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A NEW BEAKED WHALE (CETACEA, ODONTOCETI) FROM THE LATE MIOCENE OF PATAGONIA, ARGENTINA

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ABSTRACT—A new genus and species of Ziphiidae, *Notoziphius bruneti*, gen. et sp. nov., from the late Miocene of Patagonia, is described on the basis of a well-preserved skull and partial left and right dentaries. It can be diagnosed by large, triangular, and markedly asymmetric nasals that strongly point anteroventrally, the ascending process of the maxilla not expanded posteriorly, supraoccipital strongly sloped posteroventrally; elliptical fossa on the nasal process of the premaxilla, small and anterolaterally directed premaxillary crest, and the presence of well-defined alveoli in the maxilla. A phylogenetic analysis including 25 ziphiid genera and 31 characters shows *Notoziphius* as nested within Ziphiidae in a basal clade with *Aporotus*, *Beneziphius*, *Messapicetus*, and *Ziphirostrum*. This clade is diagnosed by medial fusion of the premaxillae that closes the mesorostral groove, lateral margin of prenasal basin formed by a thick strip of maxilla, premaxillary crest antero-laterally directed, and reduced contact between nasal and premaxillary crest. The presence of *Notoziphius* in the Miocene of Patagonia increases our knowledge of ziphiid diversity in South America. *Notoziphius bruneti* and other Miocene records of ziphiids reinforce the idea that during the Miocene ziphiids were widely distributed and diverse.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline/UJVP

INTRODUCTION

The Ziphiidae or beaked whales are one of the most conspicuous and little known families of the Odontoceti. Among the most striking features are their deep-diving behavior, pronounced sexual dimorphism, the presence of a high forehead or melon and ‘V’-shaped throat grooves, and the extreme reduction of the number of erupted teeth. Due to their pelagic and deep-water habitat, many of extant species are known by only for a few or even just a single-stranded specimens, and some have never been seen alive. Their life histories, behaviors, social structures, and reproductive cycles remain unknown for most of species. As a consequence, this is one of the few large-vertebrate groups for which new species continue to be described (Dalebout et al., 2004).

The evolutionary history of Ziphiidae was poorly known due to its fragmentary fossil record. However, in recent decades new finds from several localities in both hemispheres have revealed a high diversity of this family during the Neogene (e.g., Horikawa et al., 1987; Takahashi et al., 1989; Bianucci et al., 1992, 2007, 2010; Bianucci, 1997; Bianucci and Post, 2005; Lambert, 2005a; Lambert and Louwey, 2006; Post et al., 2008; Lambert et al., 2009, 2010). In South America, the ziphiid fossil record is represented by three species from the Miocene–Pliocene of Peru (*Nazcacetus urbinai* Lambert, Bianucci, and Post, 2009, middle Miocene; *Messapicetus gregarius* Bianucci, Lambert, and Post, 2010, middle Miocene; and *Ninoziphius platyrostris* Muizon, 1983, lower Pliocene) and fragmentary material from the middle Miocene of Ecuador (Bianucci et al., 2005). In addition, Cozzuol (1993, 1996) reported a well-preserved skull and partial left and right dentaries of a ziphiid recovered from the late Miocene of Chubut province, Argentina, which represents the first ziphiid record from the Southwest Atlantic. The combination of features of the synver-

tex (sensu Moore, 1968) indicates that the specimen reported by Cozzuol represents a new species of ziphiid. The purpose of this paper is to diagnose and describe a new genus and species based on this specimen and to determine its phylogenetic relationships.

Institutional Abbreviations—**CNPMAMM**, Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico, Puerto Madryn, Chubut Province, Argentina; **MPEF**, Museo Paleontológico ‘Egidio Feruglio,’ Trelew, Chubut Province, Argentina; **NMNZ**, Museum of New Zealand Te Papa, Tongarewa, Wellington, New Zealand; **PEM**, Marine Mammal Collection, Port Elizabeth Museum, Port Elizabeth, South Africa; **USNM**, Department of Paleobiology and Department of Vertebrate Zoology (Division of Mammals), National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

MATERIALS AND METHODS

Specimens and Terminology

The new ziphiid species is described on the basis of one specimen housed in the Museo Paleontológico ‘Egidio Feruglio,’ Trelew, Chubut Province. Data from the literature and specimens held in scientific collections were used in the comparative and phylogenetic studies: *Ninoziphius* (Muizon, 1983, 1984); *Messapicetus gregarius* and *M. longirostris* (Bianucci et al., 1992, 1994, 2010); *Caviziphius altirostris* (Bianucci and Post, 2005); *Aporotus dicyrtus* and *A. recurvirostris*, *Beneziphius brevirostris*, *Choneziphius planirostris*, and *Ziphirostrum marginatum* (Lambert, 2005a); *Eurhinodelphis cocheteuxi* (Lambert, 2005b); *Archaeoziphius microglenoideus* (Lambert and Louwey, 2006); *Africanacetus ceratopsis*, *Ihlengesi saldanhae*, *Izikoziphius rossi* and *I. angustus*, *Khoikhoicetus agulhasis*, *Microberardius africanus*, *Nenga meganasalis*, *Pterocetus benguelae*, and *Xhosacetus hendeyi* (Bianucci et al., 2007); *Tusciziphius*

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crispus (Bianucci, 1997; Post et al., 2008); *Nazcacetus urbinai* (Lambert et al., 2009); *Squalodon calvertensis* (USNM 24356, USNM 25910, USNM 328343, USNM 175382); *Berardius arnuxii* (NMNZ7, NMNZ1406) and *B. bairdii* (USNM 550891); *Tasmacetus shepherdii* (NMNZ2184, NMNZ1826, USNM 484878); *Indopacetus pacificus* (PEM N1960, USNM 593534); *Hyperoodon planifrons* (NMNZ1806, NMNZ 2214; CNPMAMM 0663); *Mesoplodon grayi* (NMNZ2613); *M. mirus* (USNM 504764); *M. bidens* (USNM 550204); *M. europaeus* (USNM 593437); *Ziphius cavirostris* (CNPMAMM 0657, NMNZ 2356).

The anatomical terminology used in the description follows Moore (1968), Heyning (1989), and Mead and Fordyce (2009). Measurements were taken following the standard skull measurements proposed by Perrin (1975). Others measures more specific for ziphiids were taken from Lambert et al. (2009).

Phylogenetic Analysis

In order to determine the phylogenetic affinities of the new species, a cladistic analysis was conducted using the Bianucci et al. (2010) data set with the addition of five ziphiid taxa (*Aporotus*, *Caviziphius*, *Khoikhoicetus*, *Nenga*, and *Ninoziphius*) and two characters from Lambert (2005b) (see Appendix 1 for character descriptions and Appendix 2 for characters coding). Heuristic parsimony analysis of the data set was performed in TNT version 1.1 (Goloboff et al., 2008a, 2008b) using the traditional search under implied weights ($K = 6$). All characters were treated as unordered. The analysis was performed using 1000 replicates of heuristic searches using random taxon addition sequences, followed by TBR branch-swapping (holding 10 trees per replicate). The resulting most parsimonious trees (MPTs) were summarized with a strict consensus tree with zero-length branches collapsed (i.e., 'rule 1' of Coddington and Scharff, 1994). A measure of tree support, bootstrap resampling analysis, was performed. To identify unstable taxa, we use the IterPCR procedure (Pol and Escapa, 2009) over the entire set of MPTs. This procedure allows the identification of the set of characters that positively support alternative positions of the unstable taxon and the set of characters scored with missing entries that could reduce the instability of problematic taxa if they are scored (Pol and Escapa, 2009; Escapa and Pol, 2011).

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
ODONTOCETI Flower, 1867
ZIPHIIDAE Gray, 1850
NOTOZIPHIUS, gen. nov.

Type Species—*Notoziphius bruneti* by monotypy.

Etymology—'Nótos' in Ancient Greek, the southern wind, referring to the weather conditions of Patagonia, where the holotype was found; *Ziphius*, type genus of the family.

