairs of ribs were double-headed, with both a tuberculum and a capitulum (de Muizon, 1984). All extant ziphiids except *Berardius* display a double-headed rib count lower than eight (True, 1910; Oliver, 1937; Mead, 1989a; Dalebout *et al.*, 2003; O. Lambert, pers. observ.), and therefore a more derived, shorter chest region as defined by Buchholtz (2001). In the only preserved lumbar vertebra, de Muizon (1984) noted a neural canal significantly narrower than in extant ziphiids, possibly indicating weaker innervation of the caudal region and lesser development of the musculature of that area.

Sternum

The robust first sternal element is proportionally longer than in any extant ziphiid, including *Indopacetus*, for which this element was unknown at the time of de Muizon's study. The anterolateral corner creates a triangular apophysis more prominent than in extant ziphiids (de Muizon, 1984: fig. 95). The most similar outline is seen in *Tasmacetus*, in which the anterior notch is probably deeper (see Oliver, 1937: pl. 4). Changes in the shape of the sternum suggest modifications for the insertion of hyoid muscles (e.g. sternohyoid, altering the position of the hyoid); the hyoid region is critical for the origin of muscles acting on the tongue and floor of the mouth in odontocetes, and, together with other muscles, the sternohyoid 'may create a strong piston-like motion of the tongue within the tube of the long rostrum and mandibles to produce a powerful suction force' (Reidenberg & Laitman, 1994). In this framework, and considering that suction feeding is a key adaptation of extant ziphiids (Heyning & Mead, 1996), it is interesting to note the similarities between *Ninoziphius* and *Tasmacetus*, the only extant ziphiid with a complete dentition. The anterior margin of the first sternal element is more robust in *Berardius*, *Hyperoodon*, *Indopacetus*, and *Mesoplodon*, wider with shorter anterior projections compared to the level of the articulation of the first rib. This difference might be related to a stronger sternohyoid muscle in the latter taxa, even though an important variation is observed in this area within the genus *Mesoplodon*. Data on outgroup taxa, for example eurhinodelphinids, would be important to better understand the evolution of this character.

Body size

As the postcranial skeleton of *N. platyrostris* is only partially known, we used skull measurements to estimate the total body length of the animal. From the various equations proposed in the past to estimate cetacean body length (see Pyenson & Sponberg, 2011), we chose the equation proposed by Bianucci *et al.* (2008: supplementary online material, fig. b), because it is the only one that considers the ziphiids alone. From a regression line based on the body length (y) versus postorbital width of the skull (x) for 25 specimens of extant ziphiids, Bianucci *et al.* (2008) obtained the following equation: $y = 9.464x + 1137$. The body length of *Ninoziphius* is estimated to be 4.41 m, a value close to that of *Messapicetus* (4.47 m) and in the range of several species of *Mesoplodon* (e.g. *Mesoplodon bowdoini* and *Mes. densirostris*), but smaller than members of other extant ziphiid genera (MacLeod, 2006). However, with some differences noted between the vertebral columns of *Ninoziphius* and extant ziphiids (see above; de Muizon, 1984), this body size estimate must be considered as tentative.

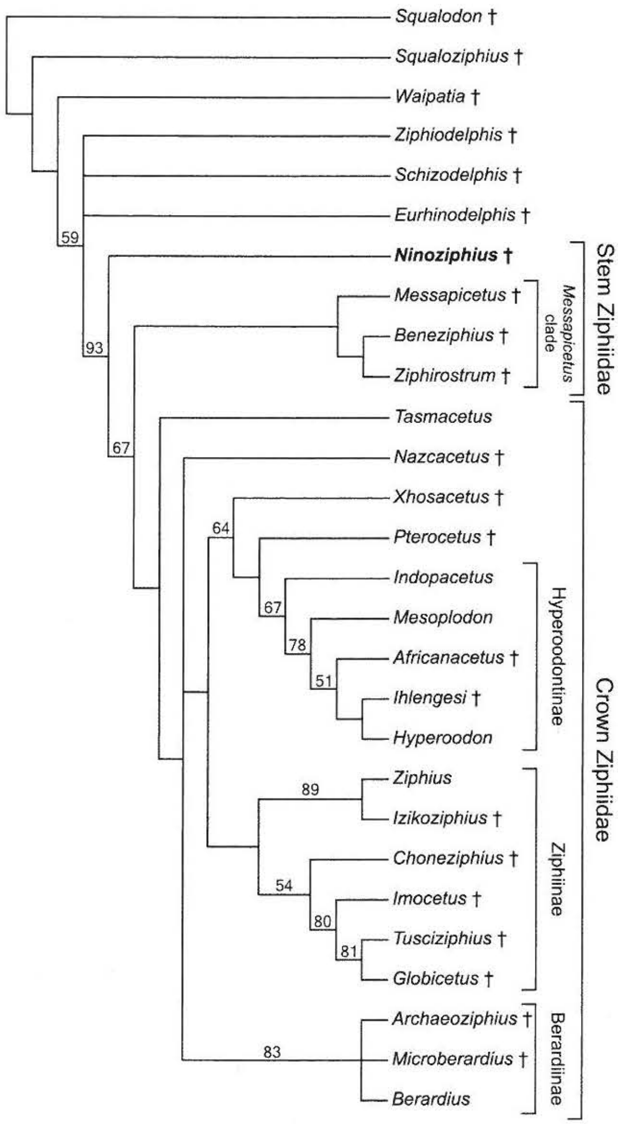


Figure 14. Consensus tree of 45 equally parsimonious cladograms showing the relationships of *Ninoziphius* with other ziphiid genera. Homoplastic characters downweighted using the method of Goloboff (1993).Tree length = 134, Goloboff fit = –36.21, consistency index = 0.54, and retention index = 0.77. Numbers associated with the branches are bootstrap values. See text for discussion and Appendices S1–S2 for description of characters and data matrix. †, strictly fossil taxa.

PHYLOGENY

The cladistic analysis produced 45 equally parsimonious trees, with tree length = 134, Goloboff fit = –36.21, consistency index = 0.54, and retention index = 0.77. The consensus tree of these cladograms and the bootstrap support values are presented in Figure 14 and are discussed below.

In our analysis, contrary to the original interpretation by de Muizon (1991) and despite the presence of distinct premaxillary crests and elongated nasals, *Squaloziphius* does not fall as sister group of the ziphiids. It lacks two key characters of the family [the elevated vertex (char. 9); the fossa for the hamular lobe of the pterygoid sinus extending anteriorly on the rostrum and ventrally until the ventral limit of the basicranium (char. 35)] and a few characters shared by ziphiids and several other odontocetes [e.g. the concave ascending process of the premaxilla in lateral view (char. 7); the postglenoid process of the squamosal higher than the ventral margin of the paroccipital process (char. 39); and the anteriorly shortened zygomatic process of the squamosal (char. 38)]. Nevertheless, some of the latter characters probably evolved independently in several odontocete clades, and the unusual morphology of the robust squamosal of *Squaloziphius* might be derived, as proposed by de Muizon (1991). Additional data on this interesting archaic odontocete, whose rostrum, ear bones, and mandibles are still unknown, might change our current view of its still-debated relationships with eurhinodelphinids and ziphiids, especially in a more widely sampled phylogenetic analysis.

