

Bizarre fossil beaked whales (Odontoceti, Ziphiidae) fished from the Atlantic Ocean floor off the Iberian Peninsula

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ABSTRACT

Forty partial fossil skulls belonging to beaked whales (Cetacea, Odontoceti, Ziphiidae) were collected by trawling and long-line fishing on Neogene (probably Late Early to Middle Miocene) layers of the Atlantic floor off the coasts of Portugal and Spain (Asturias and Galicia). The systematic study of the most diagnostic Iberian specimens, those preserving the rostrum and the dorsal part of the cranium, led to the recognition of two new genera (*Globicetus* n. gen.

and *Imocetus* n. gen.) and four new species (*Choneziphius leidy* n. sp., *G. hiberus* n. gen., n. sp., *I. piscatus* n. gen., n. sp., and *Tusciziphius atlanticus* n. sp.). Based on the matrix of a previous work, the phylogenetic analysis places all the new taxa in the subfamily Ziphiinae Gray, 1850. More fragmentary specimens are tentatively referred to the genera *Caviziphius* Bianucci & Post, 2005 and *Ziphirostrum* du Bus, 1868. Among these new ziphiids, extremely bizarre skull morphologies are observed. In *G. hiberus* n. gen., n. sp. the proximal portion of the rostrum bears a voluminous premaxillary spheroid. In *T. atlanticus* n. sp. a medial premaxillary bulge is present on the rostrum; together with asymmetric rostral maxillary eminences at the rostrum base, this bulge displays various degrees of elevation in different specimens, which may be interpreted as sexual dimorphism. Specimens of *I. piscatus* n. gen., n. sp. bear two sets of even crests: spur-like rostral maxillary crests and longitudinal maxillary crests laterally bordering a wide and long facial basin. A preliminary macroscopic observation of these elements indicates very dense bones, with a compactness comparable with that of cetacean ear bones. Questioning their function, the high medial rostral elements (the premaxillary spheroid of *G. hiberus* n. gen., n. sp. and the medial bulge of *T. atlanticus* n. sp.) remind the huge rostral maxillary crests of adult males of the extant *Hyperoodon ampullatus* (Forster, 1770). In the latter, the crests are very likely related to head-butting. However, they are made of much more spongy bone than in the fossil taxa studied here, and therefore possibly better mechanically suited for facing impacts. Other interpretations of these unusual bone specializations, related to deep-diving (ballast) and echolocation (sound reflection), fail to explain the diversity of shapes and the hypothetical sexual dimorphism observed in at least part of the taxa. The spur-like rostral maxillary crests and long maxillary crests limiting the large facial basin in *I. piscatus* n. gen., n. sp. and the excrescences on the maxilla at the rostrum base in *Choneziphius* spp. are instead interpreted as areas of origin for rostral and facial muscles, acting on the nasal passages, blowhole, and melon. From a palaeobiogeographic point of view, the newly described taxa further emphasize the differences in the North Atlantic (including Iberian Peninsula) and South African Neogene ziphiid faunal lists. Even if the stratigraphic context is poorly understood, leaving open the question of the geological age for most of the dredged specimens, these differences in the composition of cold to temperate northern and southern hemisphere fossil ziphiid faunas may be explained by a warm-water equatorial barrier.

KEY WORDS

Cetacea,
Odontoceti,
Ziphiidae,
Neogene,
Miocene,
Portugal,
Spain,
phylogeny,
skull morphology,
new genera,
new species.

RÉSUMÉ

Étranges baleines à bec fossiles (Odontoceti, Ziphiidae) pêchées sur le fond de l'Océan Atlantique au large de la péninsule ibérique.

Quarante crânes partiels fossiles de baleines à bec (Cetacea, Odontoceti, Ziphiidae), pêchés au chalut et à la palangre sur des couches du Néogène (probablement fin du Miocène inférieur à Miocène moyen) du fond de l'Atlantique au large des côtes du Portugal et d'Espagne (Asturies et Galice), sont signalés. L'étude systématique des spécimens ibériques les plus diagnostiques, ceux dont le rostre et la partie faciale sont préservés, a permis la reconnaissance de deux nouveaux genres (*Globicetus* n. gen. et *Imocetus* n. gen.) et de quatre nouvelles espèces (*Choneziphius leidy* n. sp., *G. hiberus* n. gen., n. sp., *I. piscatus* n. gen., n. sp. et *Tusciziphius atlanticus* n. sp.). Sur la base de la matrice d'un travail précédent, l'analyse phylogénique positionne l'ensemble des nouveaux taxons

dans la sous-famille Ziphiinae Gray, 1850. Des spécimens plus fragmentaires sont provisoirement attribués aux genres *Caviziphius* Bianucci & Post, 2005 et *Ziphirostrum* du Bus, 1868. Parmi ces nouveaux ziphiidés, des morphologies extrêmement bizarres sont observées. Chez *G. hiberus* n. gen., n. sp., la partie proximale du rostre porte une volumineuse sphère prémaxillaire. Une crête médiale prémaxillaire est présente sur le rostre de *T. atlanticus* n. sp.; cette crête, de même que des éminences rostrales maxillaires asymétriques, montre différents degrés d'élévation au sein de l'espèce, peut-être en lien avec du dimorphisme sexuel. Les spécimens d'*I. piscatus* n. gen., n. sp. portent deux paires de crêtes : des crêtes rostrales maxillaires en forme d'éperon et des crêtes maxillaires longitudinales bordant latéralement un long et large bassin facial. L'observation macroscopique préliminaire de ces éléments indique un os très dense, avec une compacité comparable à celle des os de l'oreille des cétacés. Au niveau de leur fonction potentielle, les éléments médians du rostre (sphère prémaxillaire de *G. hiberus* n. gen., n. sp. et crête médiane prémaxillaire de *T. atlanticus* n. sp.) rappellent les énormes crêtes maxillaires rostrales des mâles adultes de l'espèce moderne *Hyperoodon ampullatus* (Forster, 1770). Chez ce dernier, les crêtes sont très probablement utilisées lors de combats par coups de tête. Cependant, elles sont constituées d'un os beaucoup plus spongieux que chez les taxons fossiles étudiés ici, et donc peut-être plus aptes mécaniquement à subir des impacts. D'autres interprétations des ces spécialisations osseuses inhabituelles, liées aux plongées profondes (ballast) et à l'écholocalisation (réflexion des sons), échouent à expliquer la diversité des formes et le possible dimorphisme sexuel observé chez une partie des espèces. Les crêtes rostrales maxillaires en forme d'éperon et les longues crêtes maxillaires limitant le grand bassin facial d'*I. piscatus* n. gen., n. sp. et les excroissances sur le maxillaire à la base du rostre de *Choneziphius* spp. sont, elles, interprétées comme des régions d'origine pour des muscles rostraux et faciaux, agissant sur les conduits nasaux, l'évent et le melon. D'un point de vue paléobiogéographique, les nouveaux taxons confirment les différences de contenu des listes fauniques de ziphiidés néogènes de l'Atlantique Nord (incluant la péninsule ibérique) et de l'Afrique du Sud. Malgré le contexte stratigraphique peu précis, laissant ouverte la question de l'âge géologique de la plupart des spécimens pêchés sur le fond de la mer, ces différences dans la composition des faunes de ziphiidés fossiles des régions froides à tempérées des hémisphères nord et sud pourraient être expliquées par la présence d'une barrière d'eau équatoriale chaude.

MOTS CLÉS

Cetacea,
Odontoceti,
Ziphiidae,
Néogène,
Miocène,
Portugal,
Espagne,
phylogénie,
morphologie crânienne,
genres nouveaux,
espèces nouvelles.

INTRODUCTION

Including at least 21 extant species (Dalebout *et al.* 2002), beaked whales (Ziphiidae Gray, 1850) are the second most species-rich modern cetacean family, following the Delphinidae Gray, 1821. In addition to dental reduction, these deep-diving, generally teuthophagous animals are characterized by various

skull specializations, some of these specializations being sexually dimorphic, that place them as one of the most peculiar odontocete groups and lead to contrasted functional interpretations (Heyning 1984; Buffrénil *et al.* 2000; MacLeod 2002; Lambert *et al.* 2011). For a long time the fossil record of ziphiids was scarce compared to its high present diversity. Even now, the number of fossil species

based on specimens from inland deposits remains small (e.g., Muizon 1984; Bianucci *et al.* 1994, 2010; Lambert & Louwye 2006; Lambert *et al.* 2009; Bianucci *et al.* 2010). However, specimens recovered from the bottom of oceans proved to be an essential source of information. Fossils, generally isolated rostra, have been reported from the South Pacific Ocean (Fordyce & Cullen 1979; Miyazaki & Hasegawa 1992), Indian Ocean (Robineau 1973), and Sea of Japan (Horikawa *et al.* 1987; Tazaki *et al.* 1987). Whitmore *et al.* (1986) also mentioned several ziphiid fossils from other deep ocean sites and analyzed in more detail the nature of these strange and strongly phosphatized skull elements.

Later Bianucci *et al.* (2007, 2008) reported eight new fossil ziphiid genera and ten new species, based on better preserved cranial material recovered from trawling activities on the ocean bottom along the South African coasts, at depths of as much as 1000 m. Here again, the relationships with phosphorite deposits were emphasized, allowing some argument about the still problematic dating of the specimens and the high local productivity (Bianucci *et al.* 2007).

Following a preliminary note (Miján 2007), the present article describes a new large sample of well preserved fossil ziphiid skulls, some of them displaying unusual morphologies, recovered from the Atlantic Ocean floor off Portugal and Spain (Asturias and Galicia).

To our knowledge, the present article, together with the Miján (2007) note, represent the first scientific report of fossil ziphiids from Iberian Peninsula. Zbyszewski (1954) referred to the new species *Palaeoziphius melidensis* an incomplete mandible (MG5450) collected in the Tortonian of Melides (Southwest Portugal). However, the genus *Palaeoziphius* Abel, 1905, primarily used for the species *P. scaldensis* (du Bus, 1872), based on another isolated mandible, has been placed in Odontoceti *incertae sedis* by Lambert (2005). Judging from Zbyszewski's illustrations (Zbyszewski 1954: pls 1, 2), the mandible from Melides does not exhibit any ziphiid character; consequently *P. melidensis* must also be referred to Odontoceti *incertae sedis*. The only reliable previous fossil ziphiid record from Portugal (but not from Iberian Peninsula) originates from the Archipelago of Azores and was referred to *Mesopodon* sp. by Stevens & Ávila (2007).

ABBREVIATIONS

IEO	Instituto Español de Oceanografía, Gijón, Spain;
IGF	Museo di Geologia e Paleontologia dell'Università di Firenze, Florence, Italy;
MG	Museu Geológico, Lisboa, Portugal;
MHNUSC	Museo de Historia Natural Luis Iglesias, Universidad de Santiago de Compostela, Santiago de Compostela, Spain;
ML	Museu da Lourinhã, Lourinhã, Portugal;
NMB	Natuurhistorisch Museum Boekenberg, Antwerp;
NMR	Natuurhistorisch Museum Rotterdam;
SGHN	Museo da Natureza da Sociedade Galega de Historia Natural, Ferrol, Spain.

MATERIAL AND METHODS

SPECIMENS AND LOCALITIES

We examined 40 partial ziphiid skulls recovered from the sea floor off the coasts of Asturias, Galicia, and Portugal during fishing activities based on bottom set long-line and bottom trawl (Fig. 1). All the specimens were collected on the borders of the continental platform, most of them at a depth ranging between 500 and 1000 m. Most of the specimens were kept in private collections for years; the location is precise in some cases, but more approximate in others, for two reasons: some were collected before the Global Positioning System (GPS) was widely used and fishermen are often reluctant to reveal their fishing spots. The fossils collected off the Asturias coast are from the Canyon of Avilés and other imprecise localities along the platform. The fossils collected off Galicia are from several localities, among which As Paredes, A Selva, and Cortada fishing grounds. The specimens from Portugal were found in deep water off central Portugal (Lourinhã, Peniche), south of Nazaré Canyon; the latter extends about 210 km westward from the coast and reaches depths near 5000 m in its distal part (Tyler *et al.* 2009). All the fossils examined are now kept in IEO, ML, MHNUSC, and SGHN.

All the fossils are strongly phosphoritized; some of them are even partly included in a phosphatic conglomerate. Fossilization and associated sediments are actually similar for fossil ziphiids trawled off the South African coasts (Bianucci *et al.* 2007).

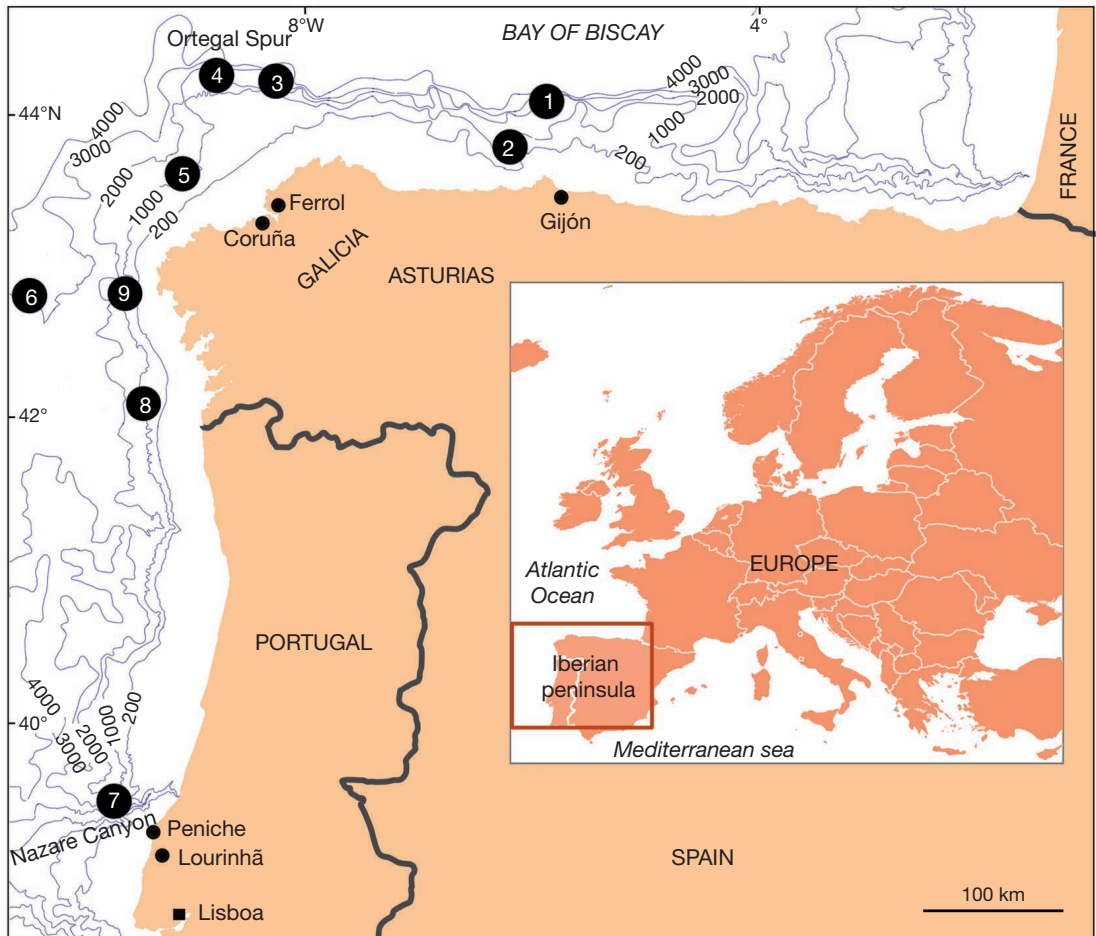


FIG. 1. — Map of Atlantic Iberian coast showing localities where fossil ziphiid skulls have been recovered by bottom set long-line and trawling: 1, Asturias continental border, imprecise location; 2, Avilés Canyon, Asturias coast; 3, As Paredes fishing ground (44°10'N, 8°20'W), depth 250-600 m; 4, A Selva fishing ground (44°10'N, 8°40'W), depth 350-600 m; 5, Cortada fishing ground (43°36'N, 9°0'W), depth 400-800 m; 6, oceanographic research at 1500 m depth (42°27'N 11°59'W); 7, south of Nazaré Canyon, imprecise location (c. 39°18'N, 9°47'W); 8, escarpote fishing ground (42°10'N, 09°26'W), depth 680-750 m; 9, 20 miles from Touriñán Cape (42°50'N, 9°40'W), depth 1500 m.

As commonly observed for the phosphoritized fossil beaked whale remains recovered from the sea floor (Fordyce & Cullen 1979; Whitmore *et al.* 1986; Horikawa *et al.* 1987; Tazaki *et al.* 1987; Bianucci *et al.* 2007), all Iberian skulls are incomplete. The preserved bones are the ones that are more compact in the living ziphiids: bones from the rostrum and in some cases from the facial area of the cranium, including the vertex (Lambert *et al.* 2011). The more spongy and/or delicate bones forming the

posteroventral portion of the braincase are generally not preserved.

Following Bianucci *et al.* (2007), we decided to use only those specimens that include at least the more diagnostic dorsal surface of the cranium, including the vertex, for the description of new taxa. More fragmentary fossils (e.g., isolated rostra) originating from the same geographic area are listed in the referred material only if their morphological features fully overlap those of the more complete

specimens. Eighteen of the 40 skulls are considered as diagnostic. All these specimens are described for the first time in this article, with the exception of SGHN MA0632 and SGHN MA0644, which were previously tentatively referred to the genus *Hyperoodon* Lacépède, 1804 (Miján 2007).

SYSTEMATICS

The systematic classification used in the following section is based on the phylogenetic analysis published by Bianucci *et al.* (2010), here confirmed with the addition of new taxa (see phylogenetic paragraph). Most of the described material is demonstrated to belong to the subfamily Ziphiinae Gray, 1850, which is redefined in this article. Following Bianucci *et al.* (2010), this subfamily excludes *Beneziphius* Lambert, 2005, *Messapicetus* Bianucci, Landini & Varola, 1992 and *Ziphirostrum* du Bus, 1868, three genera forming, possibly together with *Aporotus* du Bus, 1868, a more basal clade of the ziphiid phylogenetic tree (“*Messapicetus* clade”).

SYSTEMATIC PALAEOLOGY

Order CETACEA Brisson, 1762
Suborder ODONTOCETI Flower, 1867
Family ZIPHIIDAE Gray, 1850

Subfamily ZIPHIINAE Gray, 1850

TYPE GENUS. — *Ziphius* Cuvier, 1823.

OTHER GENERA INCLUDED. — *Choneziphius* Duvernoy, 1851, *Globicetus* n. gen., *Imocetus* n. gen., *Izikoziphius* Bianucci, Lambert & Post, 2007, *Tusciziphius* Bianucci, 1997, and possibly *Caviziphius* Bianucci & Post, 2005.