Diagnosis—As for type and only species.

NOTOZIPHIUS BRUNETI, sp. nov.
(Figs. 2–8)

Holotype—MPEF-PV 3282, partial skull and fragments of left and right dentaries belonging to the same individual. The holotype is a partial but well-preserved skull with an incomplete rostrum and cranium (Figs. 2, 3). Missing elements include anterior and dorsal portions of the rostrum, right orbital region (left counterpart partially preserved), right jugal, right lacrimal, ventral and left-lateral portions of occipital shield, occipital condyles, left parietal and squamosal, most of the basioccipital and pterygoids, portion of the vomer, both periotics, and bullae and auditory ossicles. The left portion of occipital shield and right temporal region are distorted, possibly due to diagenetic processes. Based on presence of skull sutures that are not fused

along their full lengths (Class V of Perrin, 1975), the holotype of *Notoziphius bruneti* is determined to be a subadult.

Etymology—The species name honors Rodolfo Brunet (†), who discovered the holotype, donated it for this study, and was a very productive fossil collector in the region for many years.

Type Locality—The specimen was found on the northern coast of Playa El Doradillo (42°40'S, 64°59'W), which is located 15 km north of the town of Puerto Madryn, western coast of Golfo Nuevo, Chubut Province, Argentina (Fig. 1).

Type Horizon—The holotype, MPEF-PV 3282, was collected from the lowermost level of the Puerto Madryn Formation, about 2 m above the unconformable contact with the underlying Gaiman Formation (Fig. 1). The specimen was found in a horizon of bioturbated muddy sandstones stratigraphically between two coquina horizons: one in coarse sandstones (below) and another in a conglomerate (above).

The Puerto Madryn Formation sequence comprises a transgressive-regressive cycle that was deposited in a shallow marine environment (Scasso and del Río, 1987). The age of this unit is controversial. A late middle Miocene (Del Río, 1988, 1990) and recently a late Miocene (Martínez and del Río, 2002; del Río, 2004) age was established according to paleontologic, paleobiogeographic, and paleoclimatic evidence of its marine mollusk assemblage. Available radiometric K/Ar and Sr⁸⁷/Sr⁸⁶ dates (9.41 Ma, Zinsmeister et al., 1981; 10 ± 0.3 Ma, Scasso et al., 2001), as well as the palynological evidence (Palazzesi and Barreda, 2004; Barreda and Palazzesi, 2007) also point to a late Miocene age (Tortonian). The Puerto Madryn Formation contains abundant and well-preserved marine invertebrate assemblages (del Río, 1990, 2000, 2004; del Río et al., 2001) and marine and continental vertebrate assemblages (Cione, 1978; Cione and Tonni, 1981; Cozzuol 1993, 1996, 2001; Riva Rossi et al., 2000; Dozo et al., 2002, 2007, 2010; Cione et al., 2005; Acosta Hospitaleche et al., 2007).

Diagnosis—*Notoziphius* differs from all other Ziphiidae in the following combination of characters: large, triangular and markedly asymmetric nasals, strongly point anteroventrally with the anterior margin anterior to the premaxillary crest; the ascending process of the maxilla is not expanded posteriorly; supraoccipital strongly sloped posteroventrally; elliptical fossa in the nasal process of the premaxilla (shared only with *Izikoziphius*); functional maxillary teeth (shared with *Messapicetus*, *Ninoziphius*, and *Tasmacetus*); large distance between premaxillary crest (differs from *Hyperoodon* and *Mesoplodon*); reduced contact between nasal and premaxillary crests (shared with *Aporotus*, *Beneziphius*, *Caviziphius*, *Choneziphius*, *Izikoziphius*, *Messapicetus*, *Ziphistrostrum*, and *Ziphius*); lack of inclusion of the nasal in the premaxillary crest (differs from *Nenga*, *Xhosacetus*, *Khoikhoicetus*, *Pterocetus*, *Indopacetus*, *Hyperoodon*, *Mesoplodon*, *Ihlangesi*, and *Africanacetus*); lack of prenasal basin (differs from *Aporotus*, *Beneziphius*, *Messapicetus*, *Ziphistrostrum*, and *Ziphius*); lack of constriction of the nasal process of the right premaxilla (differs from *Africanacetus*, *Beneziphius*, *Khoikhoicetus*, *Hyperoodon*, *Indopacetus*, *Ihlangesi*, *Mesoplodon*, *Messapicetus*, *Nazcacetus*, *Pterocetus*, *Tasmacetus*, *Tusciziphius*, *Xhosacetus*, and *Ziphistrostrum*); weak asymmetry of the premaxillary sac fossa (differs from *Caviziphius*, *Choneziphius*, *Hyperoodon*, *Izikoziphius*, *Tusciziphius*, and *Ziphius*); nasal process of the premaxilla concave with posterodorsal portion vertical (differs from *Archaeoziphius*, *Berardius*, *Microberardius*, *Tusciziphius*, *Izikoziphius*, *Ziphius*, *Khoikhoicetus*, *Hyperoodon*, *Mesoplodon*, *Ihlangesi*, and *Africanacetus*); lower vertex (differs from *Izikoziphius*, *Ziphius*, and *Hyperoodon*); premaxillary crest anterolaterally directed (shared with *Aporotus*, *Beneziphius*, *Messapicetus*, *Tusciziphius*, *Caviziphius*, *Choneziphius*, *Izikoziphius*, *Ziphistrostrum*, and *Ziphius*); well-defined anteromedial depression of the dorsal surface of the nasal (shared with *Aporotus*, *Beneziphius*,