Contrasting with *Squaloziphius*, *Ninoziphius* is placed as sister group to all other ziphiids; it is considered here as the most basal stem-ziphiid currently known. The monophyly of Ziphiidae has a bootstrap support value of 93; it is supported by the following six apomorphies, observed in *Ninoziphius* and all the other ziphiid genera: (1) presence of a posteroventral corner on the sigmoid process of the tympanic (char. 23, states 1–2); (2) presence of one or two pairs of tusks on the mandibles (char. 28, states 1–3); (3) hamular fossa of the pterygoid sinus extended anteriorly on the palatal surface of the rostrum and ventrally close to the ventral limit of the basicranium (char. 35, state 1); (4) ventral margin of the postglenoid process of the squamosal clearly more dorsal than the ventral margin of the paroccipital process of the exoccipital in lateral view (char. 39, state 2); (5) absence or substantial reduction of the dorsal keel on the posterior process of the periotic (char. 41, state 1); (6) presence of a precoronoid crest on the dorsal margin of the mandible (char. 44, state 1). Moreover, *Ninoziphius* exhibits an elevated vertex (char. 9, state 2), which, as pointed out above, is a feature shared with all the ziphiids apart from *Nazcacetus*.

Ninoziphius is less derived than all the other ziphiids, including *Messapicetus*, also a stem-ziphiid here, in having a sigmoid process of the tympanic with the posteroventral corner not posteriorly projected (char. 23, state 1) and in having the apex of the hamular process of the pterygoid not excavated by the fossa for the hamular lobe of the pterygoid sinus (char. 37, state 0). *Ninoziphius* differs from all the other ziphiids except *Messapicetus* in the following additional plesiomorphic characters: elongated rostrum (char. 1, state 0); posterior bullar facet of the periotic not fan-shaped (char. 20, state 0); transverse thickening of the anterior process of the periotic absent or weak (char. 21, state 0); elongated symphyseal portion of the mandibles (char. 29, state 0). Other primitive characters shared by *Ninoziphius* and a few other ziphiids are the following: ascending process of the premaxilla in lateral view only slightly concave (char. 7, state 1; also observed in the berardiines); absence of the anteromedial excavation of the dorsal surface of the of the nasal (char. 14, state 0; also observed in *Archaeoziphius*, *Berardius*, *Izikoziphius*, *Xhosacetus*, and *Ziphius*); functional maxillary teeth in individualized alveoli (char. 27, state 0; also observed in *Messapicetus* and *Tasmacetus*); eight or more pairs of double-headed ribs (char. 46, state 0; also observed in *Berardius*, but status unknown for all other fossil ziphiids).

Concerning the other ziphiids, our analysis substantially agreed with those recently published (Bianucci *et al.*, 2010; 2013) with some minor changes (e.g. the sister-group relationship between the Ziphiinae and the Hyperoodontinae + stem relatives) because of the addition of new taxa and characters. The bootstrap analysis supported the exclusion of *Squaloziphius* from the ziphiids and the basal position of *Ninoziphius* inside the family. However, it also confirmed, as already pointed out (Bianucci *et al.*, 2010; 2013), that the relationships amongst some clades and genera of this family still need to be better resolved. Further discoveries of well-preserved specimens such as those of *Ninoziphius* described here could improve the knowledge of the relationships within this family.

Considering the late early to middle Miocene age of the oldest known fossil ziphiid remains (Bianucci *et al.*, 2005; Lambert & Louwye, 2006), the basal-most position of the early Pliocene (or latest Miocene, see discussion above) *N. platyrostris* in the ziphiid phylogenetic tree suggests a long range extension (amount of stratigraphical range of a given taxon to be added to comply with the phylogenetic tree; Smith, 1994; Cavin & Forey, 2007). Indeed, *Archaeoziphius microglenoideus*, the geologically oldest fossil ziphiid crownward to the lineage of *Ninoziphius* in our phylogenetic tree, is dated from the middle Miocene (tentatively late Langhian to early Serravallian, *c.* 15–13.2 Mya; Lambert & Louwye, 2006); this implies a range extension of more than 7.3 or 7.9 Mya for the lineage of *Ninoziphius*, depending on the early Pliocene or latest Miocene age of the Sud-Sacaco level in which the specimens were found.

PALAEOECOLOGY

CLUES ON THE FEEDING STRATEGY AND HABITAT OF *NINOZIPHIUS*

One of the most obvious features of the head of *Ninoziphius* is its very elongated snout. It is striking to note that the two ziphiids with the longest snout, namely *Messapicetus* and *Ninoziphius*, and another long-snouted taxon, *Tasmacetus*, have a complete set of functional upper and lower teeth. This combination, which might be considered as primitive amongst ziphiids (see phylogeny above), suggests that teeth were still used for grasping the prey, with the help of the long snout, whereas in toothless ziphiids the prey is probably captured and ingested through suction (Heyning & Mead, 1996; Werth, 2006; Johnston & Berta, 2011). Additional arguments to support this hypothesis can be found. For example, the first sternal element of *Ninoziphius* is more similar to *Tasmacetus*, suggesting a weaker sternohyoid muscle (see above). The notch in the posterior margin of the dentary, between the mandibular condyle and angular process, might have allowed a larger gape in *Messapicetus* and *Ninoziphius* compared with 'capture' suction-feeding ziphiids (see Heyning & Mead, 1996), possibly related to the use of the jaws to grasp prey. Alternatively, the enlarged hamular processes of the pterygoids of *Ninoziphius*, observed in all other ziphiids, might have enhanced gular distension in association with suction feeding; during caudal retraction of the tongue, the ventrally extended processes would force it to move ventrally, further increasing the intraoral volume and consequently decreasing the intraoral pressure (Heyning & Mead, 1996). Apart from the non-excavated apex, the hamular process is not smaller in *Ninoziphius* than in any other ziphiids. Furthermore, *Ninoziphius* displays a distinct precoronoid crest, albeit slightly lower than in some other ziphiids. As mentioned above, this anatomical feature constitutes a rigid lateral wall for the oral cavity and has been considered as useful for the production of an increased intraoral pressure for suction (Fordyce *et al.*, 2002; Lambert *et al.*, 2009).

The intense apical tooth wear observed in most of the preserved upper and lower teeth of the holotype of *N. platyrostris* is another interesting element for discussion of the feeding strategy of the species, even though it is difficult to interpret. Such tooth wear is observed in many extant odontocetes, for example the beluga, *Delphinapterus leucas*, the sperm whale, *Physeter macrocephalus*, and some populations of the killer whale, *Orcinus orca* (Fitzgerald, 2010; Ford *et al.*, 2011; O. Lambert, pers. observ.). The wear in *Delphinapterus* is in large part because of the oblique occlusion of upper and lower teeth (Fitzgerald, 2010), whereas in *Ninoziphius* shallow occlusion facets are located on mesial and distal surfaces of teeth. In *Physeter*, which only bears erupted teeth on the lower jaw, roughly flat apical wear surfaces are mostly seen in the posterior part of the tooth row, beyond the end of the symphysis. Wear surfaces are not necessarily horizontal; they are sometimes tilted medially or laterally. It is well known that the teeth of *Physeter* are not used for grasping prey, which is directly sucked into the oropharynx (Werth, 2004, 2006). In this case, apical wear on the posterior teeth could be explained by the repeated passage of food and water through this area; the lesser wear in more anterior teeth might be explained if the animal feeds with the mouth widely open. Intense tooth wear in individuals of a north-eastern Pacific population of *Orcinus* has been proposed to be at least partly related to predation on the Pacific sleeper shark *Somniosus pacificus*; dermal denticles in the skin of this shark would produce abrasion of the apex of the teeth (Ford *et al.*, 2011). In this case mandibular wear is sometimes severe, reaching until the gum line, and wear is proposed to be more intense in anterior teeth, probably related to the preferential use of these teeth for grasping and tearing this large prey (Caldwell & Brown, 1964).