EMENDED DIAGNOSIS. — With the exception of *Izikoziphius* and *Ziphius*, members of the subfamily Ziphiinae differ from all other Ziphiidae in the dorsal closure of the mesorostral groove by medial sutural contact of the premaxillae extending posteriorly until the bony nares. With the exception of *Choneziphius* and *Imocetus* n. gen., they further differ from all other Ziphiidae in having very elongated nasals with the anterior tip of nasals located anterior to the premaxillary crests (ratio between length of medial suture of nasals and maximum width of nasals > 1.1). They further differ from all other Ziphiidae, with the exception of the clade formed by *Africanacetus*

Bianucci, Lambert & Post, 2007, *Hyperoodon*, *Ihlen-gesi* Bianucci, Lambert & Post, 2007, and *Mesoplodon* Gervais, 1850, in having the ascending process of the premaxilla concave in lateral view, with the posterodorsal portion partly overhanging the bony nares (apart from *Choneziphius planirostris* (Cuvier, 1823), with bony nares still visible in dorsal view). They further differ from all other Ziphiidae, except *Beneziphius*, *Messapicetus*, and *Ziphirostrum*, in having the left premaxillary crest anterolaterally directed.

Genus *Choneziphius* Duvernoy, 1851

TYPE SPECIES. — *Choneziphius planirostris* from southern North Sea Basin, probably Late Miocene (Lambert 2005).

OTHER SPECIES INCLUDED. — *Choneziphius leidy* n. sp.

EMENDED DIAGNOSIS. — *Choneziphius* differs from all other ziphiid genera in the mesorostral groove dorsally closed at the level of the antorbital notches by the joined medial margins of the premaxillary sac fossae, forming a prominent ridge posteriorly shifted to the left, and separating deeply concave anterior portions of the premaxillary sac fossae.

It also differs from the other ziphiine genera in the maxilla covered at the rostrum base with prominent excrescences. Moreover it differs from *Ziphius* and *Izikoziphius* in the medial fusion of the premaxillae dorsally closing the mesorostral groove; from *Globicetus* n. gen., *Imocetus* n. gen., and *Tusciziphius* in lacking an extremely ossified trapezoidal vertex with the anterior part of the nasals contacting the premaxillary crests; from *Imocetus* n. gen. in lacking a wide facial depression, a rostral maxillary spur-shaped crest, and in the location of the premaxillary foramen (not posterior to the level of the antorbital notch); from *Globicetus* n. gen. in lacking a large spherical medial premaxillary prominence at the rostrum base; from the possible ziphiine *Caviziphius* in shallower premaxillary sac fossae and in the more slender and lower right premaxillary crest.

DISCUSSION

The fossil record of *Choneziphius* is primarily based on several partial skulls and rostra referred to the type species *C. planirostris*. These fossils have been collected in sediments of North Sea, probably dated from the late Miocene (Belgium, Netherlands, and UK; see Lambert [2005] for bibliography and review). Lankester (1870) described *C. packardii* Lankester, 1870 based on an incomplete rostrum from Suffolk (UK). Leidy (1876, 1877) described

C. liops Leidy, 1876 and *C. trachops* Leidy, 1876, based on fragmentary rostra that are now lost, from the Phosphate Beds of South Carolina (USA). While reviewing the genus *Choneziphius*, Lambert (2005) considered *C. packardi* as based on too fragmentary material to allow specific or even generic determination; he considered *C. liops* as a possibly valid species (rostrum shorter and with anterior narrowing stronger than in *C. planirostris*), and *C. trachops* as possibly conspecific with *C. planirostris*. According to Lambert (2005), *Proroziphius macrops* Leidy, 1876 and probably *P. chonops* Leidy, 1876, both based on fragmentary and unfortunately lost skulls from the Phosphate Beds of South Carolina, should be included in the genus *Choneziphius*. Whitmore & Kaltenbach (2008) considered *C. trachops* as a valid taxon and assigned to this species a large rostrum collected from reworked sediments at the Lee Creek Mine, North Carolina. Although the above mentioned taxa show the apomorphies of the genus *Choneziphius* (at least on illustrations), we restrict these species, based on too fragmentary material, to their holotypes and consider them as *incertae sedis*.

Choneziphius leidyi n. sp.
(Figs 2-5; Table 1)

HOLOTYPE. — SGHN MA0633, partial skull including rostrum, facial area and vertex.

REFERRED SPECIMENS. — SGHN MA0640, partial skull including rostrum, facial area and vertex, Escarpote fishing ground, depth of approximately 685 m, off the Galician coast, 42°08'N, 09°26'W; SGHN MA0641, partial skull including posterior portion of rostrum, part of facial area and vertex, A Selva fishing ground, depth of approximately 500 m, off the Galician coast, 44°10'N, 08°40'W; SGHN MA0937, partial skull including rostrum and facial area, A Selva fishing ground, depth of approximately 500 m, off the Galician coast, 44°10'N, 08°40'W; ML 533, partial skull including rostrum and facial area, south of Nazaré Canyon, off the Portuguese coast, exact locality unknown but likely around 39°18'N, 9°47'W; ML 1366, fragment of skull including the left dorsal surface of the cranium with the left premaxillary crest, south of Nazaré Canyon off the Portuguese coast, exact locality unknown, but likely around 39°18'N, 9°47'W.

ETYMOLOGY. — In honour of the American palaeontologist Joseph Leidy (1823-1891), who described several *Choneziphius*-like fossil ziphiids from the Mid Atlantic Coastal Plain of the USA in 1876 and 1877.

TYPE LOCALITY. — A Selva fishing ground, depth of approximately 500 m, off the Galician coast, 44°10'N, 08°40'W.

DIAGNOSIS. — Large species of *Choneziphius* differing from *C. planirostris* in: longer and more pointed rostrum with apex constructed of premaxillae alone; longer dorsal opening of the mesorostral groove at the apex of the rostrum; premaxillary foramina located distinctly anterior to level of prominent notch; lower maxillary crest on the supraorbital process; shallower and wider premaxillary sac fossae; less asymmetric premaxillary sac fossae; higher vertex overhanging the bony nares.

DESCRIPTION

The rostrum, although longer than in *Choneziphius planirostris*, exhibits the same massive appearance; in both species it is relatively narrow with a subcylindrical anterior half portion. As in *C. planirostris*, the facial area is wider than long. Differing from *C. planirostris*, the bony nares are not visible in dorsal view, being hidden by the overhanging and anteriorly projected vertex.

Premaxilla

On the complete rostra of the holotype and SGHN MA0640, the apex of the rostrum is formed by the premaxillae only, contrary to *C. planirostris* where maxilla and premaxilla both reach the apex of the rostrum. Anteriorly, the premaxillae are not fused dorsally, leaving the narrow tunnel-shaped mesorostral groove open for a length of at least 80 mm. Such a dorsal exposure of the mesorostral groove is rarely present in the large sample of *C. planirostris*, and, if present, never longer than 50 mm. For most of the rostrum length, the thick premaxillae are firmly fused at midline, with a suture remaining visible until the bony nares (as in *C. planirostris*).

As in *C. planirostris*, the fused premaxillae form a prominent ridge at the rostrum base, posteriorly shifted to the left and separating the deeply excavated anterior portions of the premaxillary sac fossae (the main character defining the genus *Choneziphius*). Each premaxillary sac fossa contains a premaxillary

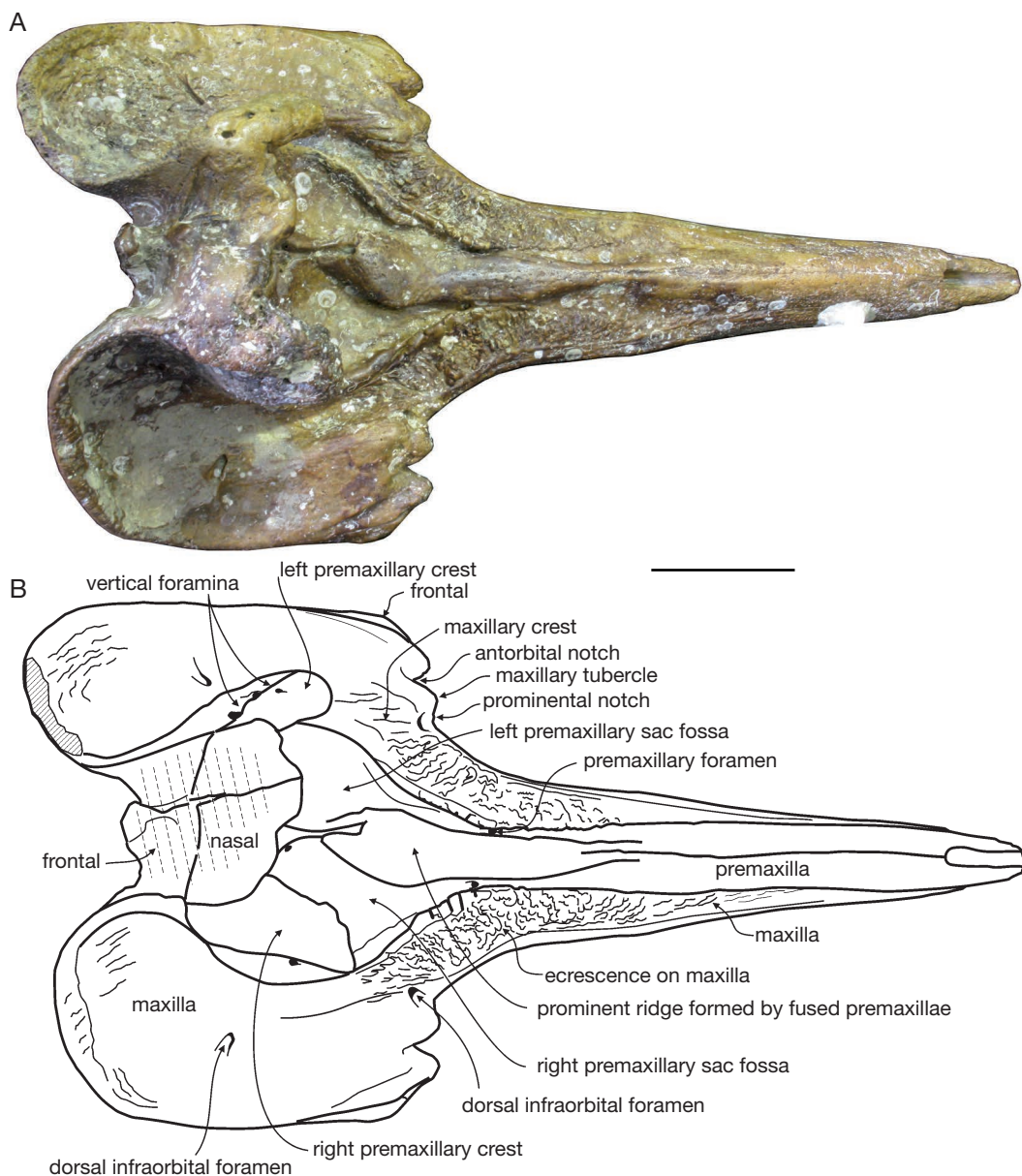


FIG. 2. — Skull of *Choneziphius leidy* n. sp. (SGHN MA0633, holotype): **A**, dorsal view; **B**, corresponding line drawing. Tight parallel lines indicate a break surface; more widely spaced parallel lines indicate superficial wear. Scale bar: 10 cm.

foramen at its anteriormost point, located well anterior to the level of the prominent notch of the maxilla (Fig. 2). In *C. planirostris*, the premaxillary foramen is located at, or just posterior to, the level of the prominent notch. An additional foramen

is observed on the medial margin of the left premaxillary sac fossa of SGHN MA0640.

The right premaxillary sac fossa is distinctly wider than the left (ratio between maximum width of left and right fossae between 0.70 and 0.76, $n = 3$), and

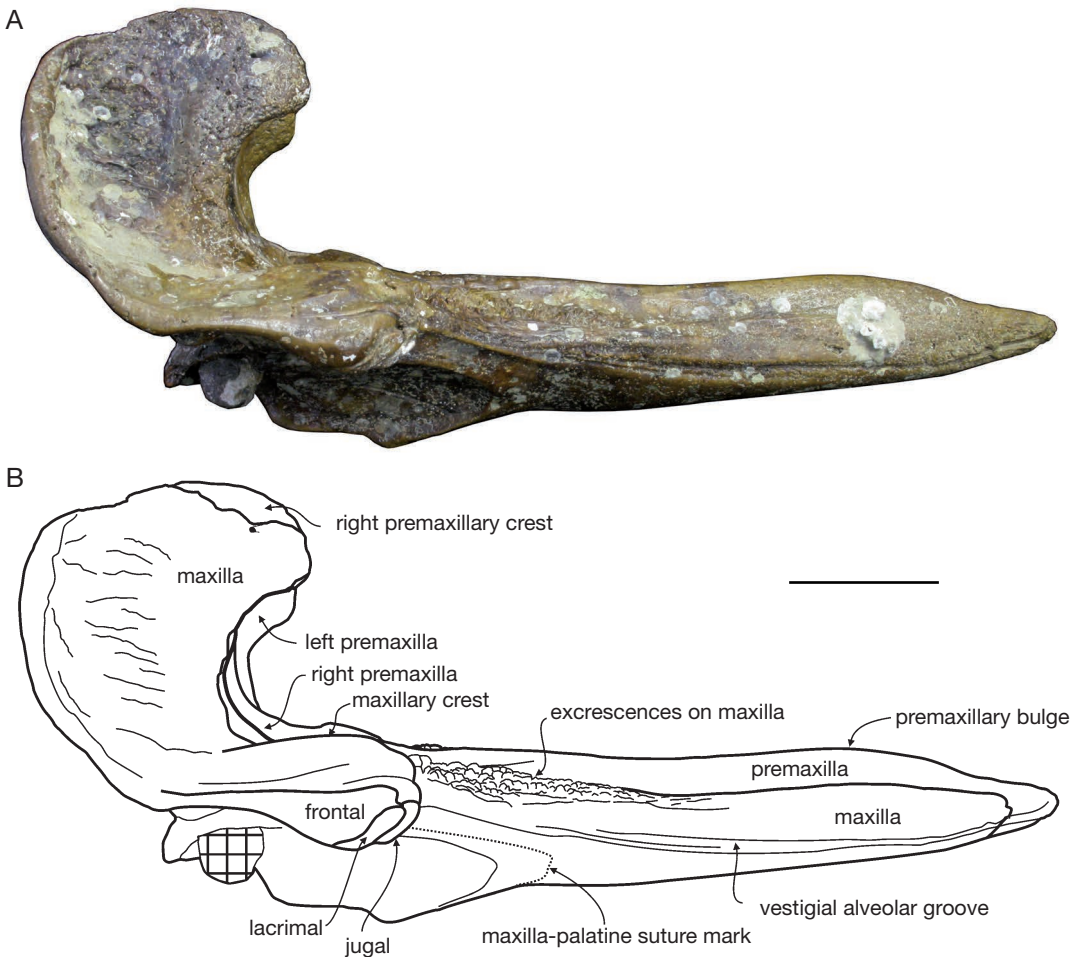


FIG. 3. — Skull of *Choneziphius leidy* n. sp. (SGHN MA0633, holotype); **A**, lateral view; **B**, corresponding line drawing. Cross-hatching indicates the presence of a concretion. Scale bar: 10 cm.

the asymmetry is therefore less pronounced than in *C. planirostris* (ratio between 0.48 and 0.65, $n = 15$).

The anterior part of the vertex, including the ascending process of the premaxilla and the premaxillary crest, is overhanging the premaxillary sac fossae and the bony nares. This condition contrasts with *C. planirostris*, in which in lateral view the ascending process forms an angle of $\leq 90^\circ$ with the horizontal plane of the skull, whereas the angle is $> 90^\circ$ in *C. leidy* n. sp. The fairly slender premaxillary crest is anterolaterally directed. The right crest is distinctly larger than the left, as in *C. planirostris*.

Maxilla

From a roughly vertical orientation on the anterior half of the rostrum, the lateral surface of the maxilla progressively shifts to a subhorizontal dorsal surface bordered by an acute lateral margin and the thick premaxilla medially. In this part, the dorsal side of the maxilla is covered with multiple, marked excrescences. Rostra of *C. planirostris* bear similar excrescences in the same area, usually less prominent than in the known specimens of *C. leidy* n. sp.

On the lateral surface of the maxilla, a marked alveolar groove is visible which sharply slopes down from its

TABLE 1. — Measurements (in mm) on the skulls of *Choneziphius leidyi* n. sp. from the Atlantic Ocean floor off the Iberian Peninsula. Abbreviations: e, estimate; +, nearly complete; –, no data.

	SGHN MA0633 (holotype)	SGHN MA0640	SGHN MA0641	ML 533
Rostrum length from level of antorbital notch	+503	+495	–	408
Rostrum length from level of prominental notch	+488	+482	–	–
Distance from apex of rostrum to bony nares	+588	+585	–	–
Length premaxillary portion of rostrum	–	+67	–	–
Height of rostrum at anterior end of maxilla	–	42	–	–
Width of rostrum at mid-length	82	74	–	94
Width of premaxillae at mid-length of rostrum	50	e50	–	–
Height of rostrum at mid-length	82	71	–	–
Width of rostrum base at prominental notch	195	–	–	–
Width of rostrum base at antorbital notch	252	–	–	205
Width of premaxillae at rostrum base (antorbital)	87	98	–	–
Minimum distance between maxillae near rostrum base	37	–	25	–
Distance rostrum base – anterior apex of palatine	e115	e109	–	–
Preorbital width of skull	354	–	–	–
Longitudinal distance right premaxillary foramen – rostrum base (antorbital)	52	49	–	–
Longitudinal distance left premaxillary foramen – rostrum base (antorbital)	63	52	–	–
Width of premaxillary sac fossae	172	168	158	150
Width of right premaxillary sac fossa	96	95	e82	92
Width of left premaxillary sac fossa	69	67	64	58
Width of bony nares	73	80	e81	–
Minimum width of right ascending process of the premaxilla	54	48	+45	–
Width of premaxillary crests	178	170	+155	–
Width of right premaxillary crest	65	71	+55	–
Width of left premaxillary crest	43	45	e48	–
Minimum distance between premaxillary crests	83	e74	e60	–
Maximum width of nasals	e89	e84	e72	–
Minimum posterior distance between maxillae	–	86	80	–

uttermost point on the maxilla until approximately $\frac{1}{5}$ of the rostrum length. Within the groove SGHN MA0640 shows 12–13 very shallow alveoli probably corresponding to vestigial teeth. A few specimens of *C. planirostris* also show traces of shallow alveoli.

From the prominent maxillary tubercle, the maxilla forms a maxillary crest on the supraorbital process, with a roughly antero-posterior direction. This crest is less prominent than in *C. planirostris*, a feature especially noticeable in anterior view.

Each maxilla is pierced by two dorsal infraorbital foramina, one just behind the prominental notch, and the other lateral to the vertex.

Nasal

The dorsal surface of the nasals is strongly worn in each specimen, but their outline is clearly discern-

able thanks to the conspicuous sutures with the premaxillary crests, frontals, and mesethmoid, with a condition similar to *C. planirostris*. In the latter the nasals are rarely preserved, and if preserved they show a more spongy aspect than surrounding bones. This is maybe the reason why they are easily damaged and lost in *Choneziphius*.