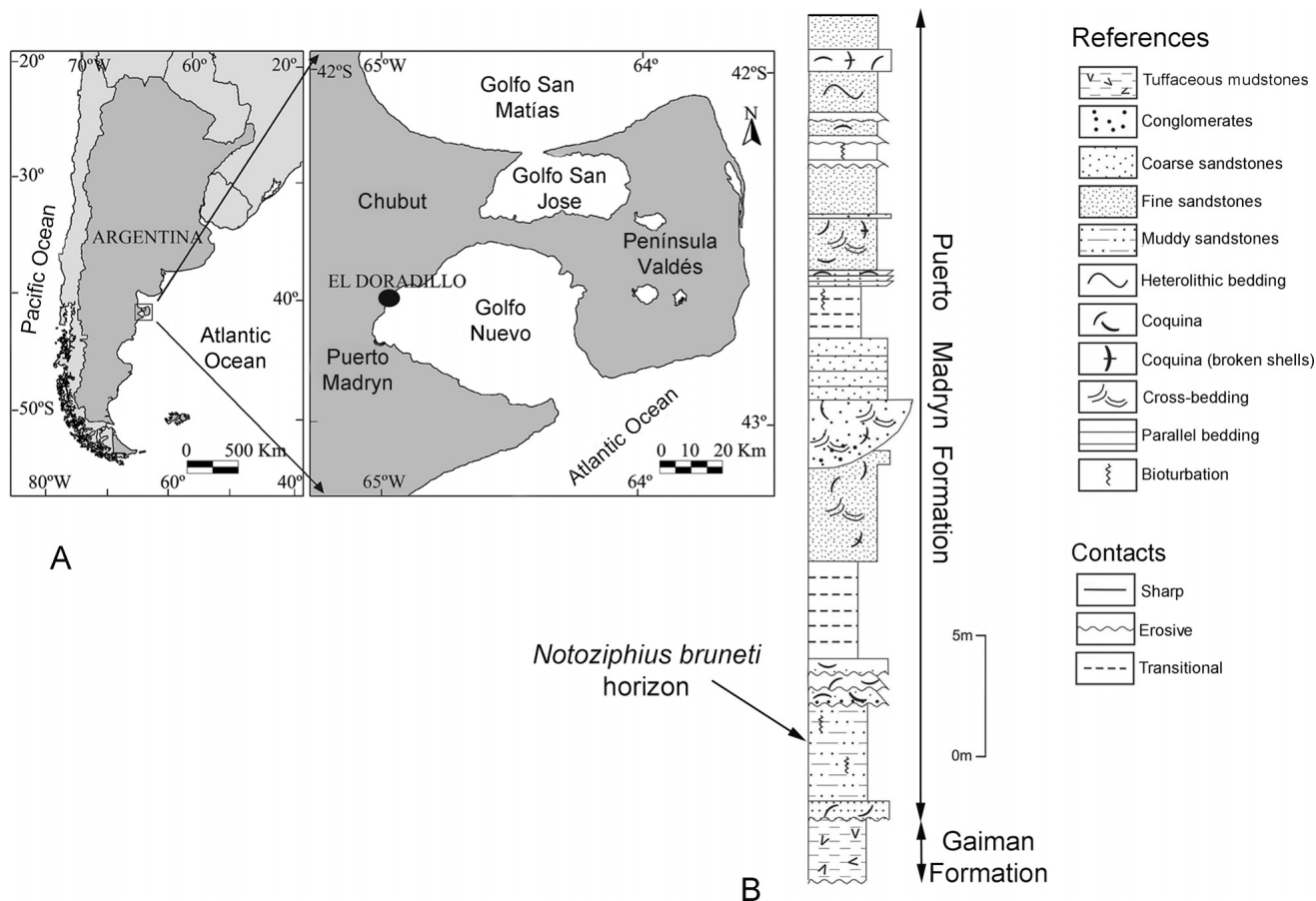


FIGURE 1. Locality and stratigraphic position of the *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). **A**, map of Península Valdés, Chubut Province (Argentina), showing El Doradillo (black circle), the locality from which the holotype was collected. **B**, stratigraphic section of Puerto Madryn Formation at the type locality, modified from Scasso et al. (2001).

Caviziphius, *Messapicetus*, *Nazcacetus*, *Tasmacetus*, and *Ziphirostrum*); and small temporal fossa (differs from *Messapicetus*).

DESCRIPTION

Skull

Cranium—The cranium is slightly wider (370 mm) than it is tall (300 mm). In lateral view, its dorsal outline is slightly concave due to the gentle posterior rising of the nasal process of the premaxilla. The synvertex is moderately elevated in lateral view and markedly asymmetric in dorsal view, the nasals being the most conspicuous elements. The external bony nares, which together are approximately as wide as they are long, open 50 mm behind the antorbital notches. In lateral view, the maxillary rostral crests are low.

Rostrum—The preserved portion of the rostrum represents 61% of the condylobasal length of the skull (Table 1). The dorsal surface is damaged so that it is not possible to see if the mesorostral groove was originally open (primitive condition) or closed due to medial fusion of the premaxillae (derived conditions observed in *Messapicetus*, *Ziphirostrum*, and other fossil ziphiids). The rostrum is robust, and in dorsal view it is broad and tapers distally as in *Berardius*, *Hyperoodon*, *Tasmacetus*, and *Ziphius*, but unlike some species of *Mesoplodon* and *Messapicetus* that have a more slender and narrow rostrum. In dorsal view, the rostrum has a triangular outline: wide at the level of the antorbital notches and narrow anteriorly. The preserved floor of the mesorostral canal is broader and deeper at the level of antorbital

notches and narrows and shallows anteriorly. In lateral view, the ventral margin of the rostrum is straight and the posterior portion slopes posteroventrally, consequently the rostrum is dorsoventrally deeper at its posterior end.

Maxilla—In the rostral region, the maxilla is transversely broad (52 mm) and dorsoventrally deep (79 mm) anterior to the antorbital notches, becoming narrower and lower toward its anterior end (width = 12 mm; depth = 43.5 mm). At the anterior-most preserved end, the dorsal surface of the rostrum is damaged and the suture with the premaxilla cannot be observed (Figs. 2, 3). In lateral view, a shallow alveolar groove is visible near the lateral margin of the maxilla and terminates approximately 130 mm from the antorbital notch; 11 maxillary alveoli can be recognized on the better-preserved left side (Fig. 4). As in *Messapicetus* and unlike *Ninoziphius*, these alveoli are elongated (length = 16 mm; width = 11 mm), with the anterior ones larger and shallower than the posterior ones. The anterior alveoli probably lodged conical teeth similar to those of *Tasmacetus*. The interalveolar septa between the posterior-most alveoli are better defined than the anterior-most ones. The alveoli are of uniform shape, lack double roots, and show no evidence of heterodonty.

Near the antorbital notch is the anteroposteriorly oriented rostral maxillary crest, which has a maximum height of 14 mm at the level of the antorbital notch. It is less pronounced than in *Aporotus* and extends to the level of the anterior margin of the external bony nares (Figs. 4, 5A). Posterodorsally, the maxilla projects toward the vertex forming the ascending process of the maxilla and extends posteriorly to a lesser extent than in other ziphiids (e.g.,

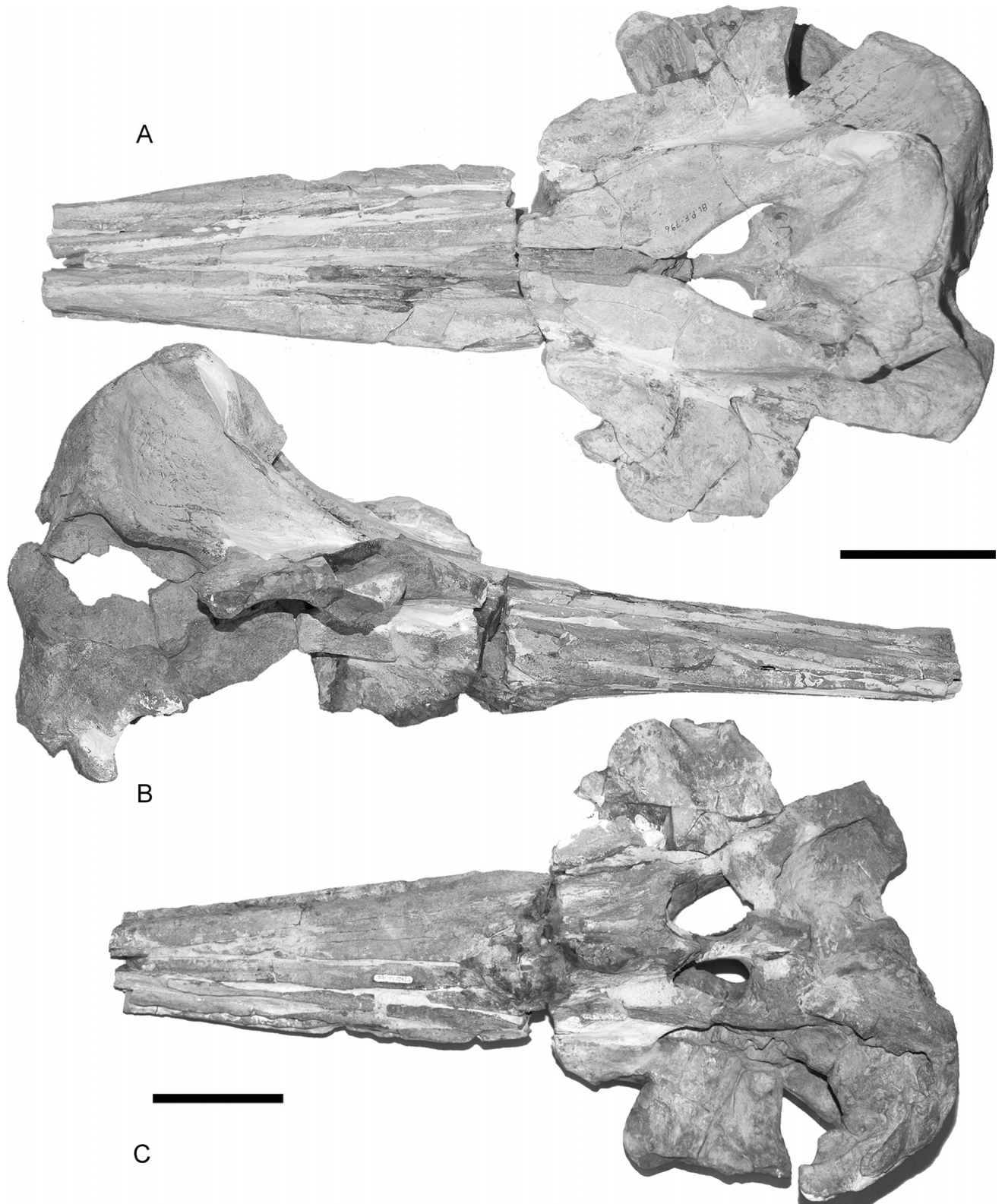


FIGURE 2. *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). Skull in (A) dorsal, (B) right lateral, and (C) ventral views. Scale bar equals 10 cm.