In *Ninoziphius*, apical tooth wear could have happened following two different scenarios: (1) direct suction or (2) capture with the teeth and ingestion by suction. In the first case, wear would be the result of repeated passage of prey with water along the teeth, implying that the prey was captured and ingested with the mouth nearly closed (both upper and lower dentitions are deeply worn). An additional abrasive element would be added if the animal was feeding on the sea floor, with sediment being ingested together with the prey and water (for comments and references about benthic feeding, see Fitzgerald, 2010). In the second hypothesis, wear would be the result of direct contact of the apex of interlocking teeth with the prey. After capture by the anterior teeth, the prey would be progressively brought posteriorly into the area where it could finally be sucked in for ingestion. The wear in the middle part of the jaws would here be linked to the progressive transfer of food from the anterior part of the elongated snout to the back, not to an initial break of the crown apex when contacting hard tissue, as all the teeth on the row have a similar level of wear. Feeding close to the sea floor could also bring abrasive sediment between the interlocking teeth and the captured prey. Considering the very long jaws of *Ninoziphius* and subhorizontal wear surfaces all along the preserved part of the tooth row, the second hypothesis is preferred here. We therefore hypothesize that *Ninoziphius* fed on medium-sized individual prey, fish and/or cephalopods, possibly at close proximity to the seafloor (Fig. 15), grasping the prey with the anterior part of the toothed jaws, transferring it to the posterior part of the mouth, and swallowing it by suction. By analogy, the long-snouted river dolphins *Inia geoffrensis* and *Platanista gangetica* are known to feed on the bottom of rivers; both have been observed probing and digging in the sediment to find prey and grasping it with their anterior teeth (Best & da Silva, 1989; Reeves & Brownell, 1989). However, in contrast to our hypothesis for *Ninoziphius*, after having grasped the prey, *I. geoffrensis* and *P. gangetica* probably rely less on suction than on movements of the jaws to move the prey posteriorly as the lateral opening of their mouths are longer than those of ziphiids (Best & da Silva, 1989; Reeves & Brownell, 1989; Werth, 2006). Microwear analyses of dental enamel and cement would be useful, even though no detailed study of this parameter in extant odontocetes is currently available for comparison. It is interesting to note that stomach content analyses have shown that several extant ziphiids feed at or close to the seafloor (MacLeod, Santos & Pierce, 2003). Recently, gouges observed in the soft sediment of the seafloor at great depths have even been interpreted as the result of bottom feeding by ziphiids (Auster & Watling, 2010).

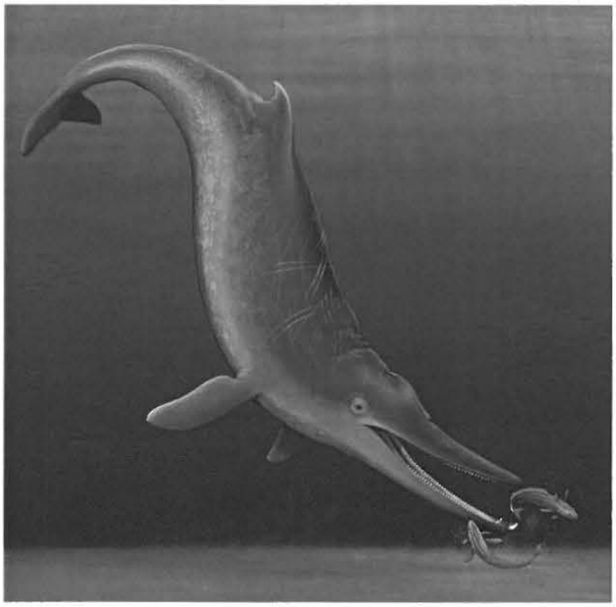


Figure 15. Life reconstruction of an adult male of *Ninoziphius platyrostris* preying upon medium-size benthic gadiform fish along the sea floor off the southern Peruvian coast during the late Neogene (scientific artist: C. Letenneur, MNHN, Paris).

Similar, although less pronounced, wear in the holotype of the other long-snouted ziphiid *Mess. gregarius* suggests that the latter fed with the same kind of strategy, as proposed in part for *Mess. longirostris* (Bianucci *et al.*, 1994: fig. 9). Few data are available on the diet of the extant *Tasmacetus*; the stomach content of one specimen revealed only cephalopod remains, whereas another only contained fish (Mead & Payne, 1975; Pitman *et al.*, 2006). The even less pronounced apical tooth wear seen in *Tasmacetus* may indicate that it feeds further from the seafloor, that its prey bears less abrasive skin, or even that only younger individuals of *Tasmacetus* were observed.

The question of feeding depth can also be discussed using the extent of the pterygoid sinuses. The considerable enlargement of the sinuses and the reduction of the lateral bony lamina limiting them in *Physeter* and the ziphiids, compared to other odontocetes (Fraser & Purves, 1960; Rommel *et al.*, 2006), led Cranford *et al.* (2008) to propose an interesting functional hypothesis. As suggested by previous authors (Fraser & Purves, 1960), Cranford *et al.* (2008) agreed that the pterygoid sinuses provide a reservoir of air that moves towards the ear bones when the animal dives because of the increased hydrostatic pressure. As air is essential for the functioning of the ossicular chain, a larger volume of air in the sinuses would ensure that a small pocket of air was retained around the ear bones during deep dives, as performed by extant ziphiids and *Physeter* (e.g. Tyack *et al.*, 2006; Minamikawa *et al.*, 2007), and would allow the animal to continue echolocating, a function crucial for prey detection (Fraser & Purves, 1960; Johnson *et al.*, 2004; Cranford *et al.*, 2008; Reidenberg & Laitman, 2008). Therefore, the volume of the pterygoid sinuses might be one of the rough indicators of the ability of an odontocete to dive at great depths. A similar argument (size of pterygoid hamuli) has been used to differentiate an offshore, presumably deeper diving, population of the delphinid *Tursiops truncatus* from a coastal ecotype (Perrin *et al.*, 2011). Except for the unexcavated apex of the hamular process, the volume of the pterygoid sinuses is not significantly smaller in *Ninoziphius* than in other extinct and extant ziphiids, meaning that this factor would not have limited the depths to which *Ninoziphius* would have been able to echolocate. The volume of the pterygoid sinuses was considerably smaller in the archaic odontocete *Squaloziphius*, although still larger than in eurhinodelphinids.

Another element worth commenting on is the similarity noted between the aspect of the pterygoid bone on the medial surface of the fossa for the hamular lobe of the pterygoid sinus in *Ninoziphius* and the gossamer-like trabeculae of the soft tissue fibrous venous plexus (FVP) laterally surrounding the pterygoid sinus in the same area in *Ziphius* (see Cranford *et al.*, 2008). The small cavities in the pterygoid are only well formed in one of the two specimens of *N. platyrostris* in which this area is preserved, but the high level of shape similarity with the FVP in *Ziphius* (Fig. 8) could suggest a similar function. In the latter, the anterior part of the FVP has been proposed to fill the volume left by the air sinuses squeezed by hydrostatic pressure during deep dives (Cranford *et al.*, 2008). The small cavities on the pterygoid bone medial to the hamular lobe of the pterygoid sinus in *N. platyrostris* might allow the retention of a small residual quantity of air along all of the bony surfaces concerned when the quantity of air is greatly reduced (T. W. Cranford, pers. comm., 2012), and possibly retain a reflective function. In the framework of this hypothesis, the bony transverse crests observed in the fossa for the hamular lobe of the pterygoid sinus of the two specimens of *N. platyrostris* would be analogous to the soft tissue transverse crests of *Ziphius*, possibly corresponding to a partial compartmentalization of the sinus volume (T. W. Cranford, pers. comm., 2012), which would also help to retain air in a given area when the sinus collapses during phases of increased pressure.