Frontal

Frontals are heavily worn on the vertex of the holotype and other referred specimens. However, judging from the short distance between the ascending processes of the maxillae, they were originally transversally narrower than the nasals, a condition similar to *C. planirostris*. The supraorbital process of the frontal is anteriorly bordered by the lacrimal and the maxilla.

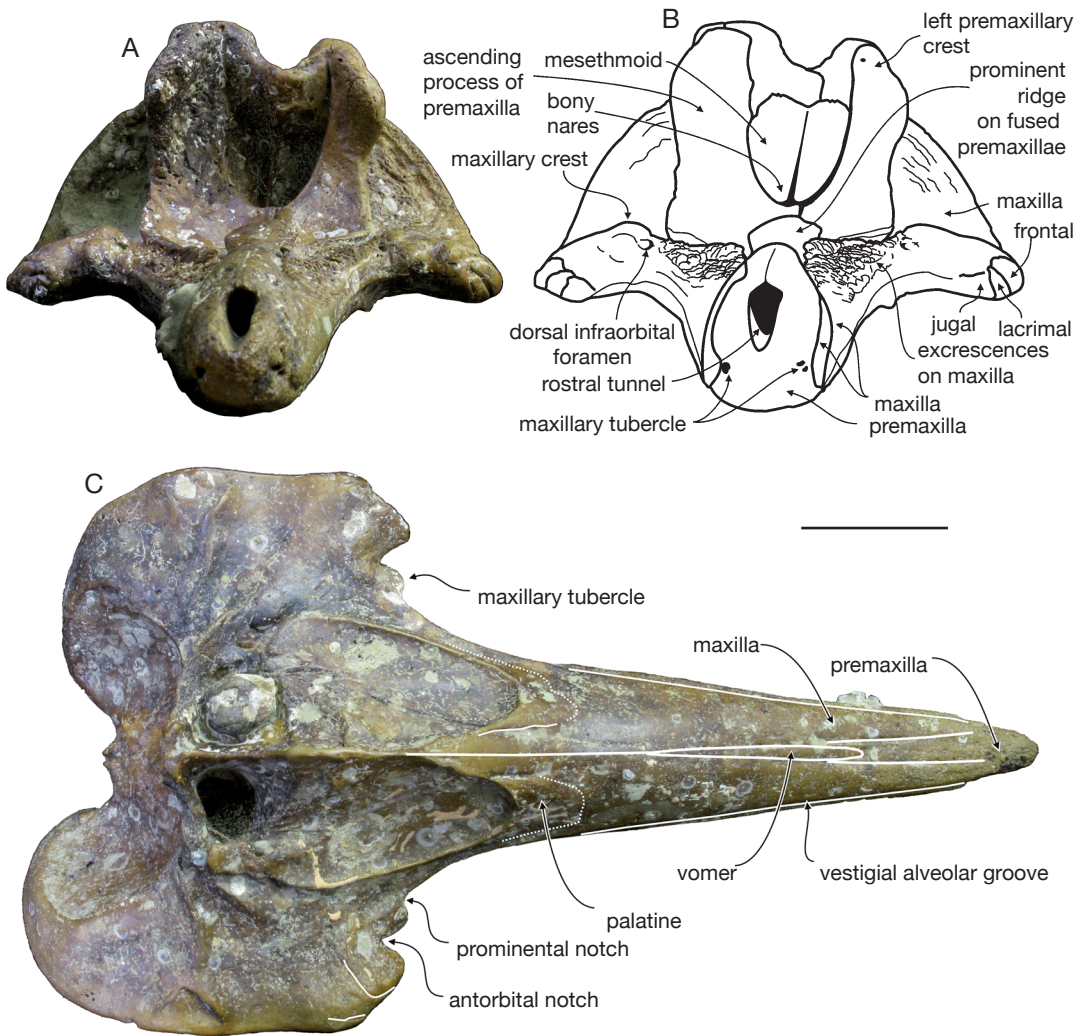


FIG. 4. — Skull of *Choneziphius leidy* n. sp. (SGHN MA0633, holotype): **A**, anterior view; **B**, corresponding line drawing; **C**, ventral view. Cross-hatching indicates the presence of a concretion. Scale bar: 10 cm.

Vomer

On the midline of the ventral side of the rostrum of the holotype, a narrow exposure of vomer is visible over a length of 166 mm, from a level 181 mm posterior to the apex of the rostrum.

Palatine

The palatine is only partially preserved in the holotype. The anteriormost point of the maxilla-palatine suture is 115 mm anterior to the level of the antorbital notch.

REMARKS

The most striking differences between *C. leidy* n. sp. and *C. planirostris* are the general size and the rostrum length. Therefore one has to wonder whether these differences (and the other differences) could be related to ontogeny and/or sexual dimorphism. Measurements of all available specimens of *C. planirostris* (all from the North Sea) show a mean rostrum length of 359 mm ($n = 27$, min = 297 mm, max = 416 mm), whereas *C. leidy* n. sp.

(from the Atlantic coast off Galicia) reports 499 mm ($n = 2$, min 495 mm, max 503 mm). It seems obvious that the large North Sea sample cannot be seen as a sexual dimorphic variant of the much larger Galician specimens. Indeed, variation within the North Sea sample (from very slender specimens to more robust specimens, see Lambert [2005: fig. 21]) shows all the aspects of sexual and/or ontogenetic variation within a same species.

Genus *Tusciziphius* Bianucci, 1997

TYPE SPECIES. — *Tusciziphius crispus* Bianucci, 1997, from Tuscany (Italy), early Pliocene, calcareous nannofossil zone MNN14-15 (Bianucci *et al.* 2001).

OTHER SPECIES INCLUDED. — *Tusciziphius atlanticus* n. sp.

EMENDED DIAGNOSIS. — *Tusciziphius* differs from all other ziphiines except *Imocetus* n. gen. and *Globicetus* n. gen. in having an extremely ossified trapezoidal vertex in which the anterior part of the nasals contact the premaxillary crests. It differs from *Globicetus* n. gen. and *Imocetus* n. gen. in the extreme widening and anterior projection of the right premaxillary crest, and in the lesser posterior constriction of the vertex; it further differs from *Globicetus* n. gen. in lacking a large spherical medial premaxillary rostral prominence; it further differs from *Imocetus* in lacking a wide facial depression, a rostral maxillary spur-shaped crest, and in having the premaxillary foramen not located posterior to the level of the antorbital notch. Among the other ziphiine genera it further differs from *Ziphius* and *Izikoziphius* in the medial fusion of the premaxillae closing the mesorostral groove; it further differs from the possible ziphiine *Caviziphius* in the shallower excavation of the premaxillary sac fossae.

Tusciziphius atlanticus n. sp. (Figs 6-9; Table 2)

HOLOTYPE. — SGHN MA0926, a partial skull including rostrum, facial area, and vertex.

PARATYPE. — NMR 9991-3020, a partial skull including rostrum, facial area, and vertex, originally referred to *Tusciziphius crispus* (see Post *et al.* 2008). Morgan River, Beaufort County, South Carolina, USA, between 32°26'50"N, 80°35'57"W and 32°27'09"N, 80°28'44"W. Found reworked on the bottom of a river, it has been proposed to originate from late Miocene-Pliocene layers (Post *et al.* 2008).

REFERRED SPECIMENS. — SGHN MA0632, a partial skull including rostrum, facial area, and vertex, As Paredes fishing ground, depth of approximately 470 m, off the Galician coast, 44°07'N, 08°07'W; SGHN MA0644, a partial skull including rostrum, facial area, and vertex, A Selva fishing ground, depth of approximately 500 m, off the Galician coast, 44°10'N, 08°40'W; SGHN MA0914, a partial skull including rostrum, facial area, and vertex, A Selva fishing ground, depth of approximately 500 m, off the Galician coast, 44°10'N, 08°40'W; ML1365, a right facial area including right side of the vertex, south of Nazaré Canyon off the Portuguese coast, exact locality unknown, but likely around 39°18'N, 9°47'W.

ETYMOLOGY. — From the Atlantic Ocean distribution of the species (South Carolina, east coast USA and Iberian Atlantic coast, western Europe).

TYPE LOCALITY. — Cortada fishing ground, depth of approximately 600 m, off the Galician coast, 43°30'N, 09°25'W.

DIAGNOSIS. — *Tusciziphius atlanticus* n. sp. differs from all other ziphiids in the prominent medial rostral bulge formed by the fused premaxillae, which elevation varies individually and is probably related to sexual dimorphism (this feature cannot be observed in *T. crispus*, of which the rostrum is unknown; in *Aporotus* the elevated premaxillae are not fused in a single bulge).

It differs from *T. crispus* in having the right premaxillary sac fossa almost completely (except the posterior portion) filled by compact bone forming a semicircular shelf and in having the excavation for the premaxillary sacs restricted to the posterior portion of both right and left premaxillary sac fossae.

DESCRIPTION

The holotype, the paratype, and the referred specimens of *Tusciziphius atlanticus* n. sp., share with *T. crispus* the similar size, the large and asymmetrical premaxillary sac fossae, and the vertex architecture with the extreme widening and anterior projection of the right premaxillary crest. All the Iberian specimens referred to this species exhibit, when preserved, a moderately elongated rostrum, suggesting that the apparently short rostrum of the paratype may be an artefact due to restoration of the broken apex with plaster (Post *et al.* 2008).

A prominent medial elevation on the rostrum, formed by the fusion of premaxillae over the mesorostral groove, is visible in three of the four specimens with a preserved rostrum. In the paratype NMR 9991-3020 and in SGHN MA0914, the

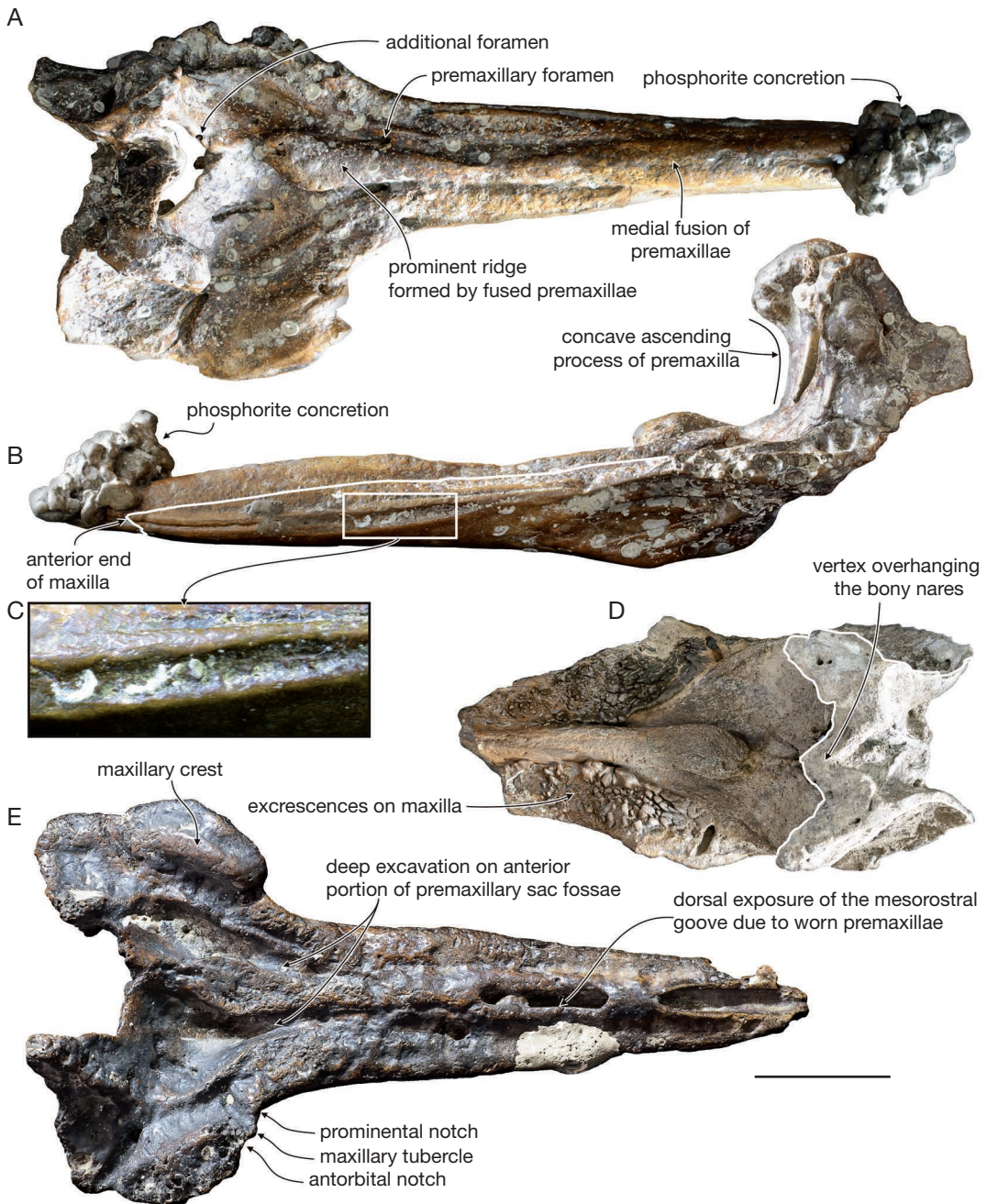


FIG. 5. — **A-C**, Skull of *Choneziphius leidy* n. sp. (SGHN MA0640); **A**, dorsal view; **B**, lateral view; **C**, detail of the rostrum in lateral view showing the vestigial alveolar groove; **D**, *C. leidy* n. sp. (SGHN MA0641), partial skull in dorsal view; **E**, *C. leidy* n. sp. (SGHN ML533), partial skull in dorsal view. Scale bar: 10 cm.

TABLE 2. — Measurements (in mm) on the skulls of *Tuszcziphius atlanticus* n. sp. from South Carolina (USA) and the Atlantic Ocean floor off the Iberian Peninsula. Abbreviations: e, estimate; +, nearly complete; –, no data.

	NMR 9991– 3020	SGHN MA0632	SGHN MA0644	SGHN MA0914	SGHN MA0926 (holotype)
Rostrum length	–	–	–	+425	+440
Length of premaxillary portion of rostrum	–	–	–	+5	–
Distance from apex of rostrum to bony nares	–	–	–	–	+525
Width of rostrum at mid-length	–	–	–	63	64
Height of rostrum at mid-length	–	–	–	89	82
Width of premaxillae at mid-length of rostrum	–	–	–	26	50
Width of rostrum base at antorbital notch	–	–	–	e150	230
Width of premaxillae at rostrum base	86	–	–	68	62
Minimum distance between maxillae near rostrum base	–	–	e51	–	62
Distance rostrum base – anterior apex of palatine	e130	–	–	e170	190
Preorbital width of skull	–	–	–	e350	320
Postorbital width of skull	+372	–	–	–	–
Width of premaxillary sac fossae	173	e171	142	170	150
Width of right premaxillary sac fossa	108	106	92	105	96
Width of left premaxillary sac fossa	51	61	46	58	41
Width of bony nares	69	e73	53	70	66
Minimum width of right ascending process of premaxilla	68	e60	60	–	–
Width of premaxillary crests	e184	188	155	–	180
Width of right premaxillary crest	+101	e87	e76	–	101
Width of left premaxillary crest	51	33	29	48	44
Minimum distance between premaxillary crests	e39	–	e58	42	61
Maximum width of nasals	–	–	–	55	58
Maximum width of right nasal	e27	–	–	29	34
Maximum width of left nasal	–	–	–	27	24
Length of right nasal	82	e67	50	72	88
Length of medial suture of nasals	68	–	–	62	71
Minimum posterior distance between maxillae	84	e105	–	88	76

rostral bulge is present but less developed. This character cannot be observed in *T. crispus* because the rostrum is not preserved on the holotype and only preserved specimen.

Premaxilla

Due to the apical erosion of the rostrum, more or less pronounced in all specimens, it is not possible to evaluate the length of the portion of the rostrum formed by the premaxillae alone. In fact, this region is partly preserved (5 mm) only in SGHN MA0914. In all the specimens, the preserved portion of the rostrum exhibits thick premaxillae with a medial suture, dorsally closing the mesorostral groove. This closure starts from the preserved apical portion of the rostrum in all specimens except in the holotype, where the first 65 mm of the groove are still dorsally open. The fused premaxillae are massive

and protuberant on the rostrum; they form a bulge, with a varying position and height, on which the medial premaxillary suture is completely obliterated.

The development of the medial premaxillary bulge extends from the apex of the rostrum to the level of the antorbital notch in the holotype, SGHN MA0632 and SGHN MA0914, and to the level of the anterior palatine suture in SGHN MA0644. The elevation of the bulge increases anteroposteriorly progressively in the holotype, and more abruptly in SGHN MA0644 and SGHN MA0632. The maximum height of the bulge above the maxilla is 90 mm in SGHN MA0632, 67 mm in SGHN MA0644, and 58 mm in the holotype. In the paratype and in SGHN M0914, only a small dome, respectively 27 and 33 mm above the maxilla, is present in the posterior part of the rostrum, just anterior to the antorbital notches.

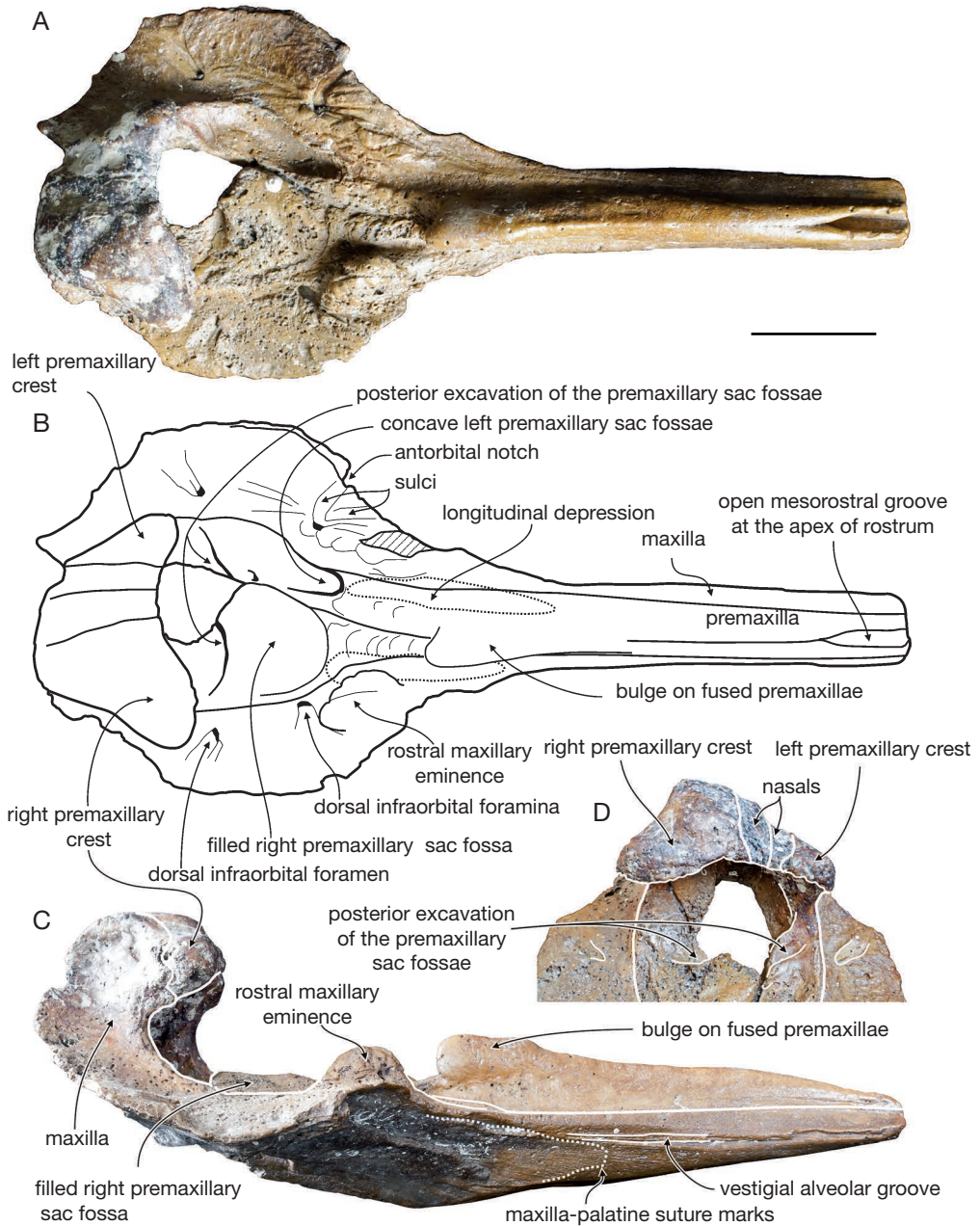


FIG. 6. — Skull of *Tusciziphius atlanticus*, n. sp. (SGHN MA0926, holotype): **A**, dorsal view; **B**, corresponding line drawing; **C**, lateral view; **D**, detail of the vertex and premaxillary sac fossae in anterior view. Parallel lines indicate a break surface. Scale bar: 10 cm.