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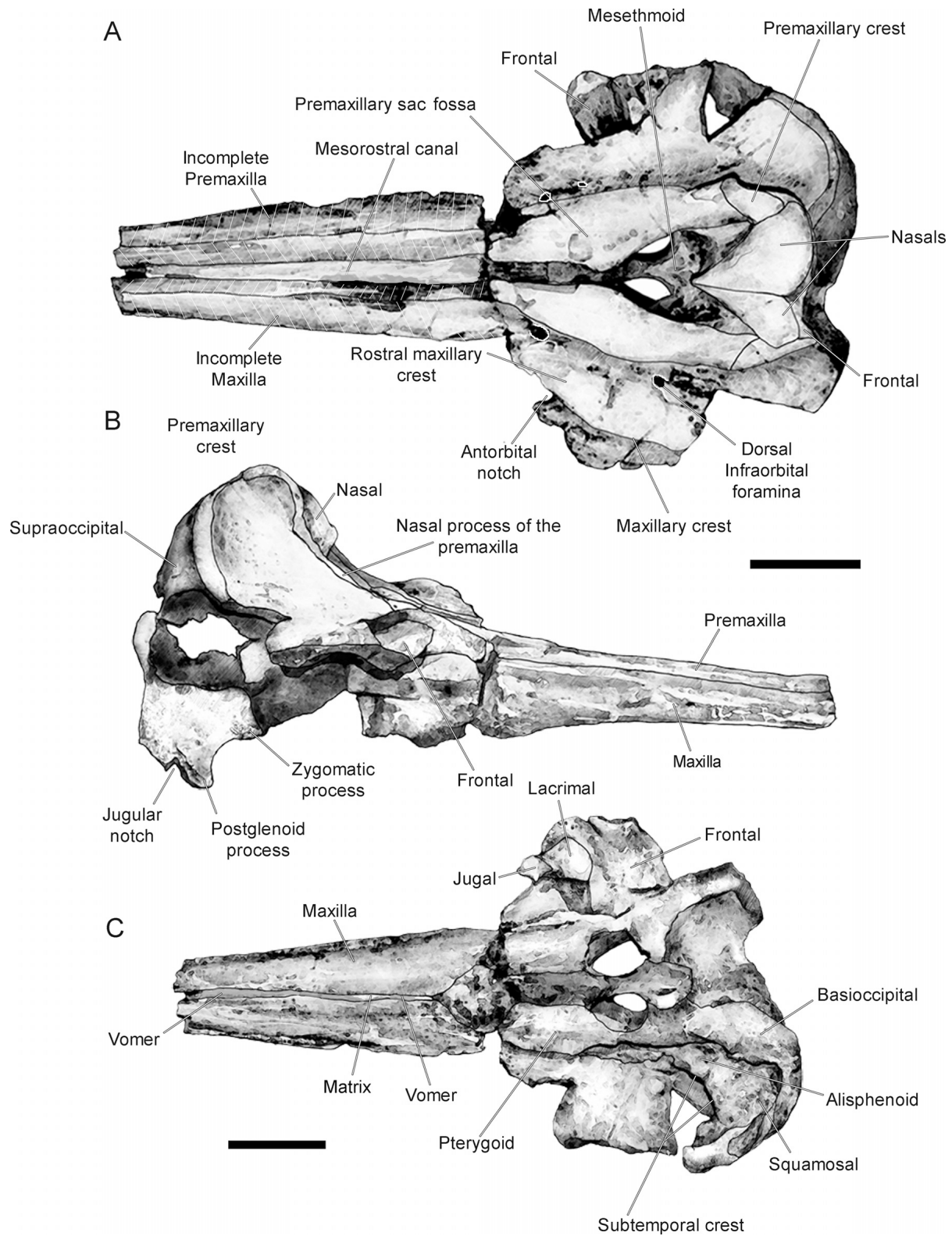


FIGURE 3. *Notoziphium bruneti*, gen. et sp. nov. (MPEF-PV 3282). Interpretive drawings of skull in (A) dorsal, (B) right lateral, and (C) ventral views. Scale bar equals 10 cm.

TABLE 1. Measurements (in mm) of skull of *Notoziphius bruneti* (MPEF-PV 3282).

Condylbasal length, from tip of rostrum to posterior of occipital condyles	+625
Length of rostrum, from tip to line across posterior limits of antorbital notches	+384
Width of the rostrum at base, along line across posterior limits of antorbital notches	e220
Width of rostrum at 60 mm anterior to line across posterior limits of antorbital notch	+127
Width of rostrum at 120 mm anterior to line across posterior limits of antorbital notch	130
Width of rostrum at 300 mm anterior to line across posterior limits of antorbital notch	90
Distance from tip of rostrum to external bony nares	+425
Distance from tip of rostrum to internal bony nares	+453
Width of premaxillae at rostrum base	123
Greatest preorbital width	331
Greatest postorbital width	+339
Greatest width of external bony nares	78
Width of premaxillary sac fossae	150
Width of right premaxillary sac fossa	74
Width of left premaxillary sac fossa	63
Minimum width of ascending process of right premaxilla	28
Minimum width of ascending process of left premaxilla	18
Maximum width of premaxillary crests	166
Width of right premaxillary crest	24
Width of left premaxillary crest	37
Minimum distance between premaxillary crests	95
Maximum width of nasals	114
Length of medial suture of nasals on vertex	71
Length of medial suture of frontals on vertex	19.5
Minimum posterior distance between maxillae	106
Length of orbit, from apex of preorbital process of frontal to apex of postorbital process	+149
Vertical distance between terminal foramen and top of vertex	124
Greatest height of temporal fossa	85
Greatest width of temporal fossa	e71
Vertical external height of braincase, from midline of basioccipital to dorsal extremity of supraoccipital	e213
Number of alveolus in the left maxillae	11

Abbreviations: e, estimate; +, nearly complete.

Aporotus, *Messapicetus*, and *Ziphirostrum*). In lateral view, the profile of the ascending process of the maxilla is concave between the nasal process of the premaxilla and the supraorbital margin of the maxilla. There it forms the facial fossa, the site of attachment of most of the nasofacial muscles. As in *Berardius* and unlike *Ziphius*, the facial fossa is slightly concave in *Notoziphius*, suggesting poor development of nasofacial muscles (Heyning, 1989). The origin of the pars anteroexternus muscle, the most super-

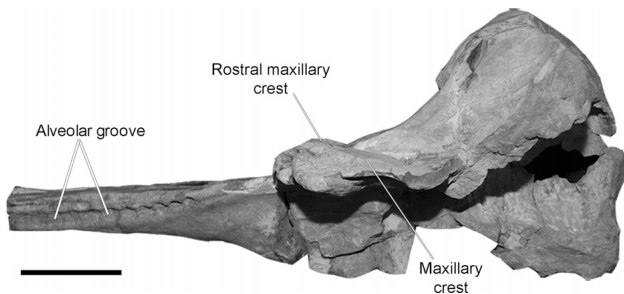


FIGURE 4. *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). Skull in left lateral view. Scale bar equals 10 cm.