Another important aspect for the process of echolocation is the morphology of the facial area, where the high frequency sounds are produced. Unfortunately, in odontocetes these echolocation sounds are produced by phonic lips in a region only made of soft tissues (e.g. Heyning, 1989; Cranford *et al.*, 2008) that do not fossilize. The only information available in fossil specimens is the morphology of the surrounding bony elements. One main change in ziphiids compared to other odontocetes is the elevation of the vertex and the development of transverse premaxillary crests lateral to the nasals (Moore, 1968; Heyning, 1989; de Muizon, 1991). Even though the crests are not completely preserved in *Ninoziphius*, they are present, on an elevated vertex that is proportionally even more elevated than in *Berardius* and *Tasmacetus*, amongst extant ziphiids. Another character of facial bones that is reflected in forehead soft anatomy and that might be related to echolocation parameters is the asymmetry of the premaxillary sac fossae, mirrored by a corresponding asymmetry of the premaxillary sacs and nasal plugs in extant ziphiids (see Heyning, 1989; Cranford, Amundin & Norris, 1996). The moderate asymmetry observed in *Ninoziphius* is, as mentioned above, much more reduced than in *Hyperoodon*, *Ziphius*, and several fossil genera, and somewhat more reduced than in some species of *Mesoplodon*, but close to the range of *Berardius* spp., *Indopacetus*, *Tasmacetus*, and other species of *Mesoplodon*. For the moment, there are to our knowledge no significant differences noted amongst the echolocation performances of the different extant ziphiid species, so nothing can be concluded from this observation. In addition, *Ninoziphius* might represent a preliminary step in the development of a prenarial basin (anterior position of the premaxillary foramen, deep posteromedial sulcus). However, it is far from the extremely wide and deep basin observed in adult males of *Ziphius* (Heyning, 1989; Cranford *et al.*, 2008), and it only approaches other fossil forms, for example *Beneziphius* or *Messapicetus*, for which no direct information about forehead anatomy and echolocation features is known. With these few elements in hand, it can only be concluded that, based on osteology, there is no argument to support a high frequency sound production area less specialized in *Ninoziphius* than in, at least, some of the extant ziphiids, the latter relying on echolocation to detect their small to medium-sized prey in deep and dark oceanic areas (e.g. Johnson *et al.*, 2004, 2008).

From a hydrodynamic standpoint, a longer and more flexible neck leads to greater manoeuvrability at low speed, but also to a loss of stability and power when swimming fast (Fish, 2002). In the case of deep diving extant ziphiids, individuals spend a long time travelling to feeding areas and back to the surface (Hooker & Baird, 1999; Johnson *et al.*, 2004; Tyack *et al.*, 2006). In some species it has been noted that the fluke rate is low for most of the descent, meaning that the animal glides for some time between the fluking periods (Tyack *et al.*, 2006). It seems obvious that a more rigid and hydrodynamic body, with, amongst other features, a short and rigid neck, would be more efficient for such a succession of fluking and gliding phases. With its longer neck, made up of a higher number of free cervicals, and a possibly shorter tail with a less powerful fluke (de Muizon, 1984), *Ninoziphius* can be considered as less adapted to deep dives than extant ziphiids. Together with the long snout, this conformation might have been better fitted for hunting elusive prey along the sea floor in shallower water (Fig. 15), in a way possibly more similar to eurhinodelphinids.

Body size is another important parameter related to diving depth and duration in air-breathing animals; larger/heavier species are often recorded to dive longer, presumably in relation to oxygen storage capacity and oxygen metabolism (Schreer & Kovacs, 1997; Watanabe *et al.*, 2011). Correlations between body mass and dive duration and between body mass and maximum diving depth have even been proposed for cetaceans or odontocetes (Schreer & Kovacs, 1997; Noren & Williams, 2000). However, concerning *Ninoziphius*, extant ziphiids with a similar body size, for example *Mes. densirostris* (MacLeod, 2006), have been recorded to dive much longer and deeper (Tyack *et al.*, 2006; Baird *et al.*, 2008) than would have been predicted by the equations of Schreer & Kovacs (1997) and Noren & Williams (2000), close to the performances of the largest extant ziphiid *Berardius bairdii* (see Minamikawa *et al.*, 2007).

Preliminary X-ray investigation of two caudal vertebrae (ninth and tenth) of the holotype did not reveal any cavity that might correspond to avascular osteonecrosis. This behaviourally induced pathology is the result of nonlethal emboli causing repeated damage to blood vessels and bones supplied by these vessels (Beatty & Rothschild, 2008). The absence of such a pathology suggests that the animal did not suffer decompression syndrome, either because it did not dive regularly at great depths, or because it already possessed the behavioural and physiological adaptations for such deep dives, as do the extant ziphiids. However, additional tests on other bones and new specimens are necessary to investigate further this question.

To summarize, most of the morphological traits of the skull of *Ninoziphius* related to echolocation (elevation of the vertex, asymmetry, volume of air sinuses . . .) are more similar to extant ziphiids than to any other odontocete. Based on these similarities, no indication has been found that *Ninoziphius* was less efficient for echolocation at depth than extant ziphiids. The morphology of the pterygoid bone at the surface of the hamular fossa further supports this hypothesis. However, considering the available postcranial elements, *Ninoziphius* was less specialized than extant ziphiids for locomotion as it appears to have been less adapted for long periods of vertical travel towards feeding areas. The elongated snout and the complete rows of upper and lower teeth suggest that *Ninoziphius* was still catching prey with its jaws, before moving it towards the posterior part of the mouth by suction. Finally, strong apical tooth wear in the holotype is tentatively interpreted as an indicator of benthic feeding.

CLUES ON THE SOCIAL BEHAVIOUR OF NINOZIPHIUS

Like all other ziphiids, *Ninoziphius* bore enlarged mandibular tusks. The apical pair probably protruded anteriorly to the end of the rostrum, and it may have been followed posteriorly by two smaller pairs (Fig. 15). Apart from *Berardius*, the tusks are sexually dimorphic in all extant ziphiids and, with some exceptions they are probably used in possibly ritualized fights between adult males (Heyning, 1984; MacLeod, 2002). A sufficiently large sample allowed the proposal of a similar sexual dimorphism in the extinct species *Mess. gregarius* (see Lambert *et al.*, 2010a). Unfortunately only one pair of mandibles of *N. platyrostris* is known to date. Therefore, considering the basal position of *Ninoziphius* in the ziphiid phylogenetic tree, we have no solid argument to support a similar sexual dimorphism in *N. platyros-*