Macroscopic observation of transverse sections along the medial bulge of SGHN MA0632 reveal a high compacity of the bone tissue and the pres-

ence of a series of growth layers, a feature already noted in the pachyostotic rostrum of several other ziphiid taxa (Lambert 2005; Buffrénil &

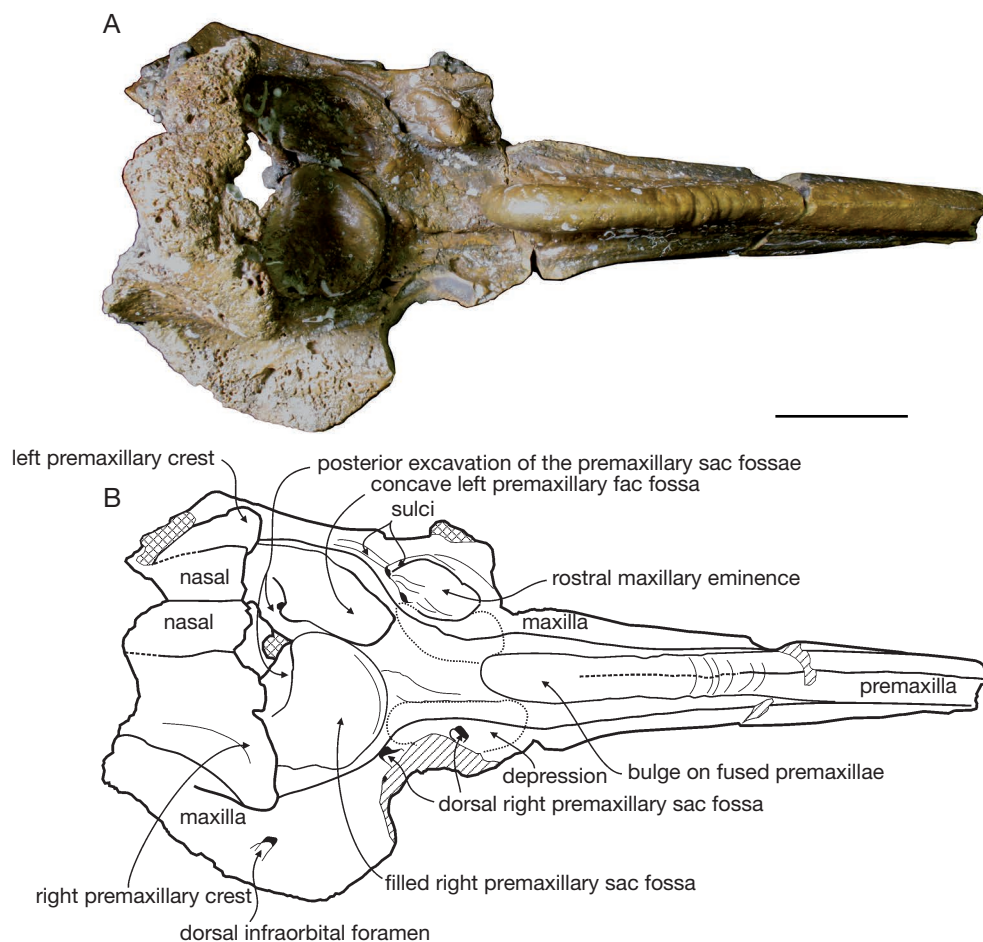


FIG. 7. — Skull of *Tuscziphius atlanticus*, n. sp. (SGHN MA0632): **A**, dorsal view; **B**, corresponding line drawing. Cross-hatching indicates the presence of a concretion; tight parallel lines indicate a break surface. Scale bar: 10 cm.

Lambert 2011; Lambert *et al.* 2011). Posterior to the premaxillary bulge, there is a low medial shelf laterally delimited by two shallow depressions and posteriorly margined by the premaxillae sac fossae. The premaxillary sac fossae are strongly asymmetric in all the specimens of *T. atlanticus* n. sp. (ratio between the left and right width ranging from 0.43 to 0.57) and in *T. crispus* (0.44). However, in all the specimens of *T. atlanticus* n. sp. the anterior part of the right premaxillary sac fossa is completely filled by compact bone, forming a thick semicircular shelf. The filling is absent in the left premaxillary fossa, which is deeply concave in all

specimens. Instead, in *T. crispus* both premaxillary sac fossae are excavated. The deep concavity of the premaxillary sac fossae is likely a derived condition shared with *Caviziphius*, *Choneziphius*, *Globicetus* n. gen., and *Imocetus* n. gen., whereas the semicircular shelf that partially fills the right premaxillary fossa in *T. atlanticus* n. sp. may be homologous with the rectangular premaxillary shelf of *Globicetus* n. gen. (see below). Due to the presence of the anterior shelf, the posterior portion of the right premaxillary sac fossa displays an abrupt anterior slope. Interestingly, a similar step is present at the same level in the fully concave left premaxillary sac

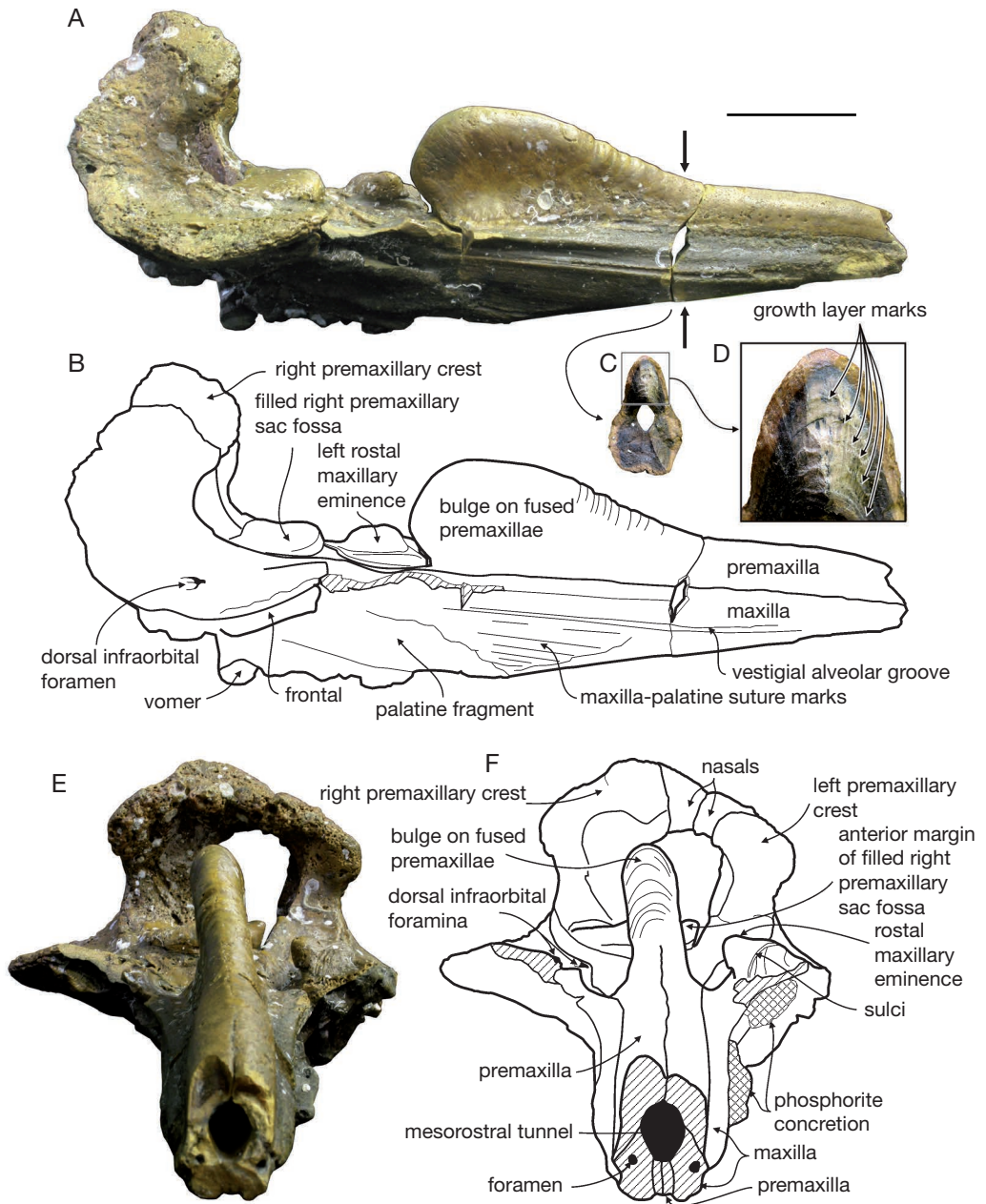


FIG. 8. — Skull of *Tusciziphius atlanticus* n. sp. (SGHN MA0632): **A**, lateral view; **B**, corresponding line drawing (the arrows indicate the level of the transverse section); **C**, transverse section through the rostrum; **D**, detail of **C** showing the growth layers; **E**, anterior view; **F**, corresponding line drawing. Cross-hatching indicates the presence of a concretion; tight parallel lines indicate a break surface. Scale bar: 10 cm.

fossa. No premaxillary foramen is observed at the anterior end of the premaxillary sac fossae. Only one foramen is visible near the medial margin of

the left fossa in the holotype, in the paratype, and SGHN MA0914, absent in SGHN MA0632 and SGHN MA0644. Similar to *T. crispus*, the ascend-

ing process of the premaxilla of *T. atlanticus* n. sp. exhibits a strong transverse constriction. Its posterior portion is anteriorly curved, overhanging the premaxillary sac fossa and bony nares. The right premaxillary crest of *T. atlanticus* n. sp. shows the extreme transverse widening typical for *Tusciziphius*. Moreover, as in *T. crispus*, the right premaxillary crest is more anteriorly projected than the left. For this character, *Tusciziphius* clearly differs from the closely related *Globicetus* n. gen., in which both crests have approximately the same anterior extent. This difference may be related to the different direction of the right premaxillary crest (anterolateral in *Tusciziphius* and more transversal in *Globicetus* n. gen.). Finally, as in *Globicetus* n. gen., *Imocetus* n. gen., and especially *Caviziphius*, the right premaxillary crest is considerably larger and especially higher than the left, a feature best seen in anterior view. Moreover, due to the fact that the right premaxillary crest is considerably higher than the left one, the dorsal surface of the right nasal is more medially inclined than that of the left nasal.

Maxilla

The distal half part of the rostrum is narrow and strongly transversally compressed. Consequently the dorsal surface of the maxilla is nearly vertical and almost invisible in dorsal view. In the proximal half portion, the lateral inclination of the maxilla decreases progressively, with a wider portion visible in dorsal view.

At the rostrum base, just medial to the right antorbital notch, the holotype and SGHN MA0644 develop a high and voluminous rostral maxillary eminence, slightly medially curved. SGHN MA0632 lacks a portion of the right maxilla that probably included, judging from the shape and the position of the broken surface, a similar eminence. On the left side of the holotype, SGHN MA0644, and SGHN MA0632, the maxilla exhibits a similar but lower rostral maxillary eminence. In the paratype and SGHN MA0914, no prominent rostral maxillary eminence is present, only some irregular excrescences. On both sides of skulls bearing rostral maxillary eminences, a shallow longitudinal depression is margined laterally by the eminence, slightly overhanging the depression, and medially

by the low medial premaxillary shelf. One to three dorsal infraorbital foramina pierce the maxilla near the rostrum base, medial and/or posterior to the rostral maxillary eminence (when the eminence is present). From these foramina, several sulci run anteriorly and posteriorly. The vestigial alveolar groove is a narrow sulcus, with no visible alveoli.

Nasal

The shape of the nasals, as the general architecture of the vertex, is rather stable in *T. atlanticus* n. sp. and *T. crispus*. The sutures of the nasals are generally hard to detect due to the extreme ossification and fusion of the vertex bones. The nasals are anteroposteriorly elongated, with lateral margins parallel or faintly convergent (but not as much as in *Globicetus* n. gen.). As in *Globicetus* n. gen. and *Imocetus* n. gen., the lateral margin of the nasal is in contact with the premaxillary crest for all its extent and the dorsal surface of the joined nasals forms a shallow depression between the premaxillary crests.

Frontal

The frontals are visible on the vertex of several specimens. They are wider than in *Globicetus* n. gen. and *Imocetus* n. gen., related to the lesser transverse constriction of the posterior part of the vertex.

Vomer

The vomer is not visible dorsally due to the complete closure of the mesorostral groove. It is visible only ventrally between the premaxillae and the maxillae along the mid-line of the rostrum, and anterior to the choanae due to the non-preservation of the palatine in that area.

Palatine

The palatine is partially preserved only in SGHN MA0914. The maxilla-palatine suture extends about 150 mm anterior to the antorbital notch, the level of the abrupt widening of the rostrum.

REMARKS

The previous assignation of the South Carolina paratype of *Tusciziphius atlanticus* n. sp. to the Italian species *T. crispus* was made at a time when only one skull was known (Post *et al.* 2008), preventing

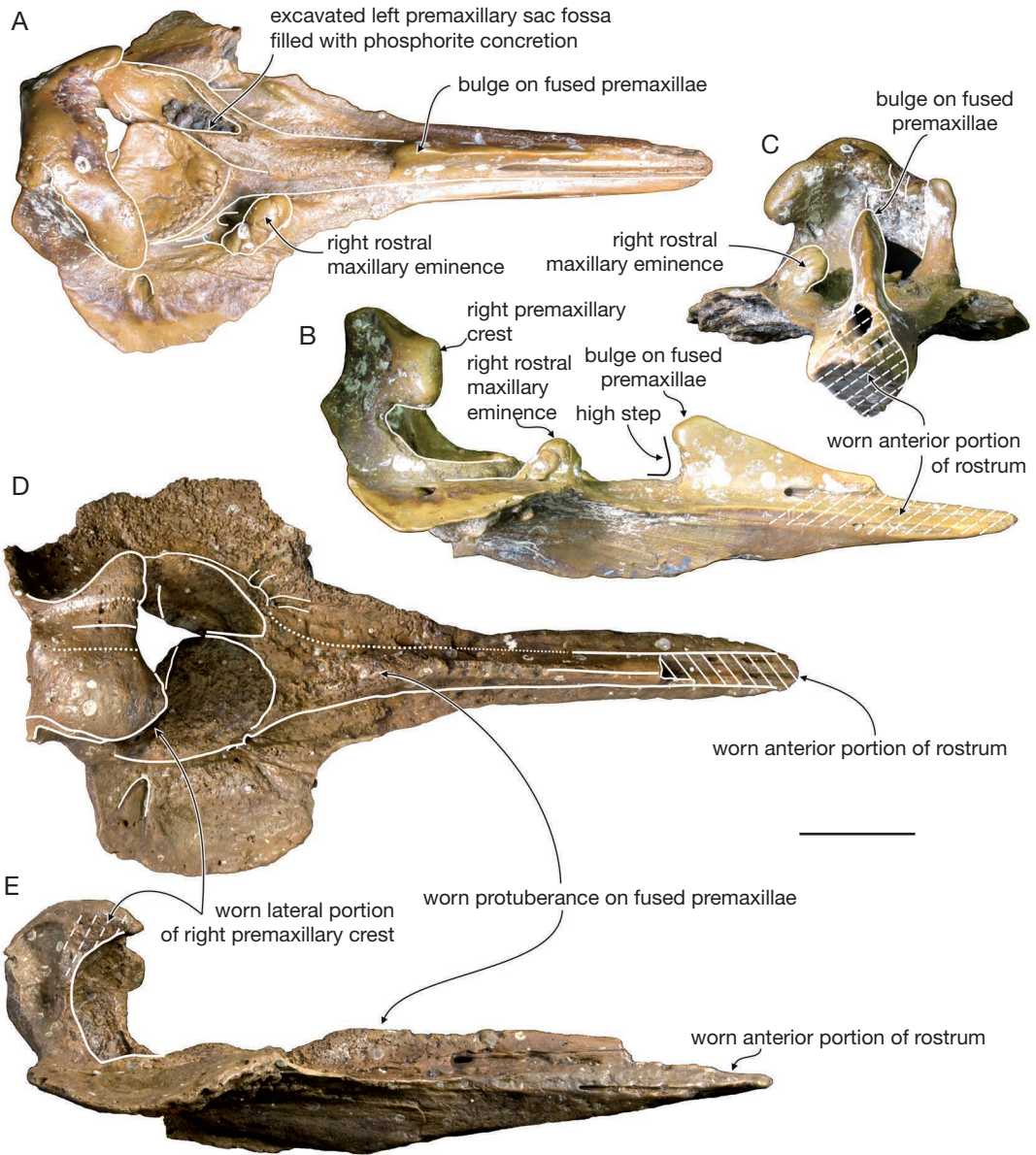


FIG. 9. — **A–C**, skull of *Tusciziphius atlanticus*, n. sp. (SGHN MA0644); **A**, dorsal view; **B**, lateral view; **C**, anterior view. **D, E**, skull of *T. atlanticus*, n. sp. (SGHN MA0914); **D**, dorsal view; **E**, lateral view. Parallel lines indicate superficial wear. Scale bar: 10 cm.

any evaluation of the intraspecific or interspecific character for the variation at the level of the premaxillary sac fossae. The observation of the same filling of the right premaxillary sac fossa in all the examined skulls from the Atlantic Ocean floor off

the Iberian Peninsula suggests that this character is valid for the definition of a new species, grouping the South Carolina specimen with the Iberian specimens. Additional specimens of *T. crispus* from Italy could confirm this interpretation in the future.