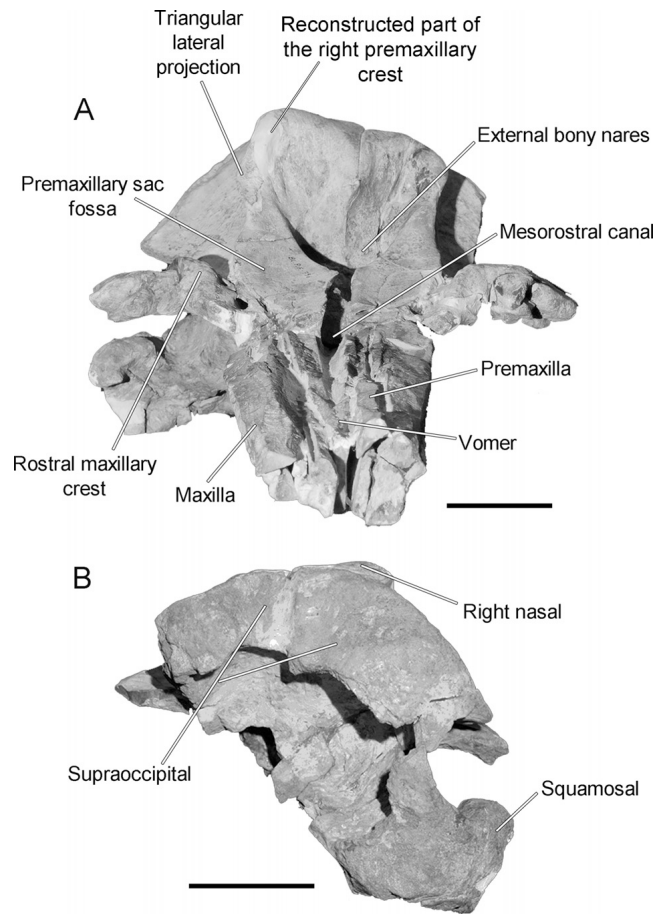


FIGURE 5. *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). Skull in (A) anterodorsal and (B) posterior views. Scale bar equals 10 cm.

ficial nasofacial muscle, is inferred to be on the maxillary crest that develops posterior to the antorbital notch on the supraorbital surface of the maxilla (Figs. 3A, 4). The origin of the deeper pars anterointernus muscle is inferred to be on the dorsal surface of the rostral maxillary crest and on the entire dorsal surface of the facial fossa, as indicated by the presence of marked striations (Heyning, 1989). The frontomaxillary suture is incompletely fused. There are several dorsal infraorbital foramina that transmitted blood vessels and infraorbital branches of the trigeminal (V) nerve: at level of the antorbital notch there are three foramina on the right side and two on the left, and posterior to these there is a larger foramen on both sides (Fig. 3A).

Premaxilla—On the rostrum, the dorsal surface of the premaxilla is damaged; therefore, the suture with maxilla and vomer as well as the presence or absence of premaxillary foramina cannot be observed. The premaxilla widens near and posterior to the antorbital notch where it forms the premaxillary sac fossa. The premaxillary sac fossae are slightly asymmetrical (ratio between the widths of the left and right fossa is 0.85). This condition differs from *Caviziphius*, *Choneziphius*, *Tusciziphius*, and *Ziphius*, in which the asymmetry between both fossae is greater. Posterodorsally, the premaxilla becomes narrower (18 mm) and forms the nasal process of the premaxilla. The nasal process of the premaxilla gradually rises posteriorly, generating a dorsal profile of the facial region that is gently concave in lateral view; the posterior portion of the nasal process is vertical (Figs. 2B, 3B). The constriction of the nasal process of the premaxilla between the

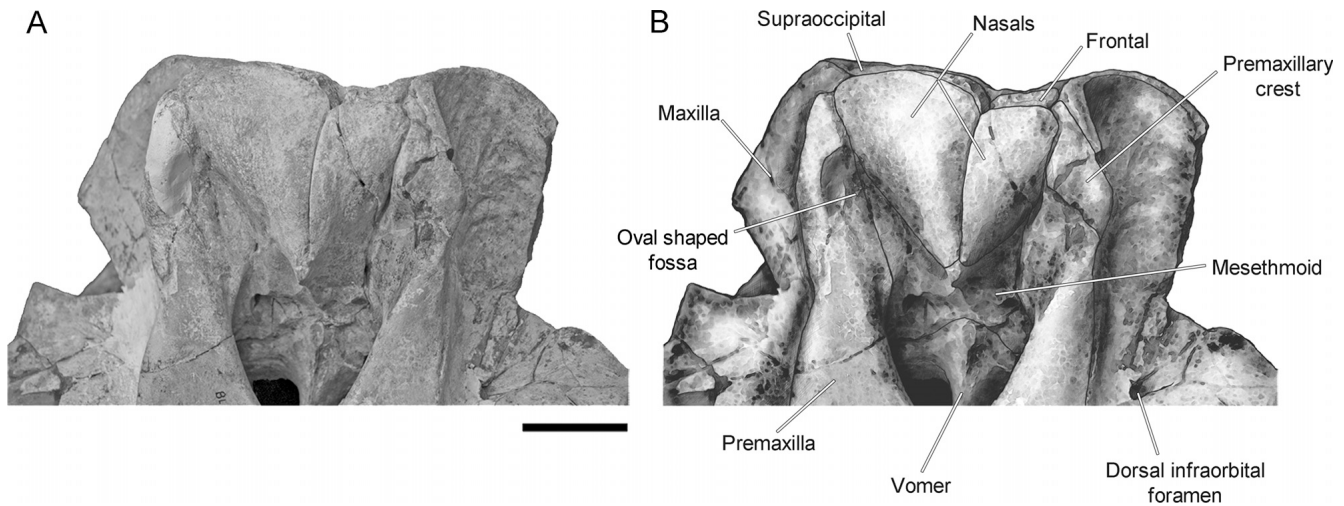


FIGURE 6. *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). Skull in (A) anterior view and (B) its interpretive drawing. Scale bar equals 5 cm.

premaxillary sac fossa and premaxillary crest is less pronounced than in *Beneziphius*, *Messapicetus*, and *Ziphirostrum*. In anterior view, the nasal process of the right premaxilla forms, together with the maxilla, a short triangular lateral projection that is not present on the left side (Fig. 5A). Both premaxillary crests extend less anteriorly than the anterior tip of the nasals. The premaxillary crests are weak, slightly asymmetrical (left larger than right) (Fig. 6), and unlike the condition in *Mesoplodon* and *Hyperoodon*, they are widely separated from each other (Table 1). The anterior ends of these crests extend anterolaterally, as in *Aporotus*, *Beneziphius*, *Caviziphius*, *Choneziphius*, *Izikoziphius*, *Messapicetus*, *Tusciziphius*, *Ziphirostrum*, and *Ziphius*. In anterior view, the right premaxillary crest is higher than the left one, as is also observed in other ziphiids (e.g., *Izikoziphius*, *Tusciziphius*, and *Ziphius*) (Fig. 5A). The posterior premaxilla-maxilla suture at the level of the premaxillary crests is concave on the right side and convex on the left. In the medial portion of each nasal process of the premaxilla, ventral to the premaxillary crests and lateral to the nasals, there is a deep and oval-shaped fossa, similar to that observed in *Izikoziphius*, which is probably related to the presence of an air sac (Fig. 6B) (Heyning, 1989; Bianucci et al., 2007). The fossa is developed on the medial surface of the nasal process of the premaxilla, unlike *Izikoziphius* where it occurs on the dorsal surface of the nasal process of the premaxilla and the lateral surface of the nasal. There is no evidence for the presence of a prenarial basin.