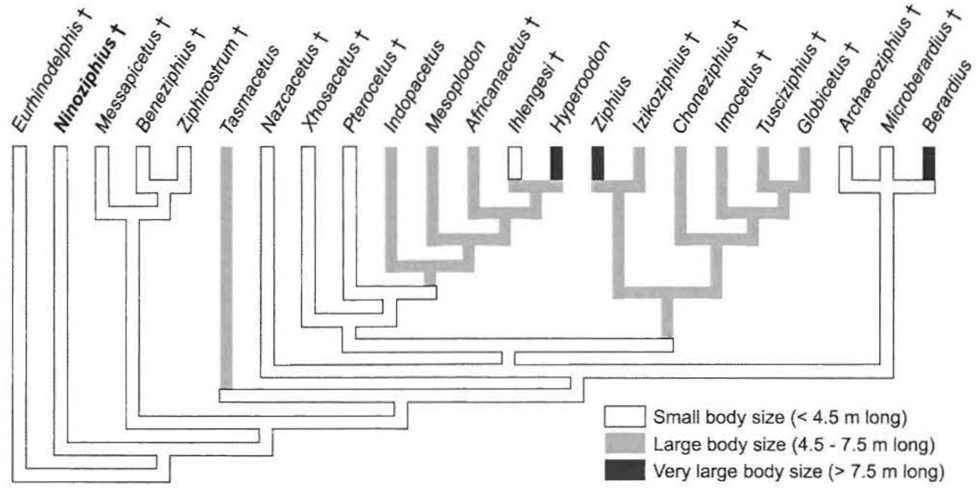


Figure 16. Consensus tree of 45 equally parsimonious cladograms as presented in Figure 14, showing the evolution of body size amongst ziphiids. Values for each genus correspond to the maximum size recorded. Note the independent size increase in several lineages and that the largest body sizes are limited to extant genera. Total body sizes of the fossil ziphiids were estimated using the equation in Bianucci *et al.* (2008: supplementary online material, fig. b). For the extant ziphiids we considered the maximum body sizes in MacLeod (2006: table 1).

tris. Nevertheless, it is interesting to note that none of the three specimens described here displays any of the changes of the rostrum morphology often observed in other ziphiids: filling of the mesorostral groove by the mesethmoid or the compact vomer, or dorsal closure of the groove by the thickened and compact premaxillae. Although no consensus exists, some of these specializations have been tentatively related to intraspecific fights (see MacLeod, 2002; Lambert *et al.*, 2010a, 2011).

ELEMENTS OF ZIPHIID EVOLUTIONARY HISTORY

REDUCTION OF DENTITION

The most parsimonious optimization of the character 'presence/absence of a full set of functional maxillary teeth' on the obtained phylogenetic tree indicates one main episode of dental reduction, at the base of the clade of crown ziphiids including *Nazcacetus* + more derived ziphiids, and one or two minor episodes in the stem-ziphiid *Messapicetus* clade (towards members of the *Beneziphius* + *Ziphirostrum* clade). However, it should be kept in mind that in several extant, and possibly fossil, ziphiid species, tiny teeth are occasionally observed in the gum (e.g. Boschma, 1951; Lambert *et al.*, 2009). This means that the genetic basis for the development of teeth is still present, even if not systematically expressed, in several ziphiid lineages. Therefore it would not be surprising if the history of the character 'presence/absence of a full set of functional maxillary teeth' proved to be more complex in the future than the simple optimization presented here.

MANDIBULAR TUSKS

The presence of apical mandibular tusks in the most basal ziphiid *Ninoziphius* (and in all the taxa for which the mandibles are known) suggests that the development of these enlarged lower teeth represents a key character in the evolution of the family, most likely present in all the crown ziphiids, even though the position of the tusks is modified in many species of *Mesoplodon* (Moore, 1968). This acquisition appears not to be related, either temporally or functionally, to the reduction of the postapical dentition, as proposed by Lambert *et al.* (2009). Considering the extensive radiation(s) of the ziphiids following this acquisition, it is hypothesized that variation in the shape, size, and position of the tusks, and possibly variation of the social behaviours related to the development of tusks, might have been, together with habitat shifts and changes in the feeding technique, one of the fundamental conditions for the diversification of the family, as already proposed for the 14 known extant species of the genus *Mesoplodon* (Dalebout, Steel & Baker, 2008).

BODY SIZE

The largest known ziphiids, with a maximum body length above 7.50 m, are all extant (*Berardius*, *Hyperoodon*, and *Ziphius*), whereas none of the stem-ziphiids has an estimated body length reaching

4.50 m (Fig. 16). Although a preservational or collection bias cannot be excluded, a size increase is observed in members of several lineages: at least amongst Berardiinae, Hyperoodontinae, and Ziphiinae. In cetaceans, an increased body size has been variously interpreted as: an adaptation to cold water, an antipredatory strategy, a way to metabolically improve the dive capacity or to minimize the drag per unit mass during swimming or diving; maximum body size has also been demonstrated to be directly related to a higher diversification rate of the clade (Noren & Williams, 2000; Fordyce & Muizon, 2001; Trammer, 2005; Fitzgerald, 2010; Lambert *et al.*, 2010b). Considering the diving performances of smaller extant species, the general distribution of extant ziphiids (e.g. Davies, 1963), the reports of attacks by killer whales, even on the largest species (Balcomb, 1989; Mead, 1989b), and the separate dietary niches of species living in the same area (MacLeod *et al.*, 2003), the parallel evolution of a larger size in several lineages could be interpreted as an adaptation to a cooler habitat, and/or as a mean to overcome predator attacks, and/or as providing the opportunity to feed on larger prey.

ECHOLOCATION AND DEEP DIVING

The known stem-ziphiids display facial and basicranial features that roughly match the anatomy of at least some of the extant ziphiids. Therefore, we cannot find strong arguments that would indicate an echolocation system less efficient in stem-ziphiids than in at least some of the extant forms (see discussion above for *Ninoziphius*). Additional data on the postcranial anatomy of other basal ziphiids, investigations of their hearing abilities, stable isotope analyses of tooth enamel, and computed tomography scans of vertebrae for the detection of avascular osteonecrosis might refine the various steps and timing of the critical ecological shift of ziphiids towards deeper and darker oceanic regions. Only after that would it be possible to confront the evolutionary history of the family with changes in the diversity of their prey, with the evolution of the other known main group of deep diving odontocetes (the sperm whales), and with physical changes in the oceans during the Neogene (e.g. Lindberg & Pyenson, 2007).

CONCLUSIONS

Based on the holotype specimen and two newly prepared partial skulls from the same Peruvian locality, we have redescribed in detail the late Neogene fossil ziphiid (beaked whale) *N. platyrostris*. This description and the comparison with other fossil and extant ziphiid taxa led to the elaboration of an emended diagnosis for *Ninoziphius*.

In our phylogenetic analysis, including 22 other fossil and extant ziphiid genera, as well as, amongst others, the strange archaic odontocete *Squaloziphius* and several eurhinodelphinids, *Ninoziphius* turned out to be the most basal stem ziphiid.

Based on the morphology of the oral apparatus, *Ninoziphius* appears to be less adapted for suction feeding than most extant ziphiids and probably relied instead on its elongated tooth-bearing snout to grasp its prey. We tentatively interpreted tooth wear observed on the holotype of *N. platyrostris* as being related to benthic feeding, even though prey type could also affect dental condition. The vertebral column of *Ninoziphius* was considered somewhat less specialized for deep diving compared with extant ziphiids.

At the level of cranial anatomy, we did not detect major differences from extant ziphiids that would suggest a less efficient echolocation system. However, more detailed analyses, both on fossil and extant taxa, are necessary to understand better the evolution of ziphiid sonar.