Genus *Globicetus* n. gen.

TYPE AND ONLY SPECIES. — *Globicetus hiberus* n. gen., n. sp., by present designation.

ETYMOLOGY. — From Latin “globus”, for the large spherical medial premaxillary prominence on the rostrum, and from Latin “cetus”, whale. Gender masculine.

DIAGNOSIS. — Same as for the species.

Globicetus hiberus n. sp. (Figs 10-13; Table 3)

HOLOTYPE. — ML 1361, partial skull including rostrum, facial area and vertex.

REFERRED SPECIMENS. — MHNUSC 3958, partial skull including facial area and vertex, 20 miles from Touriñán Cape, off the Galician coast, depth of 1500 m, 42°50'N, 9°40'W; IEO DR26 026, partial skull including rostrum and anterior portion of facial area, off the Galician coast, depth of approximately 1500 m, 42°27'N, 11°59'W.

ETYMOLOGY. — From Latin “hiberus”, Iberian, for the geographical origin of the holotype and referred specimens.

TYPE LOCALITY. — South of Nazaré Canyon off the Portuguese coast, exact locality unknown, but likely around 39°18'N, 9°47'W.

DIAGNOSIS. — *Globicetus hiberus* n. gen., n. sp. differs from all other ziphiids in the large spherical medial rostral prominence formed by the fused premaxillae, in the large prominence of the right premaxilla anterior to the right premaxillary sac fossa, and in the barely marked antorbital notch, related to the important widening of the rostrum base.

Among the other ziphiine genera it further differs from *Ziphius* and *Izikozihius* in the medial fusion of the premaxillae closing the mesorostral groove; it shares with *Imocetus* n. gen. and *Tusciziphius* the anterior part of the nasal contacting the premaxillary crest and the extreme ossification and fusion of the vertex elements, but it differs from *Imocetus* n. gen. in lacking a wide facial depression, rostral maxillary spur-shaped crest, and in having the premaxillary foramina not located posterior to the level of the antorbital notch; it differs from *Tusciziphius* in the less transversally expanded vertex (lower width between the premaxillary crests, and lower distance between maxillae posterior to the vertex), and in the posterolateral direction of the right premaxillary crest. It further differs from the possible ziphiine *Caviziphius* in shallower excavation of the premaxillary sac fossae.

DESCRIPTION

The skull is slightly smaller than in the largest specimens of *Imocetus piscatus* n. gen., n. sp. (see below), with a postorbital width estimated at 372 mm in the holotype. The rostrum is elongated and its base is wide. The posterior half of the rostrum is characterized by the extreme thickening of the premaxillae, forming a large spherical prominence followed towards the right premaxillary sac fossa by a high shelf (see below). The facial area is short with the low and wide vertex overhanging it, hiding the bony nares and most of the premaxillary sac fossae in dorsal view.

Premaxilla

On the roughly complete rostrum of the holotype the premaxilla is slightly longer apically (20 mm) than the maxilla. On the anterior half of the massive and subcylindrical rostrum, the mesorostral groove is dorsally closed by the thick premaxillae, displaying a medial sutural contact. In dorsal view, the posterior half of the rostrum is partly covered by a large, roughly spherical, element made by the joined premaxillae. Preserved on the holotype and IEO DR26 026, this unusual prominence has a maximum width of 150 mm and 141 mm respectively in these two specimens and a maximum height above the maxilla of 135 mm and 92 mm. It is slightly asymmetrical, higher on the right side of the holotype and longer on the right side of IEO DR26 026. It is made, at least superficially, by compact bone, covered with narrow and shallow anastomosed sulci likely related to vascularization. On the holotype, the anterior and anterolateral margins of the spheroid do not contact the underlying premaxilla and maxilla, leaving an open space of about 10 mm, whereas in IEO DR26 026 a high medial pad of bone joins the spheroid to the dorsal surface of the rostrum. Posteriorly, the spheroid is followed by a thick shelf predominantly constituted by the right premaxilla, whose surface is similarly compact and covered with sulci. Rectangular in dorsal view in the holotype, this shelf is distinctly narrower distally in IEO DR26 026 and in the anteriorly incomplete skull MHNUSC 3958. In lateral view the dorsal margin of the shelf of the latter raises forwards similarly to the more complete specimens, suggesting the presence of a similar large

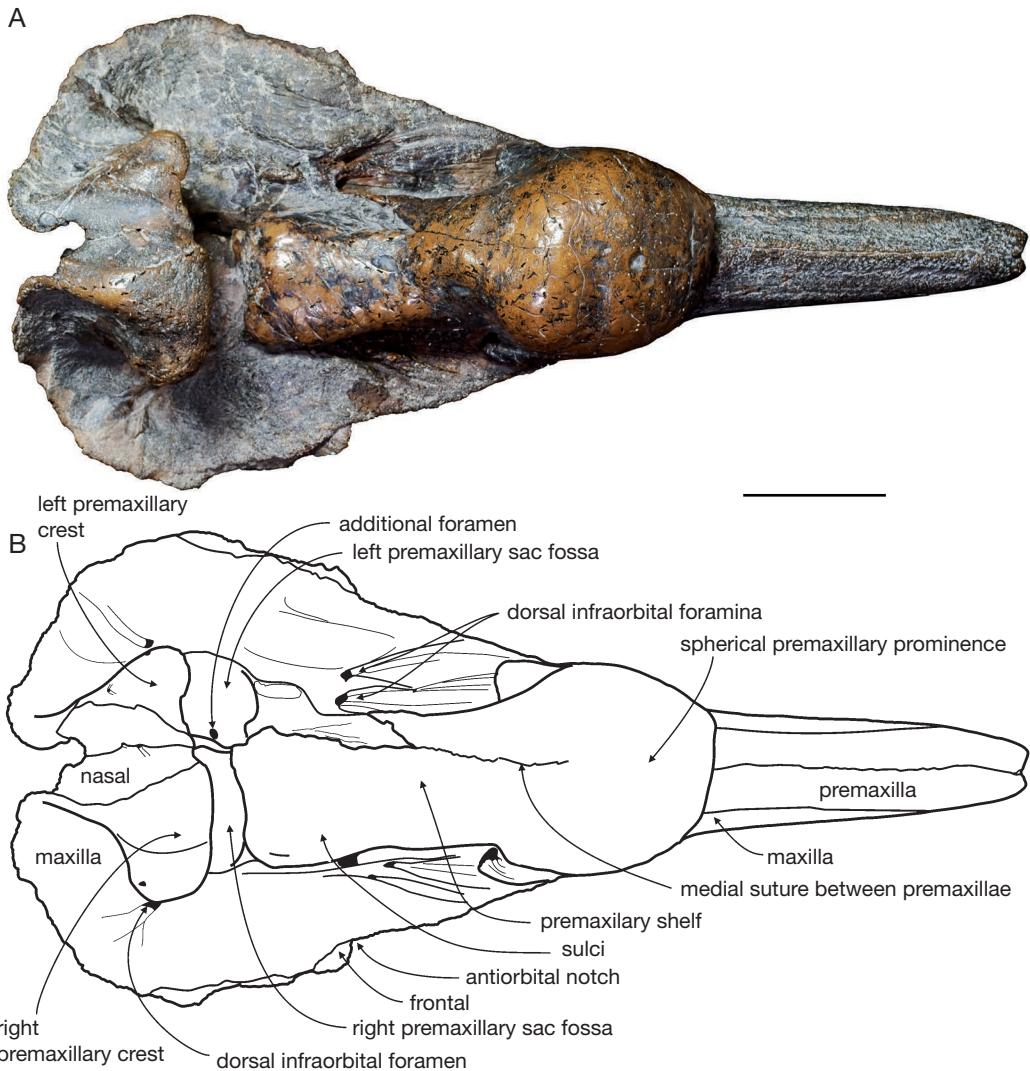


FIG. 10. — Skull of *Globicetus hiberus* n. gen., n. sp. (ML 1361, holotype): **A**, dorsal view; **B**, corresponding line drawing. Scale bar: 10 cm.

spheroid in MHNUSC 3958. The abrupt posterior margin of the shelf corresponds to the anterior limit of the right premaxillary sac fossa, which is considerably wider than the left fossa. Only a narrow and much lower longitudinal crest is located anterior to the left premaxillary sac fossa of the holotype and MHNUSC 3958. Both fossae are short anteriorly, more than in *Tusciziphius*, nearly completely dorsally overhung by the vertex. The presence of the massive shelf in *Globicetus* n. gen., associated with shorter

premaxillary sac fossae, might be interpreted as an overgrowth of the thickened anterior portion of the right premaxillary sac fossa observed in *T. atlanticus* n. sp. The surface of the premaxillary sac fossae is strongly concave and no premaxillary foramen could be detected on the bottom of any of the fossae. Only one foramen is observed on the medial margin of the left fossa of the three specimens, similar to the condition in *Choneziphius leidyi* n. sp., *Imocetus* n. gen., and *T. atlanticus* n. sp.

TABLE 3. — Measurements (in mm) on the skulls of *Globicetus hiberus* n. gen., n. sp. from the Atlantic Ocean floor off the Iberian Peninsula. Abbreviations: e, estimate; +, nearly complete; –, no data.

	ML 1361 (holotype)	MLI 3958	IEO DR 26026
Rostrum length	530	–	552
Length of premaxillary portion of rostrum	20	–	–
Distance from apex of rostrum to bony nares	665	–	e650
Width of rostrum at mid-length	99	–	93
Height of rostrum at mid-length	98	–	99
Width of rostrum base at antorbital notch	265	e285	e233
Width of premaxillae at rostrum base	104	–	–
Minimum distance between maxillae near rostrum base	–	80	–
Distance rostrum base – anterior apex of palatine	227	–	315
Preorbital width of skull	–	+335	–
Postorbital width of skull	e372	–	+305
Longitudinal distance right premaxillary foramen – rostrum base	78	–	72
Width of premaxillary sac fossae	170	+165	–
Width of right premaxillary sac fossa	100.5	83	–
Width of left premaxillary sac fossa	62.5	e74	–
Width of bony nares	79	82	–
Minimum width of right ascending process of the premaxilla	44	42	–
Minimum width of left ascending process of the premaxilla	23	e17	–
Width of premaxillary crests	185	170	–
Width of right premaxillary crest	106	84	–
Width of left premaxillary crest	70	51	–
Maximum width of nasals	69.5	68	–
Maximum width of right nasal	–	47	–
Maximum width of left nasal	–	28	–
Length of medial suture of nasals	68	e62	–

The ascending process of each premaxilla is strongly constricted and short. On the low vertex, the overhanging right premaxillary crest is much wider than the left, reaching laterally a level beyond the lateral margin of the corresponding premaxillary sac fossa. The top of the vertex is made by the right premaxilla, much higher than the left. The anterior margin of the right premaxillary crests is posterolaterally directed, whereas the anterior margin of the left premaxillary crest is roughly anterolaterally directed. In *Tusciziphius* both crests are usually anterolaterally directed.

Maxilla

Apically invisible in dorsal view, the maxilla only slightly widens along the distal half of the rostrum, with a somewhat medially convex maxilla-premaxilla suture. From the level of the large spheroid it sends a thin lateral plate whose lateral margin reaches the preorbital process in a nearly rectilinear line, forming a wide rostrum base. Differing

from *T. atlanticus* n. sp. and *Imocetus* n. gen., the antorbital notch is therefore barely individualized; a wide subhorizontal surface margins the premaxillary shelf on both sides of the rostrum base. This surface is pierced by several dorsal infraorbital foramina, three on the right side and two on the left side of the holotype, one less on the right side of MHNUSC 3958, and one less on each side of IEO DR26 026. From these foramina, several sulci are sent anteriorly and anterolaterally. A large longitudinal sulcus passes between the spheroid of the premaxillae and the maxilla, exiting on the anterior margin of the spheroid.

On the supraorbital area, the maxilla is thin, lacking any maxillary crest contrary to part of the specimens of *T. atlanticus* n. sp. and *Imocetus* n. gen. Posterior to the nasals on the vertex, left and right maxillae are close to each other, more than in *Tusciziphius*, with a minimal distance between the maxillae lower than the width of the nasals. At this level the medial margin of the right maxilla is

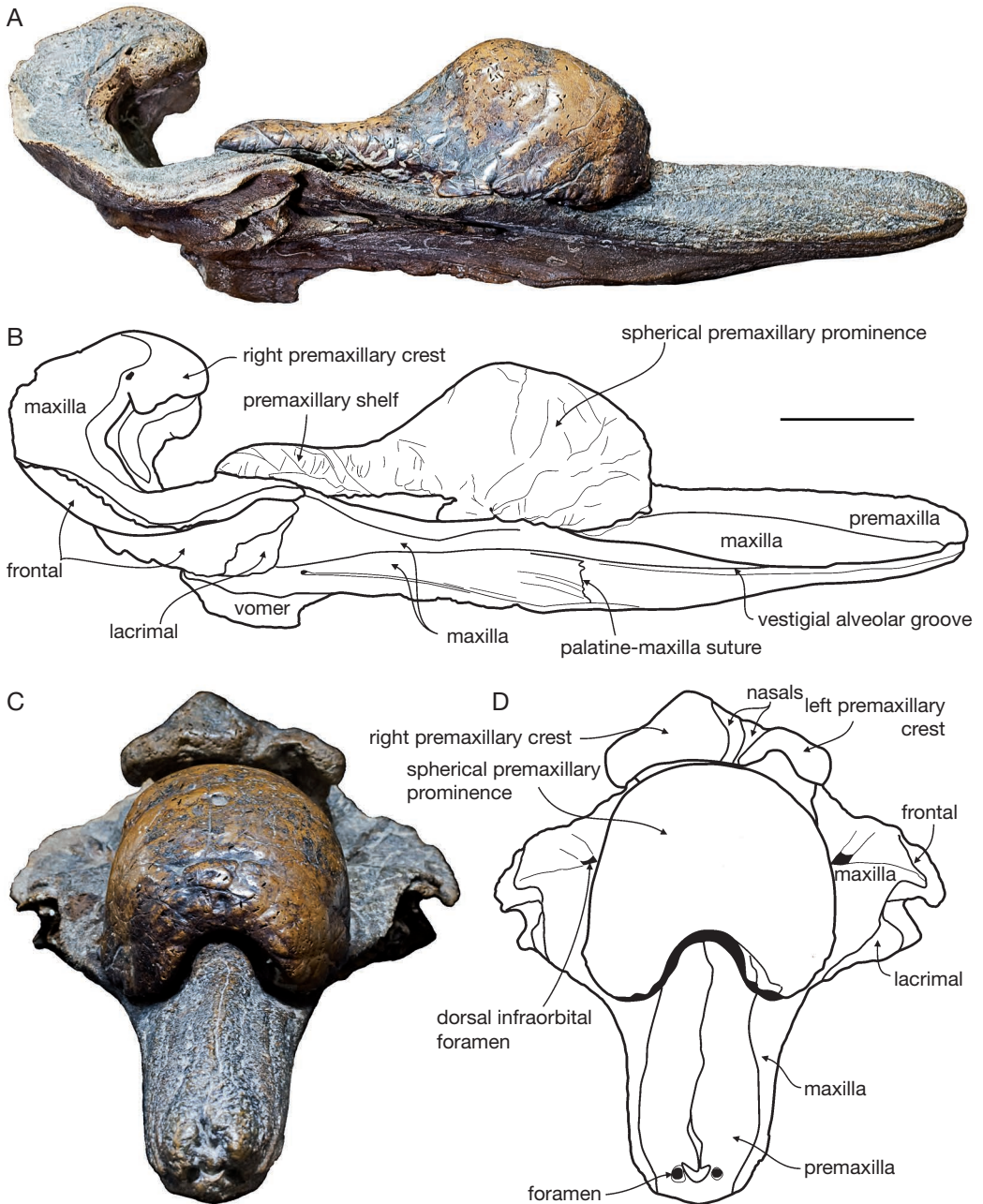


FIG. 11. — Skull of *Globicetus hiberus* n. gen., n. sp. (ML 1361, holotype): **A**, lateral view; **B**, corresponding line drawing; **C**, antero-dorsal view; **D**, corresponding line drawing. Scale bar: 10 cm.

more erected than the margin of the left maxilla; the latter is the continuation of the depressed dorsal surface of the nasals.

On the ventrolateral surface of the rostrum, the remnant of alveolar groove does not contain individualized alveoli.

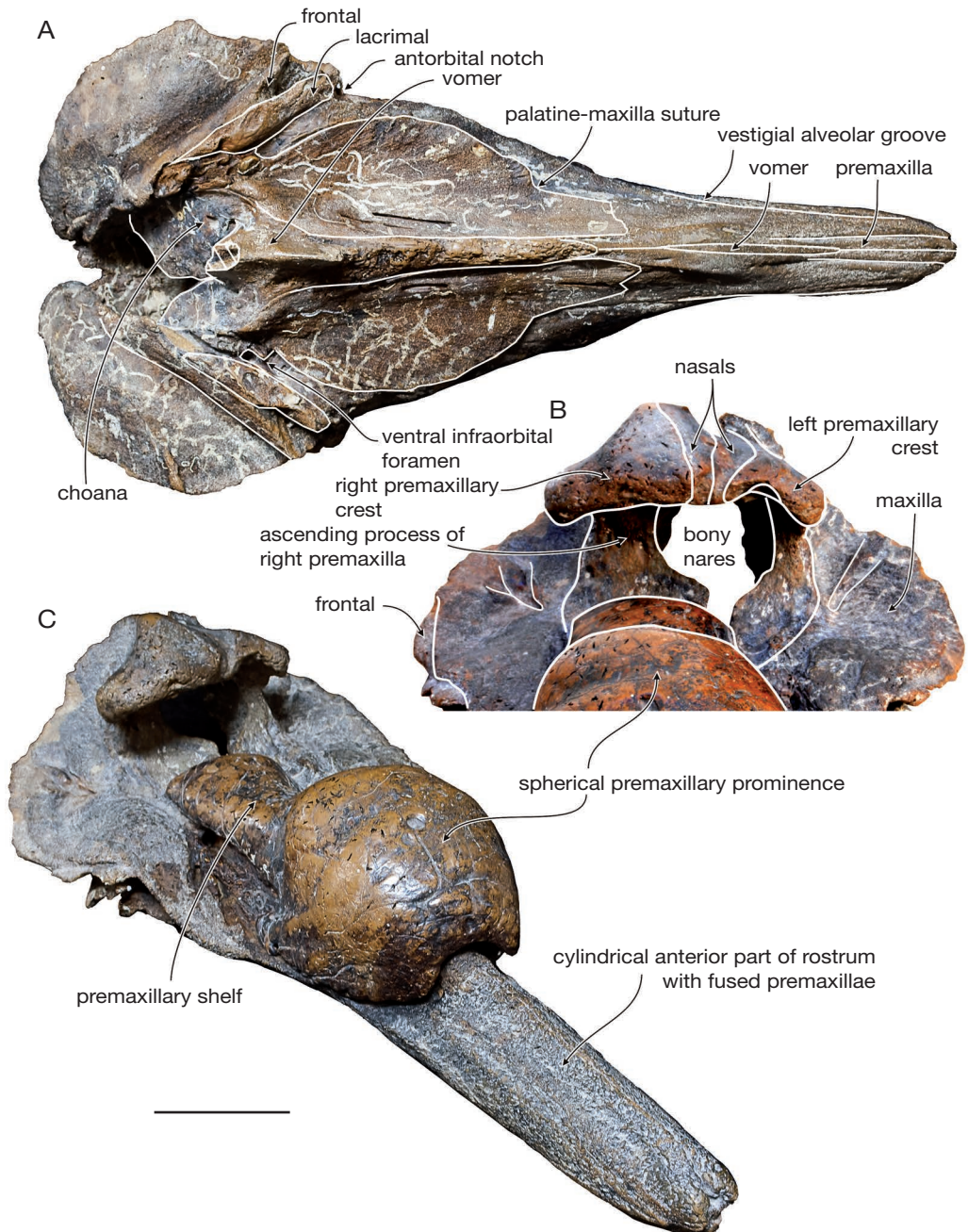


FIG. 12. — Skull of *Globicetus hiberus* n. gen., n. sp. (ML 1361, holotype): **A**, ventral view; **B**, detail of the facial area in anterior view; **C**, anterolateral view; **D**, corresponding line drawing. Scale bar: 10 cm.