Nasal—The nasals are among the most distinctive elements of the skull (Fig. 6). They form most of the synvertex and, together with the mesethmoid, the posterior narial wall. In dorsal view, the nasals are markedly asymmetric: the right nasal is almost twice the length of the left one (74 and 40 mm, respectively). In dorsal view, they are broad at their posterior ends and their lateral borders converge anteriorly, resulting in a rough triangular outline. In anterior view, the nasals have a slight anteromedial depression (Fig. 5A). The suture between the nasals is slightly deviated to the left side and the dorsal surface of the nasals strongly slopes anteroventrally. The posterior margin of each nasal is convex posteriorly and the naso-frontal suture is visible. As in *Beneziphius*, *Choneziphius*, *Ziphirostrum*, and *Ziphius*, the premaxillary crests only contact the posterior portion of the nasals, with the latter taking no part in the formation of the crests. In posterior view, the right nasal is slightly higher than the left one, and both are approximately at the same level as the frontals (Fig. 5B).

Jugal and Lacrimal—Both bones are partially preserved on the left side (Figs. 2C, 7). The jugal fragment is located ventrolateral

to the antorbital notch, and in ventral view it appears to be unfused to the lacrimal and maxilla. In contrast to some species of *M. bidens* and *M. europaeus*, in dorsal view the jugal is not visible in the antorbital notch. The lacrimal is located posterior to the jugal and contacts the maxilla along a defined suture for most of its length. The lacrimal does not form part of the preorbital process or antorbital notch.

Mesethmoid—The preserved parts include the anterior portion of the mesethmoid, which fills the posterior end of the mesorostral canal, and the dorsal projection that forms part of the posterior narial wall (Fig. 6). In the latter region, the mesethmoid has a median ridge that extends dorsoventrally and is most pronounced where it contacts the nasals. The surfaces on both sides of this ridge are slightly concave.

Vomer—In dorsal view, the vomer forms the ventrolateral wall of the mesorostral canal (Fig. 5A). At its posterior end, this canal is concave, wide (17 mm), and deep (35 mm), becoming shallower and narrower anteriorly until it terminates. There is no evidence of a mesorostral ossification of the vomer filling the mesorostral canal. In ventral view, the palatal portion of the vomer exhibits a narrow exposure between the medial margins of the maxillae from the anterior end of the preserved portion of the rostrum until about 200 mm from the anterior margin of the internal bony nares. Towards its posterior end, the vomer appears to be widely exposed. We say ‘appears’ because the ventral surface of the skull is poorly preserved and portions of the maxillae, palatines, and pterygoids that originally covered the vomer are not preserved. At the level of the internal bony nares, the vomer forms the ventral portion of the nasal septum (Figs. 2C, 3C).

Frontal—On the vertex, the frontals are exposed as a narrow transverse band that contacts the posterior margin of the nasals anteriorly and the supraoccipital posteriorly (Fig. 6). The dorsal exposure of the frontals on the vertex are shorter (anteroposteriorly) than those observed in other taxa such as *Messapicetus*. The orbital region is incomplete on both sides, but the left preorbital process of the frontal is complete except for a small part of the frontal and appears rather robust.

Temporal Fossa: Parietal, Squamosal—The parietal is part of the lateral wall of the cranium and forms, together with the squamosal, the medial wall of the temporal fossa, which is only partially preserved (Figs. 2B, 3B). The posterior wall of the temporal fossa is markedly concave and formed by the squamosal. The dorsolateral margin of the temporal fossa is defined by a weak temporal crest formed by the parietal and squamosal; this crest extends anteriorly onto the zygomatic process

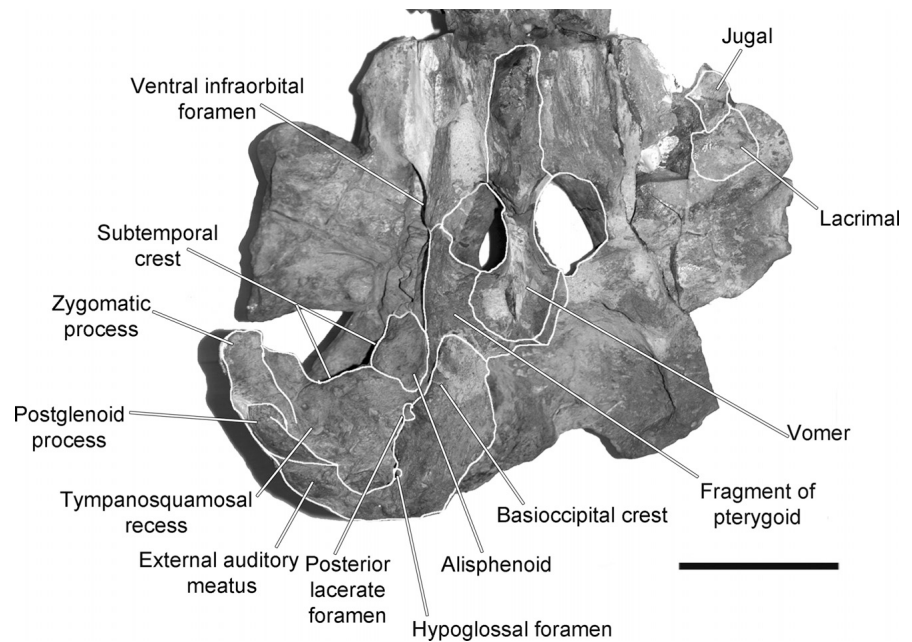


FIGURE 7. *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). Cranium in ventral view. Scale bar equals 10 cm.

of the squamosal, forming the supramastoid crest. The parieto-squamosal and fronto-parietal sutures are unclear. In lateral view, the temporal fossa is small, as in most extant ziphiids, oval, and wider anteroposteriorly (110 mm) than it is dorsoventrally high (72 mm). The zygomatic process of the squamosal is slightly ventrally deflected due to deformation of the skull. This process is robust, anteroposteriorly short (42 mm), and dorsoventrally high (56 mm). A short zygomatic process of the squamosal is a typical feature of ziphiids. The postglenoid process is anteroventrally oriented and has a rounded apex in lateral view. The posteroventral surface of the zygomatic process of the squamosal forms the glenoid fossa, which is transversely short (length = 38 mm). Posterior to the postglenoid process, the external auditory meatus extends laterally as a short and deep canal.

Supraoccipital—The supraoccipital is part of the occipital shield, which is only partially preserved (Fig. 5B). Unlike the condition in *Berardius*, *Archaeoziphius*, and *Microberardius*, the anteromedial projection of the supraoccipital between the posterior margins of the maxillae extends dorsally to the level of the synvertex so that, in posterior view, the dorsal surface of the synvertex is not visible. The supraoccipital-frontal suture is straight on the right side but anteriorly concave on the left side, possibly due to intense deformation of the skull in that sector. In lateral and dorsal views, the supraoccipital strongly slopes posteroventrally and a low sagittal crest occurs on its posterodorsal surface.

Basioccipital—Only the right lateral portion of the basioccipital is preserved, and it retains a much deteriorated basioccipital crest (Fig. 7). Anteriorly, the basioccipital contacts with the preserved portion of the pterygoid. The estimated angle formed by both basioccipital crest is about 41 degrees, similar to the condition observed in *Messapicetus* and *Ninoziphius*, and unlike extant and some extinct ziphiids (i.e., *Archaeoziphius* and *Tusciziphius*).

Pterygoid—Most of the pterygoids and both pterygoid hamuli are missing, and the ventral surface of the basicranium is heavily damaged, making it difficult to determine the extent of the pterygoid sinus fossa. The preserved portion of the pterygoid extends posteriorly on the right side of the basicranium to reach the midpoint (anteroposteriorly) of the alisphenoid, thus showing less posterior extension than in some extant ziphiids.

Alisphenoid—The alisphenoid is large, quadrangular-shaped, and has a wide ventral exposure in the basicranium. It contacts anteromedially the basioccipital and pterygoid and posterolaterally the squamosal. Anteromedially, its ventral surface is smooth and slightly concave, suggesting the presence of the pterygoid fossa. The wide exposure of the alisphenoid is related to the lack of the pterygoid; however, we infer that even if the pterygoid was entirely preserved, it would still not completely cover the alisphenoid.