Taking account of the basal position of *Ninoziphius* in the phylogenetic tree of ziphiids, the evolution of several morphological characters within the family has been discussed, namely dental reduction, the development of tusks early in the history of the family, and the increased body size evolving in parallel in at least three ziphiid lineages.

ACKNOWLEDGEMENTS

G. Avery, D. J. Bohaska, M. Fornasiero, C. Lefèvre, G. Lenglet, J. G. Mead, S. Ploen, C. Potter, N. D. Pyenson, A. Rol, R. Salas-Gismondi, H. van Grouw, and K. van Willingh provided access to specimens under their care. At the MNHN, F. Goussard took preliminary computed tomography scan images of the caudal vertebrae of MNHN SAS 941, C. Lemzaouda undertook most of the photographic work, C. Letenneur prepared the lifelike and aesthetic life reconstruction of *Ninoziphius*, and R. Vacant helped with the construction of a plaster support for the acid-etching preparation of the skull MNHN SAS 1628. Discussions on various ziphiid-related topics with B. L. Beatty, T. W. Cranford, V. de Buffrénil, C. D. MacLeod, J. G. Mead, C. Potter, I. Miján, and K. Post were much appreciated. The constructive comments and suggestions of an anonymous reviewer and the associate editor significantly improved the quality of an earlier version of this work. T. W. Cranford kindly provided beautiful photographs from his dissection of the pterygoid sinus of *Ziphius cavirostris*. The research of O. Lambert at the IRSNB for 2012–2013 is carried out in the framework of the action 'Mandats de retour 2011' of the Belgian Federal Science Policy.

REFERENCES

Auster PJ, Watling L. 2010. Beaked whale foraging areas inferred by gouges in the seafloor. *Marine Mammal Science* **26:** 226–233.

Baird RW, Webster DL, Schorr GS, McSweeney DJ, Barlow J. 2008. Diel variation in beaked whale diving behavior. *Marine Mammal Science* **24:** 630–642.

Balcomb KC. 1989. Baird's beaked whale *Berardius bairdii* Stejneger, 1883: Arnoux's beaked whale *Berardius arnuxii* Duvernoy, 1851. In: Ridgway SH, Harrison R, eds. *Handbook of marine mammals, vol. 4: river dolphins and the larger toothed whales*. London: Academic Press, 260–288.

Beatty BL, Rothschild BM. 2008. Decompression syndrome and the evolution of deep diving physiology in the Cetacea. *Die Naturwissenschaften* **95:** 793–801.

Best RC, da Silva VMF. 1989. Amazon river dolphin, Boto. *Inia geoffrensis* (de Blainville, 1817). In: Ridgway SH, Harrison R, eds. *Handbook of marine mammals, vol. 4: river dolphins and the larger toothed whales*. London: Academic Press, 1–23.

Bianucci G, Lambert O, Post K. 2007. A high diversity in fossil beaked whales (Odontoceti, Ziphiidae) recovered by trawling from the sea floor off South Africa. *Geodiversitas* **29:** 5–62.

Bianucci G, Lambert O, Post K. 2010. High concentration of long-snouted beaked whales (genus *Messapicetus*) from the Miocene of Peru. *Palaeontology* **53:** 1077–1098.

Bianucci G, Landini W, Valleri G, Ragaini L, Varola A. 2005. First cetacean fossil records from Ecuador, collected from the Miocene of Esmeraldas Province. *Rivista Italiana di Paleontologia e Stratigrafia* **111:** 345–350.

Bianucci G, Landini W, Varola A. 1994. Relationships of *Messapicetus longirostris* (Cetacea, Ziphiidae) from the Miocene of South Italy. *Bollettino della Società Paleontologica Italiana* **33:** 231–241.

Bianucci G, Miján I, Lambert O, Post K, Mateus O. 2013. Bizarre fossil beaked whales (Odontoceti, Ziphiidae) fished from the Atlantic Ocean floor off the Iberian Peninsula. *Geodiversitas*. In press.

Bianucci G, Post K. 2005. *Caviziphius altirostris*, a new beaked whale from the Miocene southern North Sea basin. *Deinsea* **11:** 1–6.

Bianucci G, Post K, Lambert O. 2008. Beaked whale mysteries revealed by sea floor fossils trawled off South Africa. *South African Journal of Science* **104:** 140–142.

Boschma H. 1951. Rows of small teeth in ziphioid whales. *Zoologische Mededelingen* **31:** 139–148.

Bouetel V, Muizon C. 2006. The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae s.s. from the early Pliocene of Peru. *Geodiversitas* **28:** 319–395.

Brisson M-J. 1762. *Regnum Animale in classes IX distributum, sine synopsis methodica*. Paris: Theodorum Haak.

Buchholtz EA. 2001. Vertebral osteology and swimming style in living and fossil whales (Order Cetacea). *Journal of Zoology* **253:** 175–190.

Caldwell DK, Brown DH. 1964. Tooth wear as a correlate of described feeding behavior by the killer whale, with notes on a captive specimen. *Bulletin of the Southern California Academy of Sciences* **63:** 128–140.

Cavin L, Forey PL. 2007. Using ghost lineages to identify diversification events in the fossil record. *Biology Letters* **3:** 201–204.

Cranford TW, Amundin M, Norris KS. 1996. Functional morphology and homology in the Odontocete nasal complex: implications for sound generation. *Journal of Morphology* **228:** 223–285.

Cranford TW, Krysl P, Hildebrand JA. 2008. Acoustic pathway revealed: simulated sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*). *Bioinspiration & Biomimetics* **3**(016001)**:** 1–10.

Cranford TW, McKenna MF, Soldevilla MS, Wiggins SM, Goldbogen JA, Shadwick RE, Krysl P, St. Leger JA, Hildebrand JA. 2008. Anatomic geometry of sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*). *The Anatomical Record* **291:** 353–378.

Dalebout ML, Mead JG, Baker CS, Baker AN, van Helden AL. 2002. A new species of beaked whale *Mesoplodon perrini* sp. n. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Marine Mammal Science* **18:** 577–608.

Dalebout ML, Ross GJB, Baker CS, Anderson RC, Best PB, Cockcroft VG, Hinsz HL, Peddemors V, Pitman RL. 2003. Appearance, distribution, and genetic distinctiveness of Longman's beaked whale, *Indopacetus pacificus*. *Marine Mammal Science* **19:** 421–461.

Dalebout ML, Steel D, Baker CS. 2008. Phylogeny of the beaked whale genus *Mesoplodon* (Ziphiidae: Cetacea) revealed by nuclear introns: implications for the evolution of male tusks. *Systematic Biology* **57:** 857–875.

Davies JL. 1963. The antitropical factor in cetacean speciation. *Evolution* **17:** 107–116.

Ehret DJ, MacFadden BJ, Jones DS, DeVries TJ, Foster DA, Salas-Gismondi R. 2012. Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. *Palaeontology* **55:** 1139–1153.

Fish FE. 2002. Balancing requirements for stability and manoeuvrability in cetaceans. *Integrative and Comparative Biology* **42:** 85–93.

Fitzgerald EMG. 2010. The morphology and systematics of *Mammalodon colliveri* (Cetacea: Mysticeti), a toothed mysticete from the Oligocene of Australia. *Zoological Journal of the Linnean Society* **158:** 367–476.

Flower WH. 1867. Description of the skeleton of *Inia geoffrensis* and the skull of *Pontoporia blainvillii*, with remarks on the systematic position of these animals in the Order Cetacea. *Transactions of the Zoological Society of London* **6:** 87–116.