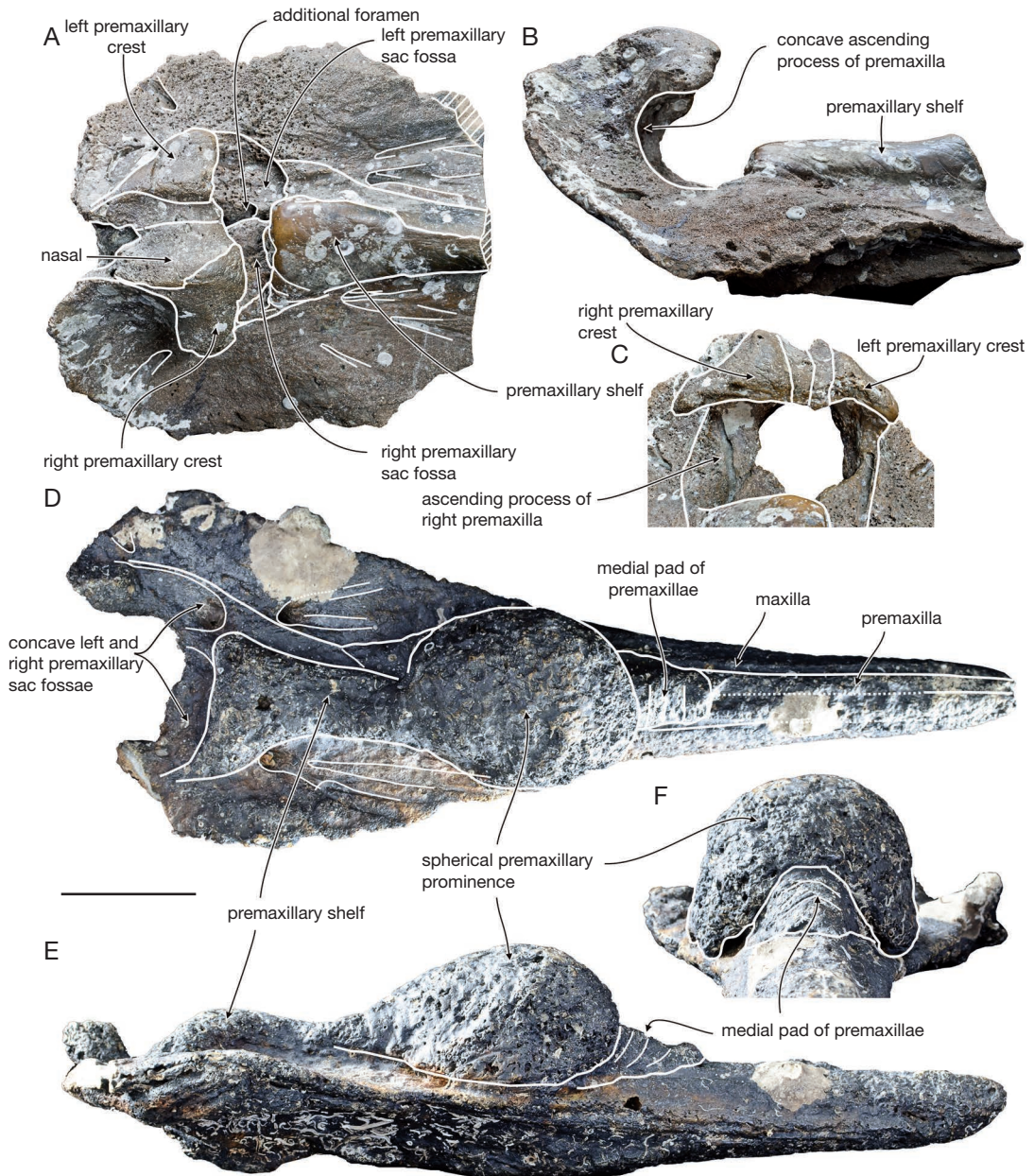


FIG. 13. — **A-C**, partial skull of *Globicetus hiberus* n. gen., n. sp. (MHNUSC 3958): **A**, dorsal view; **B**, lateral view; **C**, detail of the vertex and premaxillary sac fossae in anterior view; **D-F** partial skull of *G. hiberus* n. gen., n. sp. (IEO DR26 026): **D**, dorsal view; **E**, lateral view; **F**, detail of the spherical premaxillary prominence in anterior view. Parallel lines indicate a break surface. Scale bar: 10 cm.

Nasal

Excluded from the premaxillary crest, the nasal is considerably narrower anteriorly than posteriorly. The dorsal surface of the joined nasals forms a depression between the premaxillary crests, as in *Imocetus* n. gen. and *Tusciziphius*. The anterior tip of the nasals does not reach a level anterior to the premaxillary crests, differing from *Izikoziphius* and *Ziphius*. The medial suture is distinctly shifted to the left side compared to the sagittal plane of the skull.

Frontal

Only parts of the frontal are preserved on the heavily worn supraorbital area. Frontals are lost on the vertex; they apparently originally formed an anteromedial projection between nasals.

Vomer

Hidden dorsally by the development of the premaxillae, the vomer is only visible ventrally between the premaxillae and between the maxillae. At the rostrum base, its ventral exposure between the maxillae of the holotype is likely due to partial wear of the latter and loss of the palatines.

Palatine

Most parts of the palatine are likely lost in the three specimens. A large depression with a distinct outline marks the original anterior extent of the palatine on the rostrum, far anterior from the antorbital notch. The palatine was longer in IEO DR26 026, reaching a level 315 mm anterior to the notch.

Lacrima

The lacrima is only partly preserved ventral to the maxilla on the preorbital process of the holotype. Its ventral exposure appears rather narrow but its original extension cannot be estimated due to the bad preservation of the ventral surface of the skull.

REMARKS

A series of arguments support the interpretation of the conspicuous spheroid at the rostrum base of *Globicetus hiberus* n. gen., n. sp. as a non-pathological element. First, it is present with a very similar outer shape in two of the described specimens, it has also been observed by us in additional undescribed skulls kept

in private collections, and its presence is very likely in the third described specimen. In addition, from a morphological point of view, it is nearly symmetrical, with smooth surfaces contrasting with different kinds of pathological bone growths. Furthermore, canals for vascularization/innervation at the base of the spheroid are not interrupted. Finally no fracture or pathological bone tissue has been detected ventral to the spheroid in any of the described specimens.

From a systematic point of view, a dorsomedial sutural contact between the premaxillae is observed on the rostrum of part of the ziphiines (*Choneziphius*, *Imocetus* n. gen., and *Tusciziphius*) and members of the “*Messapicetus* clade”. The general morphology of the low and wide, trapezoidal, extremely ossified, and strongly asymmetric vertex, overhanging the bony nares and the premaxillary sac fossae, closely resembles *Tusciziphius* and, in a lesser extent, *Imocetus* n. gen. A superficially similar morphology is also observed in the hyperoodontine *Hyperoodon*, but in this case the nasal is deeply thrust in the premaxillary crest and the left premaxillary crest is distinctly directed posterolaterally. The development of a high medial prominence of the joined premaxillae on the rostrum is similarly observed in some specimens of *Tusciziphius atlanticus* n. sp. and in a fragmentary skull referred here to aff. *Caviziphius* sp. (see below). In none of these specimens the prominence displays a spherical volume shape. Additional differences with *Tusciziphius* are: large prominence of the right premaxilla anterior to the right premaxillary sac fossa; barely marked antorbital notch, related to the important widening of the rostrum base; less transversally expanded vertex (lower width between the premaxillary crests and lower distance between the maxillae posterior to the vertex); and posterolateral direction of the right premaxillary crest.

Genus *Imocetus* n. gen.

TYPE AND ONLY SPECIES. — *Imocetus piscatus* n. sp., by present designation.

ETYMOLOGY. — From Latin “imum”, bottom, because it was trawled on the sea floor, and from Latin “cetus”, whale. Gender masculine.

DIAGNOSIS. — Same as for the species.

TABLE 4. — Measurements (in mm) on the skulls of *Imocetus piscatus* n. gen., n. sp. from the Atlantic Ocean floor off the Iberian Peninsula. Abbreviations: e, estimate; +, nearly complete; –, no data.

	ML 1358 (holotype)	ML 1359	ML 1360
Rostrum length as preserved	495	382	326
Distance from apex of rostrum to bony nares	–	+392	–
Width of rostrum 100 mm from apex	68	+58	–
Width of premaxillae 100 mm from apex	–	46	–
Width of rostrum 200 mm from apex	99	101	–
Width of premaxillae 200 mm from apex	–	51	–
Width of rostrum 300 mm from apex	149	145	–
Width of premaxillae 300 mm from apex	–	52	–
Width of rostrum 400 mm from apex	212	–	–
Width of rostrum base at antorbital notch	256	199	165
Width of premaxillae at antorbital notch	–	63	–
Distance rostrum base – apex of palatine-pterygoid suture	158	85	110
Maximum distance between lateral margins of rostral maxillary crests	198	205	162
Minimum distance between maxillary crests (on neurocranium)	186	–	–
Distance rostrum base – anterior end of premaxillary sac fossa	211	367	–
Width of right premaxillary sac fossa	e64	–	–
Width of left premaxillary sac fossa	e60	–	–
Width of bony nares	76	–	–
Minimum width of right ascending process of the premaxilla	29	–	–
Width of premaxillary crests	+139	–	–
Maximum width of nasals	70	–	–
Minimum posterior distance between maxillae	51	–	–

Imocetus piscatus n. sp.
(Figs 14–17; Table 4)

HOLOTYPE. — ML 1358, partial skull including rostrum, facial area and vertex.

REFERRED SPECIMENS. — ML 1359, partial skull including rostrum and anterior portion of facial area and ML 1360, partial skull including rostrum and anterior portion of facial area, south of Nazaré Canyon off the Portuguese coast, exact locality unknown, but likely around 39°18'N, 9°47'W.

ETYMOLOGY. — From Latin “piscatus”, fished, because the holotype and the referred specimens were collected at sea by fishermen.

TYPE LOCALITY. — South of Nazaré Canyon off the Portuguese coast, exact locality unknown, but likely around 39°18'N, 9°47'W.

DIAGNOSIS. — *Imocetus piscatus* n. gen., n. sp. differs from all other ziphiids in a wide and anteroposteriorly elongated facial depression laterally margined by acute longitudinal maxillary crests, a rostral maxillary crest forming a posterodorsally directed spur, and premaxillary foramen located very posterior to the level of the antorbital notch. Among other ziphiines it further differs from *Izikoziphius* and *Ziphius* in the medial fu-

sion of the premaxillae closing the mesorostral groove; it shares with *Globicetus* n. gen. and *Tusciziphius* the anterior part of the nasal contacting the premaxillary crest, and the extreme ossification and fusion of the vertex elements, but it differs from *Globicetus* n. gen. in lacking a large spherical medial premaxillary rostral prominence and in the presence of a distinct antorbital notch. It differs from *Tusciziphius* in the less transversally expanded vertex (lower width between the premaxillary crests and lower distance between the maxillae posterior to the vertex), and in the posterolateral direction of the right premaxillary crest. It further differs from the possible ziphiine *Caviziphius* in the less excavated premaxillary sac fossae.

DESCRIPTION

The skull is large for a fossil ziphiid; based on the width of the rostrum it is close to the size of the modern *Mesoplodon layardii*. At the apex, the tapered rostrum is cylindrical, whereas it is wider at its base. The anteroposterior length of the rostrum is less than half the estimated condylobasal length. The rostrum is proportionally longer in the holotype, in which the antorbital notch is more posteriorly located than in ML 1359 and ML 1360. The ros-

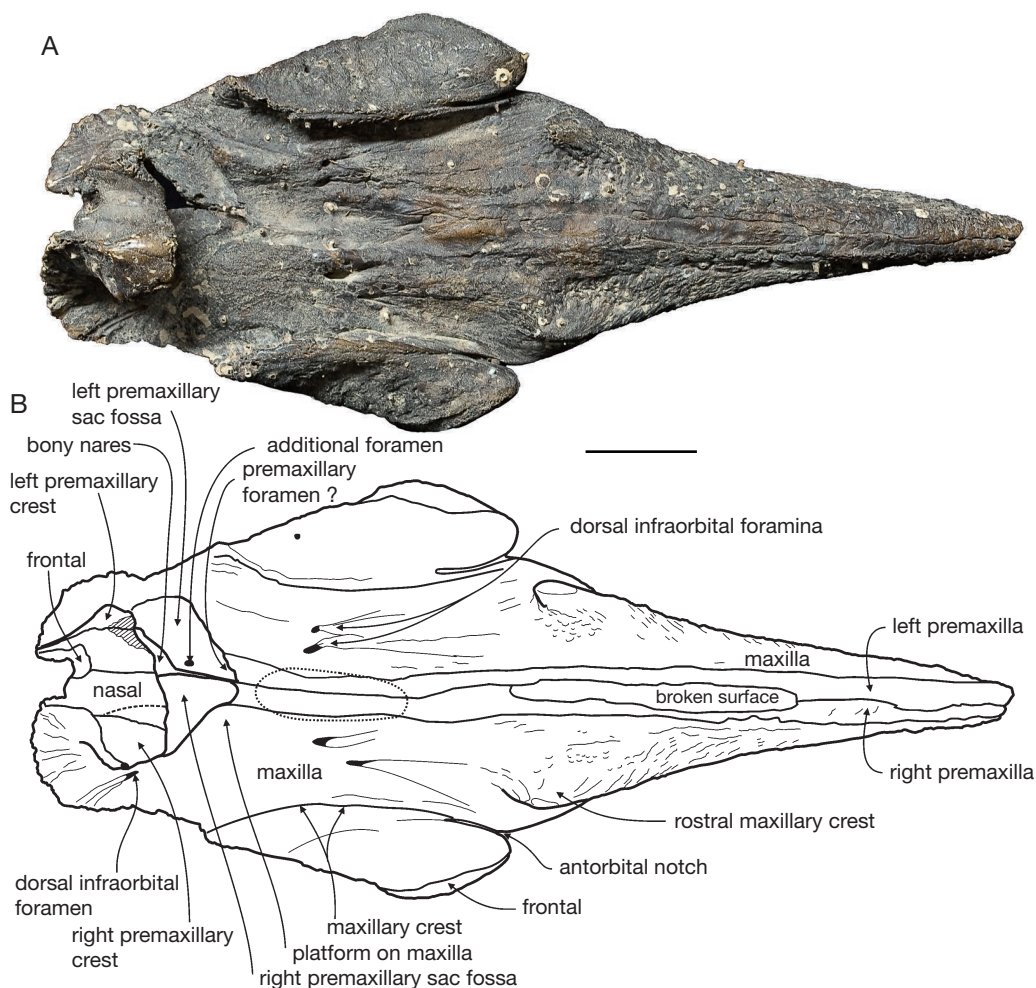


FIG. 14. — Skull of *Imocetus piscatus* n. gen., n. sp. (ML 1358, holotype): **A**, dorsal view; **B**, corresponding line drawing. Parallel lines indicate a break surface. Scale bar: 10 cm.

trum base is also considerably wider in the holotype. The facial area, between the antorbital notch and the vertex, is very long. The vertex is proportionally low, overhanging the bony nares. The supraorbital area is only partly preserved and the basicranium is completely missing.

Premaxilla

On the anterior portion of the rostrum, the half-cylindrical robust premaxillae display a sutural contact above the mesorostral groove. Their medial suture is sinuous on the holotype and more

rectilinear in ML 1359 (not preserved in ML 1360). 195 mm posterior to the apex of the rostrum of the holotype, an artificial medial opening between the superficial layers of the premaxillae exposes bone that we interpret as deeper regions of the premaxillae. Alternatively this element could correspond to the thickened vomer, but we prefer the first hypothesis taking into account the anteriorly open mesorostral groove. Considering the preserved parts, the premaxillae seem considerably thicker on the rostrum of ML 1359 than in the holotype, and even more than in ML

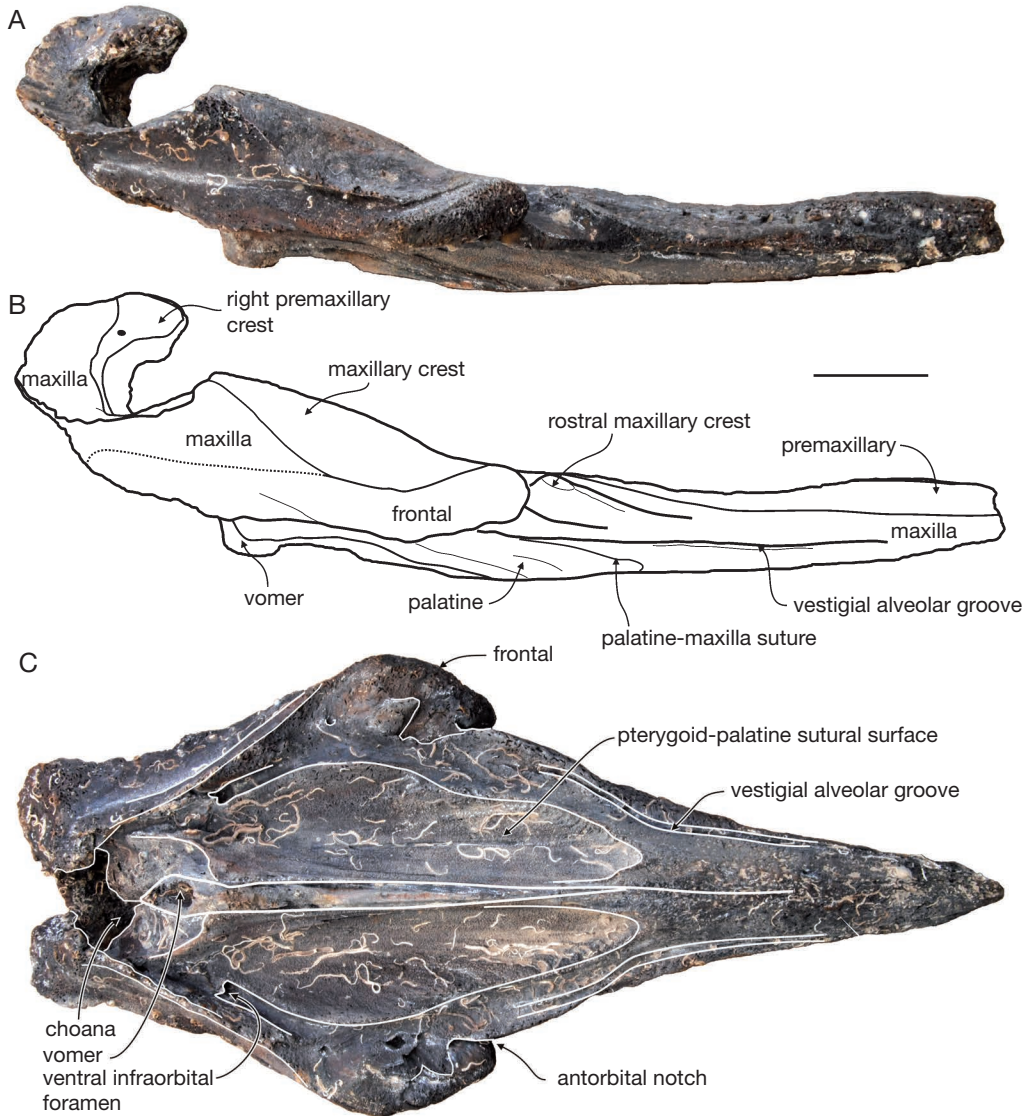


FIG. 15. — Skull of *Imocetus piscatus* n. gen., n. sp. (ML 1358, holotype): **A**, lateral view; **B**, corresponding line drawing; **C**, ventral view. Scale bar: 10 cm.