Dentary

Two dentary fragments are preserved: a larger one (length = 253 mm) corresponding to a portion of the left dentary and a smaller piece (135 mm) from the right dentary (Fig. 8). Both fragments are from the alveolar portion of the dentary. The internal surface is flat, whereas the external surface is slightly curved laterally. In dorsal view, the alveolar groove is deeper than that in the maxilla, with large alveoli (length = 27 mm; width = 21 mm) lacking well-defined interalveolar septa.

PHYLOGENETIC ANALYSIS AND DISCUSSION

The cladistic analysis produced three MPTs with a tree length of 89 steps, Goloboff fit of 4.15. The phylogenetic results are summarized in the strict consensus tree (Fig. 9), which has a consistency index of 0.56 and retention index of 0.69.

All the MPTs nested *Notoziphius* within Ziphiidae in a basal clade including *Aporotus*, *Beneziphius*, *Messapicetus*, and *Ziphirostrum*, which partially corresponds to the *Messapicetus* clade recovered by Bianucci et al. (2010). This position is supported by four synapomorphies: mesorostral groove closed by medial fusion of the premaxillae (character 3: state 1, but unknown in *Notoziphius*); prenasal basin laterally bordered by a thick strip of maxilla (character 4: state 2, but a reversal in *Notoziphius* to state 0); reduced contact between nasal and premaxillary crest (character 16: state 1); and premaxillary crest anterolaterally directed (character 10: state 1). In the strict consensus tree, the relationships within this clade are unresolved; however, in two of the MPTs *Notoziphius* is placed as the sister taxon to a clade of *Aporotus*, *Beneziphius*, *Messapicetus*, and *Ziphirostrum*.

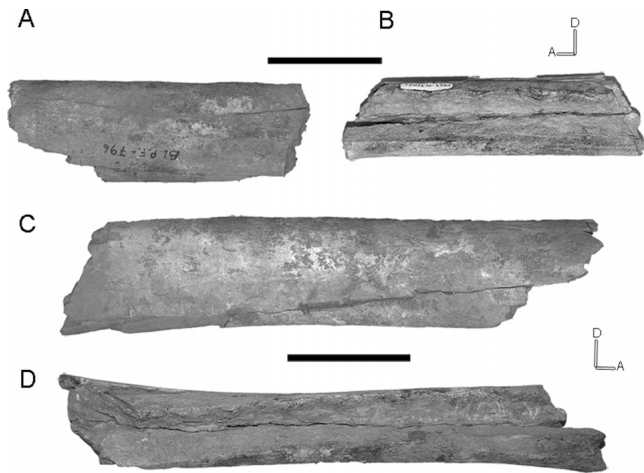


FIGURE 8. *Notoziphius bruneti*, gen. et sp. nov. (MPEF-PV 3282). **A**, medial view of right dentary fragment; **B**, dorsal view of right dentary fragment; **C**, medial view of left dentary fragment; **D**, dorsal view of left dentary fragment. **Abbreviations:** **A**, anterior; **D**, dorsal. Scale bar equals 5 cm.

Notoziphius differs from *Aporotus*, *Beneziphius*, *Messapicetus*, and *Ziphiostrum* in the absence of a prenarial basin (character 4: state 0); in the larger size and greater asymmetry of the nasals; and in the presence of the elliptical fossa on the nasal process of the premaxilla. *Notoziphius* differs from *Beneziphius*, *Messapicetus*, and *Ziphiostrum* in the lack of constriction of the nasal process of the right premaxillae (character 8: state 0); from *Beneziphius* and *Ziphiostrum* in the smaller size of the premaxillary crest; from *Messapicetus* in the elongated nasals (character 13: state 1), wider rostrum, smaller premaxillary crest, shorter exposure of the frontal on the vertex, and smaller temporal fossa; and from *Aporotus* in the presence of functional maxillary teeth (character 27: state 0).

The relationships among the remaining ziphiids are similar to those obtained by Bianucci et al. (2010); however, there are some differences that resulted from the addition of other taxa. *Ninoziphius* is placed as the sister taxon of the clade formed by *Tasmacetus*, *Nazcacetus*, and more-derived ziphiids, and this clade is diagnosed by the presence of an anterior spine of the tympanic with a rectilinear anterior margin (character 22: state 2). Unlike Lambert et al. (2009) and Bianucci et al. (2010), the position of *Nazcacetus* is resolved. It is recovered as the sister taxon of the most inclusive clade including the subclades Berardiinae (*Berardius*, *Microberardius*, and *Archaeoziphius*), Ziphinae (*Tusciziphius*, *Caviziphius*, *Choneziphius*, *Izikozihius*, and *Ziphius*), and an unnamed clade (which includes *Nenga*, *Xhosacetus*, *Khoikhoicetus*, *Pterocetus*, *Indopacetus*, *Hyperoodon*, *Mesoplodon*, *Ihlengesi*, and *Africanacetus*). This position of *Nazcacetus* is supported by the lack of functional maxillary teeth (character 27: state 1). *Tusciziphius*, *Caviziphius*, *Choneziphius*, *Izikozihius*, and *Ziphius* form a clade that partially corresponds to the Ziphinae as defined by Bianucci et al. (2010). It is supported by four synapomorphies: mesorostral groove closed by medial fusion of the premaxillae (character 3: state 3, reversal in *Izikozihius* and *Ziphius* to state 0); marked asymmetry of the premaxillary sac fossae (character 5: state 1, reversal in *Izikozihius* to state 0); posterodorsal portion of the nasal process of the premaxilla overhanging the external bony nares (character 7: state 3); and premaxillary crest anterolaterally directed (character 10: state 1). The latter character is also present in the clade formed by *Aporotus*, *Beneziphius*, *Messapicetus*, *No-*

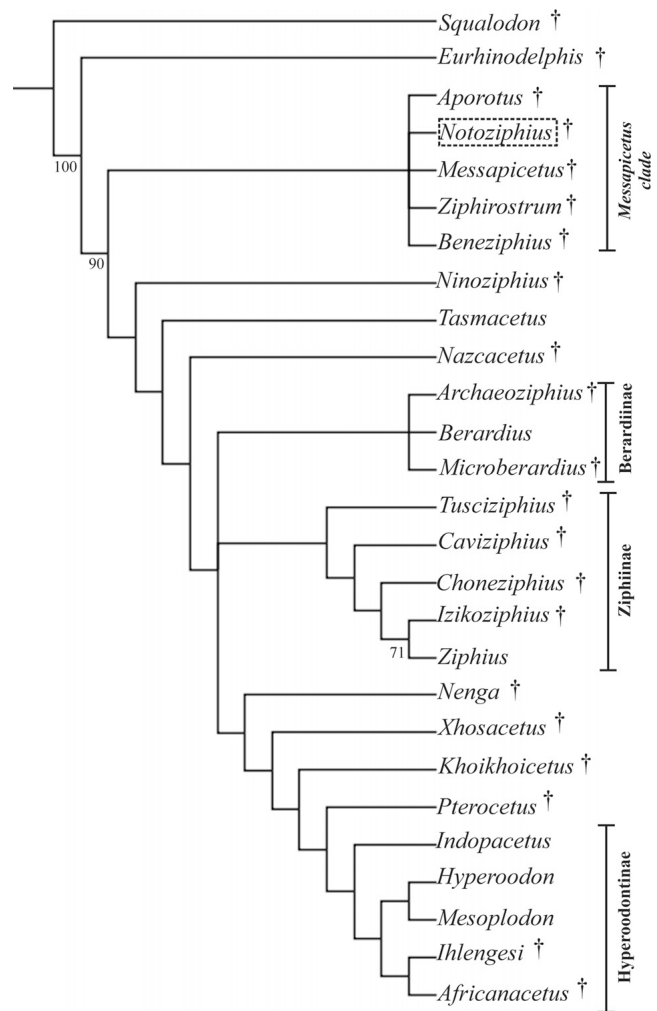


FIGURE 9. Strict consensus tree depicting the phylogenetic relationships of *Notoziphius bruneti* and other ziphiids (tree length = 91, CI = 0.56, RI = 0.69). Bootstrap support values greater than 50% are presented above the branches. †, extinct taxa.

toziphius, and *Ziphiostrum*, which implies convergent acquisition of this character in two lineages. *Caviziphius* has not been included in previous cladistic analyses of Ziphidae, although Bianucci and Post (2005) suggested a close relationship with *Choneziphius*. Our analysis corroborates their hypothesis, and the placement of *Caviziphius* as the sister taxon of the clade *Choneziphius*, *Izikozihius*, and *Ziphius* is supported by reduced contact between the nasal and the premaxillary crest (character 16: state 1). This character is also present in the clade composed of *Aporotus*, *Notoziphius*, *Messapicetus*, *Ziphiostrum*, and *Beneziphius*, which may indicate convergent evolution.