Ford JKB, Ellis GM, Matkin CO, Wetklo MH, Barrett-Lennard LG, Withler RE. 2011. Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology* **11:** 213–224.

Fordyce RE. 1994. *Waipatia maerewhenua*, new genus and new species (Waipatiidae, new family), an archaic late Oligocene dolphin from New Zealand. In: Berta A, Deméré TA, eds. *Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History*. Vol. 29. San Diego: San Diego Natural History Museum, 147–178.

Fordyce RE. 2002. *Simocetus rayi* (Odontoceti: Simocetidae) (new species, new genus, new family), a bizarre new archaic Oligocene dolphin from the eastern North Pacific. *Smithsonian Contributions to Paleobiology* **93:** 185–222.

Fordyce RE, Barnes LG. 1994. The evolutionary history of whales and dolphins. *Annual Review of Earth and Planetary Science* **22:** 419–455.

Fordyce RE, Muizon C. 2001. Evolutionary history of cetaceans: a review. In: Mazin JM, Buffrénil V, eds. *Secondary adaptations of tetrapods to life in water*. München: Verlag Dr. Friedrich Pfeil, 169–233.

Fordyce RE, Quilty PG, Daniels J. 2002. *Australodelphis mirus*, a bizarre new toothless ziphiid-like fossil dolphin (Cetacea: Delphinidae) from the Pliocene of Vestfold Hills, East Antarctica. *Antarctic Science* **14:** 37–54.

Fraser FC, Purves PE. 1960. Hearing in cetaceans: evolution of the accessory air sacs and the structure of the outer and middle ear in recent cetaceans. *Bulletin of the British Museum (Natural History), Zoology* **7:** 1–140.

Geisler JH, MacGowen MR, Yang G, Gatesy J. 2011. A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. *BMC Evolutionary Biology* **11:** 112. doi:10.1186/1471-2148-11-112.

Geisler JH, Sanders AE. 2003. Morphological evidence for the phylogeny of Cetacea. *Journal of Mammalian Evolution* **10:** 23–129.

Goloboff P. 1993. Estimating character weights during tree search. *Cladistics* **9:** 83–91.

Gray JE. 1850. *Catalogue of the specimens of Mammalia in the collections of the British Museum. Part I – Cetacea.* London: Taylor R & JE.

Heyning JE. 1984. Functional morphology involved in intraspecific fighting of the beaked whale, *Mesoplodon carlhubbsi*. *Canadian Journal of Zoology* **62:** 1645–1654.

Heyning JE. 1989. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. *Contributions in Science, Natural History Museum of Los Angeles County* **405:** 1–64.

Heyning JE, Mead JG. 1996. Suction feeding in beaked whales: morphological and observational evidence. *Contributions in Science, Natural History Museum of Los Angeles County* **464:** 1–12.

Hooker SK, Baird RW. 1999. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings of the Royal Society B* **266:** 671–676.

Johnson M, Hickmott LS, Aguilar Soto N, Madsen PT. 2008. Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). *Proceedings of the Royal Society B* **275:** 133–139.

Johnson M, Madsen PT, Aguilar Soto N, Zimmer WMX, Tyack PL. 2004. Beaked whales echolocate for prey. *Proceedings of the Royal Society B* **271:** 383–386.

Johnston C, Berta A. 2011. Comparative anatomy and evolutionary history of suction feeding in cetaceans. *Marine Mammal Science* **27:** 493–513.

Kellogg R. 1932. A Miocene long-beaked porpoise from California. *Smithsonian Miscellaneous Collections* **87:** 1–11.

Lambert O. 2005a. Review of the Miocene long-snouted dolphin *Priscodelphinus cristatus* du Bus, 1872 (Cetacea, Odontoceti) and phylogeny among eurhinodelphinids. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **75:** 211–235.

Lambert O. 2005b. Phylogenetic affinities of the long-snouted dolphin *Eurhinodelphis* (Cetacea, Odontoceti) from the Miocene of Antwerp. *Palaeontology* **48:** 653–679.

Lambert O. 2005c. Systematics and phylogeny of the fossil beaked whales *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium). *Geodiversitas* **27:** 443–497.

Lambert O, Bianucci G, Post K. 2009. A new beaked whale (Odontoceti, Ziphiidae) from the middle Miocene of Peru. *Journal of Vertebrate Paleontology* **29:** 911–922.

Lambert O, Bianucci G, Post K. 2010a. Tusk-bearing beaked whales from the Miocene of Peru: sexual dimorphism in fossil ziphiids? *Journal of Mammalogy* **91:** 19–26.

Lambert O, Bianucci G, Post K, de Muizon C, Salas-Gismondi R, Urbina M, Reumer J. 2010b. The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* **465:** 105–108.

Lambert O, de Buffrénil V, de Muizon C. 2011. Rostral densification in beaked whales: diverse processes for a similar pattern. *Comptes Rendus Palevol* **10:** 453–468.

Lambert O, Louwye S. 2006. *Archaeoziphius microglenoideus*, a new primitive beaked whale (Mammalia, Cetacea, Odontoceti) from the Middle Miocene of Belgium. *Journal of Vertebrate Paleontology* **26:** 182–191.

Lindberg DR, Pyenson ND. 2007. Things that go bump in the night: evolutionary interactions between cephalopods and cetaceans in the tertiary. *Lethaia* **40:** 335–343.

MacCann C. 1975. A study of the genus *Berardius* Duvernoy. *Scientific Reports of the Whales Research Institute* **27:** 111–137.

MacLeod CD. 2002. Possible functions of the ultradense bone in the rostrum of Blainville's beaked whale (*Mesoplodon densirostris*). *Canadian Journal of Zoology* **80:** 178–184.

MacLeod CD. 2006. How big is a beaked whale? A review of body length and sexual size dimorphism in the Family Ziphiidae. *Journal of Cetacean Research and Management* **7:** 301–308.

MacLeod CD, Herman JS. 2004. Development of tusks and associated structures in *Mesoplodon bidens* (Cetacea, Mammalia). *Mammalia* **68:** 175–184.

MacLeod CD, Santos MB, Pierce GJ. 2003. Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association of the United Kingdom* **83:** 651–665.

Maddison DR, Maddison WP. 2005. *MacClade 4 release version 4.08 for OS X*. Sunderland, MA: Sinauer Associates.

Maddison WP, Donoghue MJ, Maddison DR. 1984. Outgroup analysis and parsimony. *Systematic Zoology* **33:** 83–103.

Mead JG. 1989a. Beaked whales of the genus *Mesoplodon*. In: Ridgway SH, Harrison R, eds. *Handbook of marine mammals, vol. 4: river dolphins and the larger toothed whales*. London: Academic Press, 349–430.

Mead JG. 1989b. Bottlenose whales *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* Flower, 1882. In: Ridgway SH, Harrison R, eds. *Handbook of marine mammals, vol. 4: river dolphins and the larger toothed whales*. London: Academic Press, 321–348.

Mead JG. 2008. Beaked whales, overview. In: Perrin WF, Würsig BG, Thewissen JGM, eds. *Encyclopedia of marine mammals*, 2nd edn. San Diego, CA: Academic Press, 94–97.

Mead JG, Fordyce RE. 2009. The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology* **627:** 1–248.

Mead JG, Payne RS. 1975. A specimen of the Tasman beaked whale, *Tasmacetus sheperdi*, from Argentina. *Journal of Mammalogy* **56:** 213–218.