1360. From the level of the antorbital notch, the premaxillae descend in a depression between the more prominent maxillae, until the premaxillary sac fossae. This depression seems homologous to the prenarial basin described in *Beneziphius*, *Messapicetus*, and *Ziphirostrum* (Lambert 2005; Bianucci *et al.* 2010). The premaxillary sac fos-

sae, only well preserved on the holotype, are even more depressed compared to the maxillae, with a distinctly concave surface. The posteromedial portion of the right fossa is slightly elevated. The left fossa is lower than the right, and narrower. However, the asymmetry at this level is less pronounced than in *Caviziphius*, *Globicetus*

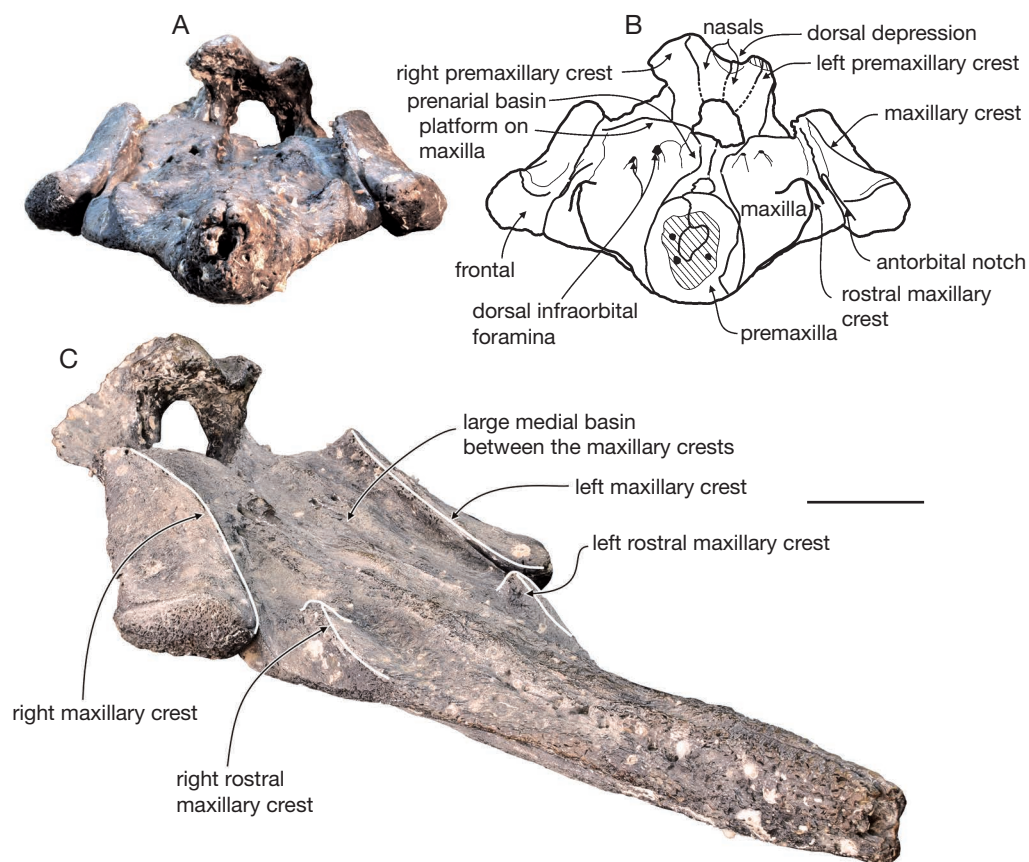


FIG. 16. — Skull of *Imocetus piscatus* n. gen., n. sp. (ML 1358, holotype): **A**, anterior view; **B**, corresponding line drawing; **C**, antero-lateral view. Parallel lines indicate a break surface. Scale bar: 10 cm.

n. gen., and *Tusciziphius*. If present (area partly covered with phosphorite concretions), right and left premaxillary foramina are close to each other and much more distant from the level of the antorbital notch than in any other known ziphiid, even more than in *Hyperoodon*. This condition stresses the unusual elongation of the facial area between antorbital notches and bony nares in *Imocetus* n. gen. An additional foramen is present on the medial margin of the left premaxillary sac fossa of the holotype and ML 1360, in the same position as in *Globicetus* n. gen., *Choneziphius leidy* n. sp., and *Tusciziphius atlanticus* n. sp.

The ascending process of the premaxilla is short and erected. Its upper part overhangs the corresponding premaxillary sac fossa. On the vertex,

the premaxillary crests are highly asymmetric: the right crest is more voluminous, distinctly higher and more anteriorly bulging. Similar to *Globicetus* n. gen., the right premaxillary crest is posterolaterally directed whereas the left crest is anterolaterally directed.

Maxilla

In dorsal view the maxilla is visible along the premaxilla on the whole length of the rostrum. On the second third of the rostrum, the lateral margin is acute. This margin only thickens considerably before the antorbital notch, in relation with the development of the rostral maxillary crest located medial to the notch. Compared to the holotype, this spur-like posterodorsally projecting

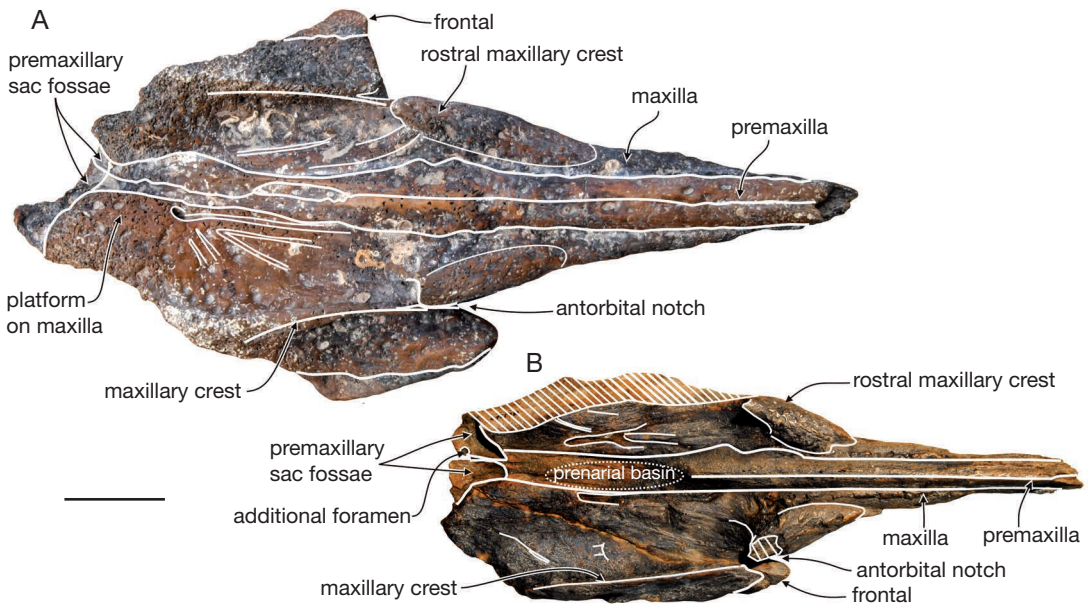


FIG. 17. — **A**, skull of *Imocetus piscatus* n. gen., n. sp. (ML 1359), dorsal view; **B**, skull of *I. piscatus* n. gen., n. sp. (ML 1360), dorsal view. Parallel lines indicate a break surface. Scale bar: 10 cm.

crest is more laterally directed, larger, and more posteriorly located compared to the antorbital notch in ML 1359 and ML 1360. The crests are asymmetric in the holotype and ML 1359; in the former the left crest is slightly higher, whereas in the latter the incomplete right crest was originally more robust than the left crest. The antorbital notch is deep and narrow in the three specimens, medial to the robust and long preorbital process. The notch is more slit-like in the holotype and V-shaped in the two other skulls. From the bottom of the notch, the maxilla forms an acute longitudinal crest on the supraorbital area of the skull. This crest is probably not homologous to the huge rostral crest observed medial to the antorbital notch in adults of *Hyperoodon* spp. (see Mead & Fordyce 2009 for terminology). This maxillary crest is rectilinear and posteriorly diverging in ML 1359 and ML 1360, whereas it is medially convex in dorsal view and slightly overhangs the medial area of the maxilla in the holotype. Right and left crests limit a vast and depressed facial area, where dorsal infraorbital

foramina are present along the prenarial basin (two on each side of the holotype, one on each side of ML 1359 and ML 1360). In addition to these large foramina, the surface of the maxilla is covered with shallow and narrow anastomosed sulci and tiny foramina. Between the dorsal infraorbital foramina and the premaxillary sac fossa, the maxilla is distinctly thickened, forming a platform with a convex surface, much wider on the right side (and also more elevated on the right side of the holotype and ML 1359). The lateral flank of the maxillary crest is a wide and slightly concave surface with a steep slope. Due to the non-preserved lateral part of the supraorbital process, in lateral view the crest of the holotype displays a high triangular section.

No alveoli could be detected on the heavily post-mortem worn alveolar groove. In relation with the anterior shift of the preorbital process and antorbital notch compared to other ziphiids, the position of the ventral infraorbital foramen is strongly modified. This foramen is about 200 mm posterior to the antorbital notch in the three specimens, whereas

it is a short distance from the notch in other ziphiids. The foramen is followed anteriorly by a deep and long groove, edging the pterygoid sinus fossa laterally until the antorbital notch. The location of the ventral infraorbital foramen also gives a clue about the level of the non-preserved orbit. Indeed, in other ziphiids and other odontocetes the frontal groove and optic canal are posterior to the infraorbital foramen.

Nasal

The nasals are wide anteriorly. Each of them occupies a considerable portion of the corresponding premaxillary crest and the nasal-premaxilla suture reaches the anterior surface of the crest, a condition more similar to *Hyperoodon*. The part of the nasal thrust in the premaxillary crest is more compact than the smoothly depressed medial area. The difference of compactness only partly explains this internasal fossa, extending posteriorly on the left frontal and maxilla. The premaxilla-nasal suture being hard to distinguish in this very ossified vertex, an alternative interpretation would be a more medial suture more similar to the condition in *Globicetus* n. gen. and *Tusciziphius* (hatched line in Fig. 14B).

Frontal

Only fragments of the frontals are preserved posterior to the nasals on the vertex. The frontal sends a short anterior projection between the nasals. In lateral view, the frontal is the main element of the robust anterior part of the preorbital process, covered by a thin sheet of maxilla. More posteriorly the bone is incomplete laterally; the whole orbit area is lost and the extent of the temporal fossa cannot be assessed.

Vomer

Our interpretation of the rostral bones suggests that the vomer does not fill the mesorostral groove of *Imocetus* n. gen., dorsally covered by the joined premaxillae.

Palatine

The palatine is preserved on its rostral portion in the three specimens. The palatine-maxilla suture is visible at some levels, but the best seen structure is the surface of suture with the lost pterygoid, marked by grooves, and limiting a large depression corre-

sponding to the vast anterior part of the pterygoid sinus fossa. The palatine-ptyergoid suture extends far anterior to the antorbital notch in the three specimens, even more in the holotype, which is characterized by a more posteriorly located notch.

Lacrima

Fragments of the lacrimal are preserved on the holotype, but its original outline cannot be precisely drawn.

REMARKS

The significant morphological variations between the holotype and the more fragmentary referred specimens is interpreted here as due to intraspecific variation (possibly related to sexual dimorphism, see below); pending the discovery of new more complete specimens, we choose to maintain ML 1359 and ML 1360 in the same species as the holotype.

Despite similarities of *Imocetus* n. gen. with some hyperoodontines (nasal probably included in the premaxillary crest and reaching the anteromedial margin of the crest; excavation of the dorsomedial surface of the nasal; right premaxillary crest posterolaterally directed) and more specifically with *Hyperoodon* (low vertex overhanging the premaxillary sac fossae; premaxillary foramen posterior to the level of the antorbital notch), this new genus is interpreted here as a member of the subfamily Ziphiinae. Indeed, it shares with all ziphiines, except *Izikoziiphius* and *Ziphius*, the medial fusion of the thickened premaxillae dorsally closing the mesorostral groove, with *Globicetus* n. gen. and *Tusciziphius* the extreme ossification and fusion of the vertex elements, and with *Choneziphius*, *Globicetus* n. gen., and *T. atlanticus* n. sp. the deep premaxillary sac fossae.

Family ZIPHIIDAE
Incertae sedis

Genus *Caviziphius* Bianucci & Post, 2005

TYPE AND ONLY SPECIES. — *Caviziphius altirostris* Bianucci & Post, 2005, known from a single specimen from Steendorp (Belgium), probably late Miocene (Bianucci & Post 2005).

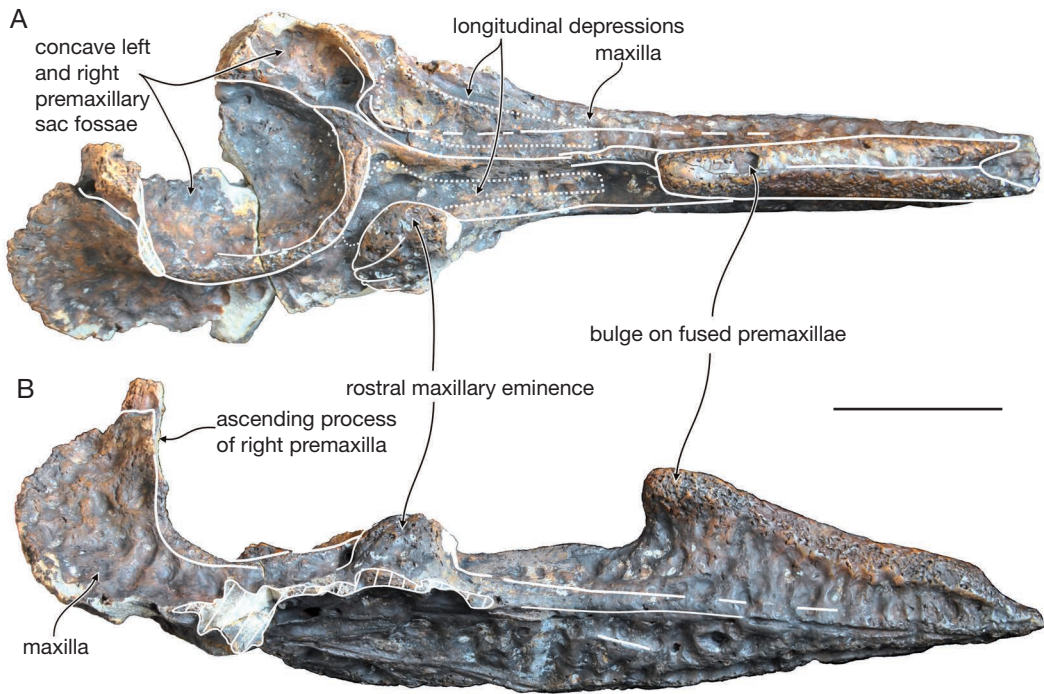


FIG. 18. — Skull of aff. *Caviziphius* sp. (SGHN MA0920): **A**, dorsal view; **B**, lateral view. Parallel lines indicate a break surface. Scale bar: 10 cm.

aff. *Caviziphius* sp.
(Fig. 18)

REFERRED SPECIMEN. — SGHN MA0920, partial skull including rostrum and right part of facial area, Cortada fishing ground, off the Galician coast, depth of approximately 400–800 m, 43°36'N, 9°0'W.

DESCRIPTION

The original shape of this badly preserved fragmentary skull might have been partially modified by an intense wear. The sutures between the bones are also almost completely obliterated. Nevertheless some typical features of the premaxilla and maxilla (medial rostral premaxillary bulge, strongly asymmetric premaxillary sac fossae, and prominent right rostral maxillary eminence) are conspicuous and allow a relevant comparison with other ziphiids.

Premaxilla

In dorsal view, the premaxillae are medially sutured for all their rostral length except for the

apical 55 mm portion, where the premaxillae abruptly diverge and leave the mesorostral groove dorsally open. From the anteriormost point of their junction, the height of the premaxillae increases progressively, reaching an elevation of 78 mm above the maxilla at 186 mm from the anterior margin of the right premaxillary sac fossa, forming a protuberant bulge. Posteriorly, the height of the premaxillae decreases abruptly, generating a clear step on the dorsal outline of the rostrum seen in lateral view. On the whole, this premaxillary bulge is similar to the bulge observed in some skulls of *Tusciziphius atlanticus* n. sp. (holotype, SGHN MA0632, and SGHN MA0644) even if its posterior margin is distinctly more anterior. In fact, the distance from the posterior margin of the bulge and the anterior margin of the premaxillary sac fossa is 186 mm in SGHN MA0920, whereas it varies from 81 to 128 mm in *T. atlanticus* n. sp. A similar anterior premaxillary bulge is present in a partial skull

from the Neogene of Antwerp, Belgium (NMB 002), referred by Lambert (2005: fig. 27A-C) to Ziphiidae aff. *Eboroziphius*.