Unlike Bianucci et al. (2007) and Lambert et al. (2009), *Nenga* is recovered as the sister taxon of the clade that includes *Xhosacetus*, *Khoikhoicetus*, *Pterocetus*, *Indopacetus*, *Hyperoodon*, *Mesoplodon*, *Ihlengesi*, and *Africanacetus*, and this grouping is diagnosed by the inclusion of the nasal in the premaxillary crest (character 15: state 1). The internal relationships of Hyperoodontinae are congruent with those obtained by Lambert et al. (2009), except that *Pterocetus* and *Khoikhoicetus* are placed within Hyperoodontinae clade. *Khoikhoicetus* has been previously considered as a hyperoodontine based on the presence of a deep anteromedian excavation of the nasals (character 14: state

3), whereas *Xhosacetus* and *Pterocetus* have been excluded from Hyperoodontinae by the lack of this key character (Bianucci et al., 2007, 2010; Lambert et al., 2009). Our analysis shows *Pterocetus* nested within Hyperoodontinae and the presence of a slight anteromedian depression could be interpreted as a reversal. The morphology in *Pterocetus* (character 14: state 1), as well as that of *Indopacetus* (character 14: state 2), could be considered as an intermediate state between the primitive state (character 14: state 0), which is present in *Nenga* and *Xhosacetus*, and the derived condition, which is present in *Africanacetus*, *Hyperoodon*, *Ihlangesi*, and *Mesoplodon* (character 14: state 3). Given the uncertainty in the evolution of this character, it might be best to restrict the composition of Hyperoodontinae to *Indopacetus*, *Hyperoodon*, *Mesoplodon*, *Ihlangesi*, and *Africanacetus* and then this clade would still be diagnosed by the presence of premaxillary crest posterolaterally directed (character 10: state 2).

Low support values for most of the ziphiid clades were obtained (standard bootstrap, 1000 replicates), and the only clade that reported a bootstrap value above 50% was the clade formed by *Izikoziphius* and *Ziphius* (Fig. 9).

In previous phylogenetic analyses, taxa that are only represented by fragmentary specimens were excluded to avoid the negative effects of abundant missing entries, which may impact phylogenetic resolution (e.g., differing topologies for fragmentary taxa in the MPTs; Lambert et al., 2009; Bianucci et al., 2010). Recent empirical and simulation studies have demonstrated that extensive taxon sampling, even including fossil taxa with abundant missing entries, improves the performance of phylogenetic studies (e.g., Zwickl and Hillis, 2002; Hillis et al., 2003). A recent protocol, IterPCR (Pol and Escapa, 2009) and associated script, detects difficult-to-place taxa and the characters related to taxon instability. IterPCR identified *Aporotus* as an unstable taxon, and it was also pruned from the reduced strict consensus because of lack of information (i.e., missing data; characters 1 and 8) (see Supplementary Data). A reduced consensus tree shows *Notoziphius* in a resolved position as the sister taxon to a clade formed by *Beneziphius*, *Messapicetus*, and *Ziphirostrum*. The results of the IterPCR script indicated that the instability of taxa in the strict consensus is more related to the lack of information for some taxa than to contradictory information in the data matrix. Accordingly, we recommend that future workers score as many taxa as possible for their data matrices and then use the IterPCR script to produce a reduced strict consensus. This method allows for the identification of floating taxa based on a strict methodological approach, which is preferred over the arbitrary pruning of taxa.

In summary, our phylogenetic analysis determined that *Notoziphius* is one of the most basal ziphiids. It is also the first ziphiid reported from the southwestern Atlantic Ocean, and it improves our knowledge of the distribution and diversity of ziphiids during the Miocene. Furthermore, this new record reinforces the idea that the worldwide distribution that we observe for extant ziphiids was already well established as early as the Miocene.

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APPENDIX 1. Descriptions of the additional characters used in the phylogenetic analysis added to the Bianucci et al. (2010) data set. The numbering of these characters continues the numbering found in Bianucci et al. (2010).

- (30) Relative ventral projection of postglenoid and posttympanic processes of the squamosal: postglenoid process more ventral or at the same level as posttympanic process (0); apex of the postglenoid process clearly higher (1) (Lambert, 2005b).
- (31) Anterior level reached by the pterygoid sinus fossae: interrupted before or at the level of antorbital notches (0); extending clearly beyond that level (Lambert, 2005b).

APPENDIX 2. Modifications to the data matrix of Bianucci et al. (2010). Character codings for six additional taxa and two phylogenetic characters were added to the Bianucci et al. (2010) matrix. *Messapicetus* has been scored as polymorphic (0, 1) for character 29. *Squalodon* was used as outgroup. ? = missing data; C = states 2 and 3.

		5	10	15	20
<i>Notoziphius</i>	? 0 ? 0 0	0 2 0 1 1	1 0 1 1 0	1 0 2 0 ?	
<i>Khoikhoicetus</i>	? 2 0 0 0	0 3 1 1 0	0 0 1 3 1	0 0 2 ? ?	
<i>Nenga</i>	? 0 0 0 0	0 2 0 1 0	0 0 1 0 1	0 0 2 ? ?	
<i>Aporotus</i>	? 0 1 1 0	0 C ? ? 1	1 ? ? 1 0	1 0 2 ? ?	
<i>Caviziphius</i>	? 0 3 0 1	0 3 ? ? 1	? ? ? 1 0	1 0 ? ? ?	
<i>Ninoziphius</i>	0 0 0 0 ?	? ? ? ? ?	? ? ? ? ?	? ? ? 0 0	
		25	30	31	
<i>Notoziphius</i>	? ? ? ? ?	? 0 ? ? ?	? ? ? ? ?	? ? ? ? ?	
<i>Khoikhoicetus</i>	? ? ? ? ?	? 1 ? ? ?	? ? ? ? ?	? ? ? ? ?	
<i>Nenga</i>	? ? ? ? ?	? 1 ? ? ?	? ? ? ? ?	? ? ? ? ?	
<i>Aporotus</i>	? ? ? ? ?	? 1 ? ? ?	? ? ? ? ?	? ? ? ? ?	
<i>Caviziphius</i>	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	
<i>Ninoziphius</i>	0 2 1 1 ?	? 0 2 1 1	? ? ? ? ?	? ? ? ? ?	
		30	31		
<i>Squalodon</i>	0 0				
<i>Eurhinodelphis</i>	0 0				
<i>Xhosacetus</i>	? 1				
<i>Pterocetus</i>	? ?				
<i>Indopacetus</i>	1 1				
<i>Africanacetus</i>	? 1				
<i>Ihlangesi</i>	? ?				
<i>Mesoplodon</i>	1 1				
<i>Hyperoodon</i>	1 1				
<i>Ziphius</i>	1 1				
<i>Izikoziphius</i>	? ?				
<i>Choneziphius</i>	? ?				
<i>Tusciziphius</i>	0 ?				
<i>Microberardius</i>	? ?				
<i>Berardius</i>	1 1				
<i>Archaeoziphius</i>	0 1				
<i>Nazcacetus</i>	1 1				
<i>Tasmacetus</i>	1 1				
<i>Beneziphius</i>	? ?				
<i>Ziphirostrum</i>	? 1				
<i>Messapicetus</i>	1 1				