Mickevich MF, Johnson MS. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. *Systematic Zoology* **25:** 260–270.

Minamikawa S, Iwasaki T, Kishiro T. 2007. Diving behaviour of a Baird's beaked whale, *Berardius bairdii*, in the slope water region of the western North Pacific: first dive records using a data logger. *Fisheries Oceanography* **16:** 573–577.

Moore JC. 1968. Relationships among the living genera of beaked whales. *Fieldiana: Zoology* **53:** 209–298.

Morgan GS. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of central Florida. In: Berta A, Deméré TA, eds. *Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History*. Vol. 29. San Diego: San Diego Natural History Museum, 239–268.

de Muizon C. 1981. Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie : deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocène inférieur de Sud-Sacaco. *Travaux de l'Institut Francais d'Etudes andines* **22:** 1–22.

de Muizon C. 1983. Un Ziphiidae (Cetacea) nouveau du Pliocène inférieur du Pérou. *Comptes rendus de l'Académie des Sciences de Paris* **297:** 85–88.

de Muizon C. 1984. Les Vertébrés de la Formation Pisco (Pérou). Deuxième partie: Les Odontocètes (Cetacea, Mammalia) du Pliocène inférieur du Sud-Sacaco. *Travaux de l'Institut Français d'Etudes Andines* **27:** 1–188.

de Muizon C. 1988a. Les Vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les Odontocètes (Cetacea, Mammalia) miocènes. *Travaux de l'Institut Français d'Etudes Andines* **42:** 1–244.

de Muizon C. 1988b. Les relations phylogénétiques des Delphinida. *Annales de Paléontologie* **74:** 115–183.

de Muizon C. 1988c. Le polyphylétisme des Acrodelphidae, odontocètes longirostres du Miocène européen. *Bulletin du Muséum National d'Histoire Naturelle, Paris* **10:** 31–88.

de Muizon C. 1991. A new Ziphiidae (Cetacea) from the Early Miocene of Washington State (USA) and phylogenetic analysis of the major groups of odontocetes. *Bulletin du Muséum National d'Histoire Naturelle, Paris* **12:** 279–326.

de Muizon C, Bellon H. 1980. L'âge mio-pliocène de la Formation Pisco (Pérou). *Comptes Rendus de l'Académie des Sciences de Paris* série 2 **290:** 1063–1066.

de Muizon C, Bellon H. 1986. Nouvelles données sur l'âge de la Formation Pisco (Pérou). *Comptes Rendus de l'Académie des Sciences de Paris* série 2 **303:** 1401–1404.

de Muizon C, DeVries TJ. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* **74:** 547–563.

Noren SR, Williams TM. 2000. Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration. *Comparative Biochemistry and Physiology, Part A* **126:** 181–191.

Oliver WRB. 1937. *Tasmacetus sheperdi*: a new genus and species of beaked whale from New Zealand. *Proceedings of the Zoological Society of London B* **107:** 371–381.

Omura H. 1972. An osteological study of the Cuvier's beaked whale, *Ziphius cavirostris*, in the northwest Pacific. *The Scientific Reports of the Whales Research Institute* **24:** 1–34.

Perrin WF, Thieleking JL, Walker WA, Archer FI, Robertson KM. 2011. Common bottlenose dolphin (*Tursiops truncatus*) in California waters: cranial differentiation of coastal and offshore ecotypes. *Marine Mammal Science* **27:** 769–792.

Pitman RL, van Helden AL, Best PB, Pym A. 2006. Shepherd's beaked whale (*Tasmacetus shepherdi*): information on appearance and biology based on strandings and at-sea observations. *Marine Mammal Science* **22:** 744–755.

Post K, Lambert O, Bianucci G. 2008. First record of *Tusciziphius crispus* (Cetacea, Ziphiidae) from the Neogene of the US east coast. *Deinsea* **12:** 1–10.

Pyenson ND, Sponberg SN. 2011. Reconstructing body size in extinct crown Cetacea (Neoceti) using allometry, phylogenetic methods and tests from the fossil record. *Journal of Mammalian Evolution* **18:** 269–288.

Reeves RR, Brownell RL, Jr. 1989. Susu *Platanista gangetica* (Roxburgh, 1801) and *Platanista minor* Owen, 1853. In: Ridgway SH, Harrison R, eds. *Handbook of marine mammals, vol. 4: river dolphins and the larger toothed whales*. London: Academic Press, 69–99.

Reidenberg JS, Laitman JT. 1994. Anatomy of the hyoid apparatus in Odontoceti (toothed whales): specializations of their skeleton and musculature compared with those of terrestrial mammals. *The Anatomical Record* **240:** 598–624.

Reidenberg JS, Laitman JT. 2008. Sisters of the sinuses: cetacean air sacs. *The Anatomical Record* **291:** 1389–1396.

Rommel SA. 1990. Osteology of the bottlenose dolphin. In: Leatherwood S, Reeves RR, eds. *The bottlenose dolphin*. San Diego, CA: Academic Press, 29–49.

Rommel SA, Costidis AM, Fernández A, Jepson PD, Pabst DA, Houser DS, Cranford TW, van Helden AL, Allen DM, Barros NB. 2006. Elements of beaked whale anatomy and diving physiology and some hypothetical causes of sonar-related stranding. *Journal of Cetacean Research and Management* **7:** 189–209.

Schreer JF, Kovacs KM. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* **75:** 339–358.

Smith AB. 1994. *Systematics and the fossil record. Documenting evolutionary patterns.* Oxford, UK: Blackwell Scientific.

Swofford DL. 2001. *PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4b10.* Sunderland, MA: Sinauer Associates.

Trammer J. 2005. Maximum body size in a radiating clade as a function of time. *Evolution* **59:** 941–947.

True FW. 1910. An account of the beaked whales of the family Ziphiidae in the collection of the United States National Museum, with remarks on some specimens in other American museums. *Bulletin of the United States National Museum* **73:** 1–89.

Tyack PL, Johnson M, Soto NA, Sturlese A, Madsen PT. 2006. Extreme diving of beaked whales. *Journal of Experimental Biology* **209:** 4238–4253.

Uhen MD. 2008. A new *Xenorophus*-like odontocete cetacean from the Oligocene of North Carolina and a discussion of the basal odontocete radiation. *Journal of Systematic Palaeontology* **6:** 433–452.

Watanabe YY, Sato K, Watanuki Y, Takahashi A, Mitani Y, Amano M, Aoki K, Narazaki T, Iwata T, Minamikawa S, Miyazaki N. 2011. Scaling of swim speed in breath-hold divers. *Journal of Animal Ecology* **80:** 57–68.

Werth AJ. 2004. Functional morphology of the sperm whale tongue, with reference to suction feeding. *Aquatic Mammals* **30:** 405–418.

Werth AJ. 2006. Mandibular and dental variation and the evolution of suction feeding in Odontoceti. *Journal of Mammalogy* **87:** 579–588.

Whitmore FC, Jr, Kaltenbach JA. 2008. Neogene cetacea of the Lee Creek Phosphate Mine, North Carolina. *Virginia Museum of Natural History Special Publication* **14:** 181–269.

Wiens JJ. 2003. Incomplete taxa, incomplete characters, and phylogenetic accuracy: is there a missing data problem? *Journal of Vertebrate Paleontology* **23:** 297–310.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of characters used in the cladistic analysis.
Appendix S2. Character/taxon matrix.