Between the bulge and the premaxillary sac fossae, the premaxillae form a shallow medial elevation laterally delimited by two longitudinal depressions. A similar architecture is present in *T. atlanticus* n. sp. (even if this area is anteroposteriorly shorter), NMB 002, *Eboroziphius coelops* Leidy, 1876, and *Caviziphius altirostris*. The incompletely preserved premaxillary sac fossae are strongly asymmetric (ratio between maximum width of left and right fossae approximately 0.5) and deeply excavated, even more than in *T. crispus*. The fossae are separated by a narrow septum corresponding to the medial overlap of the premaxillae. For these characters, the premaxillary sac fossae are similar to those of NMB 002, *Caviziphius*, *E. coelops*, and *Pelycorhamphus pertortus* Cope, 1895 (see Lambert 2005: fig. 28). It is important to outline that the holotypes and only referred specimens of *E. coelops* and *P. pertortus* are fragmentary and considerably worn; consequently we restrict the genera to their type-species and the type-species to their holotypes, and consider them as *incertae sedis*.

Only the incomplete ascending portion of the right premaxilla is preserved. It abruptly rises from the level of the premaxillary sac fossa; consequently, in lateral view, the outline of the anterior margin of the vertex displays a deep concavity, followed ventrally by a semicircular deep excavation corresponding to the premaxillary sac fossa. A similar lateral profile is observed in *Caviziphius*.

Although no premaxillary crest is preserved, the thin broken surface at the posterior end of the right ascending process suggests that the right crest was not massive and wide as seen in *Globicetus* n. gen. and *Tusciziphius*. Nevertheless, the right premaxillary crest of *Caviziphius*, even if not completely preserved, seems to have been more robust than in SGHN MA0920, judging from the wider break surface on the ascending process of the right premaxilla of the holotype and only referred specimen.

Maxilla

Due to the incompleteness and the strong erosion, the maxilla does not show any significant features, with the exception of a prominent right rostral maxillary eminence. Roughly located at the rostrum base, this semicircular crest is tilted medially. A similar crest is present in several skulls of *T. atlanticus* n. sp. and in NMB 002.

REMARKS

SGHN MA0920 shares with some skulls of *Tusciziphius atlanticus* n. sp. and the fragmentary skull NMB 002 the medial bulge on the fused premaxillae, the strongly asymmetric premaxillary sac fossae, and the prominent right rostral maxillary eminence. Considering the deep excavation of both premaxillary sac fossae, the anterior location of the premaxillary bulge, and the diverging premaxillae near the anterior end of the bulge, SGHN MA0920 is more similar to NMB 002 than to *T. atlanticus* n. sp. SGHN MA0920 also shares with *Caviziphius* the deeply excavated asymmetric premaxillary sac fossae, the longitudinal depressions that laterally margin the shallow medial elevation of the sutured premaxillae at the rostrum base, and the abrupt elevation of the ascending process of the right premaxilla. Unfortunately the anterior part of the rostrum and the antorbital area of the maxillae are not preserved in the holotype and only referred specimen of *Caviziphius altirostris* (see Bianucci & Post 2005); consequently it is not possible to establish if the premaxillary bulge and the prominent right rostral maxillary eminence are also present in the latter. Nevertheless, considering that the holotype of *C. altirostris* and NMB 002 are nearly identical for the parts preserved in both specimens and show similar dimensions, it is likely that both these incomplete skulls belong to the same species. Furthermore they were collected in the same area (Antwerp). If this hypothesis is confirmed with future discoveries, *C. altirostris* will be redefined with the combination of the characters of the holotype and NMB 002. The only significant differences between SGHN MA0920 and these two skulls from Antwerp are the smaller size and probably the thinner right premaxillary crest.

“*Messapicetus* clade”

Genus *Ziphirostrum* du Bus, 1868

TYPE SPECIES. — *Ziphirostrum marginatum* du Bus, 1868, from Antwerp (Belgium), late Miocene (Lambert 2005).

OTHER SPECIES INCLUDED. — *Ziphirostrum recurvus* (du Bus, 1968) and *Z. turniense* du Bus, 1868.

aff. *Ziphirostrum* sp.
(Fig. 19; Table 3)

REFERRED SPECIMEN. — SGHN MA0936, partial skull including rostrum and left part of facial area, A Selva fishing ground, depth of approximately 500 m, off the Galician coast, 44°10'N, 08°40'W.

DESCRIPTION

The rostrum of this medium-size ziphiid is narrow and elongated, with size and proportions close to *Ziphirostrum turniense* (see Lambert 2005).

Premaxilla

The premaxillae are distinctly swollen on the rostrum, contacting each other dorsomedially above the hollow mesorostral groove for most of the rostral length. The nearly fused medial suture is asymmetric, shifted to the right side on the posterior half of the rostrum. A similar asymmetry has been noted, but on the other side, on an isolated ziphiid rostrum from the Miocene of Maryland, USA (Lambert *et al.* 2010). In lateral view, the maximum height and width of the premaxilla is more anterior than in *Z. marginatum*, more similar to *Z. turniense*. From mid-length of the rostrum, the premaxilla narrows considerably, and a medial separation appears 110 mm anterior to the level of the antorbital notch, with a progressive descent of the premaxilla in the prenarial basin, a feature absent in *Choneziphius*. The extent and depth of the basin is again more similar to *Z. turniense*, shallower than in *Z. marginatum*. Less anteriorly located than in the latter, the premaxillary foramen is on the floor of the basin, slightly anterior to the prominent notch. The partly preserved surface of the left premaxillary sac fossa is transversely convex, as in *Ziphirostrum*, differing from the concave surface in *Choneziphius* and related taxa. The ascent towards the vertex is not abrupt.

Maxilla

Even if the anterior part of the maxilla-premaxilla suture is difficult to detect, the anterior end of the maxilla is located 50–60 mm from the apex of the rostrum. Barely visible in dorsal view for the anterior half of the rostrum, the maxilla considerably widens towards the prominent notch, forming an elongated triangular surface. The posterior part of this surface, along the prenarial basin, displays a steep slope, with an elevated and thin lateral margin, more similar to *Z. turniense*. Considerably wider on the right side than on the left, the triangular surface is covered with numerous and high excrescences, a character found in *Choneziphius*, but also in *Beneziphius* and an isolated ziphiid rostrum from the Neogene of the North Sea (see Lambert 2005: fig. 26). The prominent notch and maxillary tubercle are conspicuous; this area is not well preserved in any specimen of *Z. turniense*. No marked maxillary crest extends posteriorly from the maxillary tubercle, differing from *Choneziphius*.

The alveolar groove is vestigial, with shallow remains of alveoli still visible, a condition observed in several specimens of *Z. marginatum* and *Z. turniense*.

Palatine

The palatine is preserved at the rostrum base, with a maxilla-palatine suture easy to distinguish. The rounded anterior end of the palatine is 130 mm anterior to the antorbital notch. An abrupt step in the surface of the palatine indicates the suture with the lost pterygoid.

REMARKS

Except for the development of excrescences on the dorsal surface of the maxilla on the posterior half of the rostrum and the distinct asymmetry of the premaxillae on the rostrum, this specimen is similar to the two specimens from the Neogene of the North Sea referred to *Ziphirostrum turniense*. The low diagnostic value of the excrescences on the maxilla has previously been demonstrated (Lambert 2005) and the development of the premaxillae on the rostrum is known to vary within one species. The main features differentiating *Z. turniense* from the better-known *Z. marginatum* are observed here: maximum width and height of the premaxillae at

TABLE 5. — Measurements (in mm) on the skull of aff. *Ziphirostrum* sp. SGHN MA0936 from the Atlantic Ocean floor off the Iberian Peninsula. Abbreviation: e, estimate.

	SGHN MA0936
Rostrum length	557
Distance from apex of rostrum to bony nares	e635
Width of rostrum at mid-length	71
Width of premaxillae at mid-length of rostrum	49
Height of rostrum at mid-length	90
Width of rostrum base at prominent notch	e120
Width of rostrum base at antorbital notch	e208
Distance rostrum base – anterior apex of palatine	130
Preorbital width of skull	e314
Longitudinal distance left premaxillary foramen-rostrum base	40
Width of left premaxillary sac fossa	49

mid-length of the rostrum, shallower prenarial basin, with dorsal exposure of the maxillae wider and more steeply sloping along the basin. The third species of the genus, *Z. recurvus*, is characterized by a more elevated rostrum with a complete filling of the mesorostral groove by the vomer, a feature lacking here. Because this specimen originates from a remote area, and because the vertex is lacking, as in specimens of *Z. turniense* and *Z. recurvus*, we prefer to maintain the attribution Ziphiidae aff. *Ziphirostrum* sp., pending the discovery of more complete specimens.

PHYLOGENY

To explore the phylogenetic relationships of the new ziphiids described here (*Choneziphius leidy* n. sp., *Imocetus piscatus* n. gen., n. sp., *Globicetus hiberus* n. gen., n. sp., and *Tusciziphius atlanticus* n. sp.), we included the new taxa in the matrix of 29 morphological characters published by Bianucci *et al.* (2010) and undertook a similar cladistic analysis, using the same outgroups (the squalodontid *Squalodon* and the eurhinodelphinid *Eurhinodelphis*). The only change in the matrix is the addition of a new state (3) for the unordered character 10 (premaxillary crest direction): left crest anterolaterally directed and right crest posterolaterally directed, a condition observed in *Globicetus* n. gen. and *Imocetus* n. gen. The coding of characters for the Iberian new taxa is given in the Appendix 1.

The cladistic analysis was achieved with the software PAUP (version 4.0b10; Swofford 2001), using the Branch-and-bound algorithm with the homoplastic characters down-weighted using the default value of 3 for the constant k of the Goloboff method (1993). The analysis produced 875 equally parsimonious trees, with tree length 94, Goloboff fit-20.98, Consistency Index (CI) 0.53 and Retention Index (RI) 0.72. The consensus tree (Fig. 20) displays the same general topology as in Bianucci *et al.* (2010). All the Iberian ziphiids are placed inside the Ziphiinae. *Choneziphius leidy* n. sp. appears as sister taxon of *C. planirostris*, the species coded in the previous analysis for the genus *Choneziphius*. The unresolved relationships between *T. atlanticus* n. sp. and *T. crispus* are probably due to the incompleteness of the holotype and only referred specimen of *T. crispus*. Nevertheless, both species are more basal than the *Choneziphius* + *Izikoziphius* + *Ziphius* clade, similar to the position of *T. crispus* in Bianucci *et al.* (2010). *Globicetus* n. gen. and *Imocetus* n. gen. have a more basal position inside the Ziphiinae, redefined here (see the emended diagnosis above) with the inclusion of these two new genera.

INTRASPECIFIC VARIATION

Significant morphological variation, considered as possibly related to sexual dimorphism and/or ontogeny, is observed in the samples of skulls referred to *Tusciziphius atlanticus* n. sp. and *Imocetus piscatus* n. gen., n. sp.

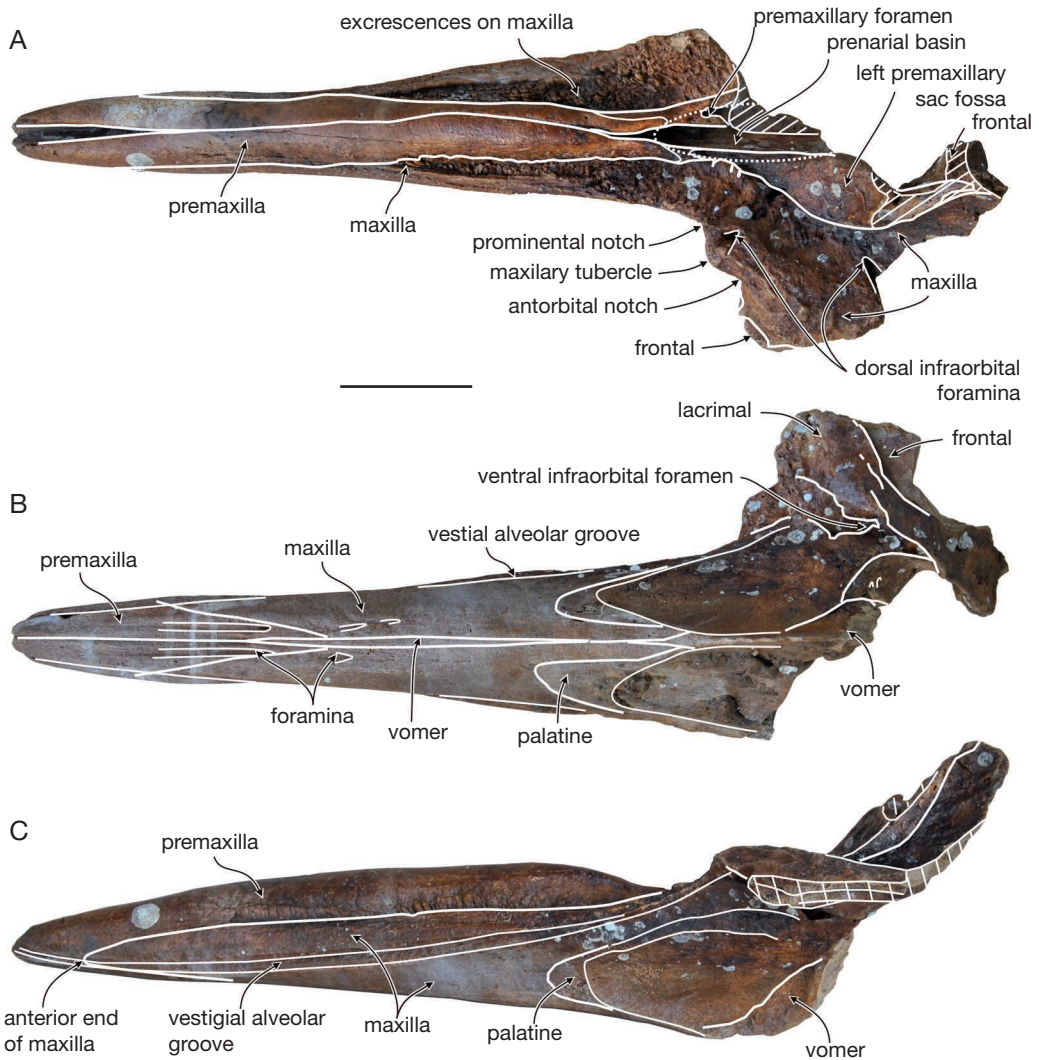


FIG. 19. — Skull of aff. *Ziphirostrum* sp. (SGHN MA0936): **A**, dorsal view; **B**, ventral view; **C**, lateral view. Parallel lines indicate a break surface. Scale bar: 10 cm.

The intraspecific variation observed at the level of the medial premaxillary bulge within the species *T. atlanticus* n. sp. is very conspicuous, the most significant found until now in a fossil ziphiid considering the range of sizes for the concerned element. Interestingly, the development and extension of the medial premaxillary bulge shows a correlation with the development of rostral maxillary eminences. Indeed, the speci-

mens that display a high medial premaxillary bulge (holotype, SGHN MA0644, and SGHN MA0632) also bear rostral maxillary eminences, more developed on the right side. Such a variation could be related to sexual dimorphism. In several extant ziphiids, a high intraspecific variation related to sex and age has been reported: filling of the mesorostral groove by the vomer more pronounced in adult males of *Mesoplodon*

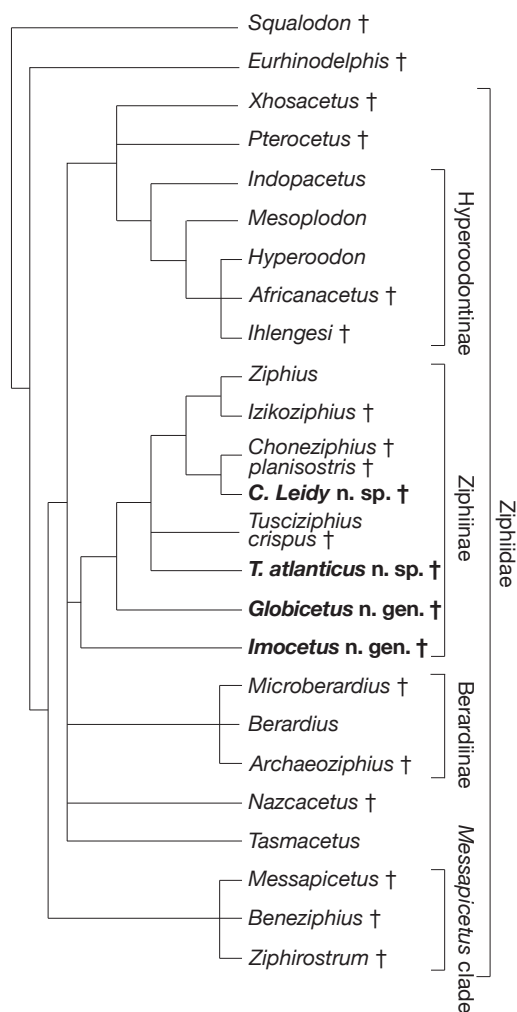


FIG. 20. — Consensus tree of 875 equally parsimonious cladograms showing the relationships of the Iberian fossil ziphiids (in bold) with other fossil and extant ziphiid genera. Tree length 94, Goloboff fit – 20.98, CI 0.53 and RI 0.72. See Bianucci *et al.* (2011) for the description of characters and matrix, and Appendix 1 for the coding of characters of taxa not included in that previous analysis. †, strictly fossil taxa.

spp. and *Ziphius cavirostris* Cuvier, 1823, further development of the prenarial basin in adult males of *Z. cavirostris*, much higher rostral maxillary crests in adult males of *Hyperoodon ampullatus* (Forster, 1770), and larger mandibular tusks in adult males of many extant ziphiids, and possibly fossil ziphiids (e.g., Heyning 1984, 1989a, b; Mead 1989a, b; MacLeod & Her-

man 2004; Lambert *et al.* 2010). Based on the development of the medial premaxillary bulge and the rostral maxillary eminences in *T. atlanticus* n. sp., we propose that the holotype, SGHN MA0644, SGHN MA0632, and SGHN MA0926 are males, whereas the paratype and SGHN MA0914 are interpreted as females or immature males, by analogy with extant ziphiids, especially *H. ampullatus*. In adult males of the latter, further development of the rostral maxillary crests starts at the onset of sexual maturity, leading to a larger size, massive proportions, and a flattened anterodorsal surface (Hardy 2005). Similarly the different degrees of development of the medial premaxillary bulge and of the rostral maxillary eminences observed in *T. atlanticus* n. sp. might be explained by sexual dimorphism and maturity.

In *I. piscatus* n. gen., n. sp., the significant morphological variation observed between the holotype and the more fragmentarily known referred specimens is also related to bony structures influenced by high sexual dimorphism in several modern ziphiids. Indeed, the most striking difference, namely the length of the preorbital process and the related position of the antorbital notch, might be linked to the development of the maxillary crest on the supraorbital process. This crest forms a lateral boundary to a wide facial depression seemingly analogous (but not homologous) to the wide prenarial basin of adult male *Z. cavirostris* (see Heyning 1989a; Cranford *et al.* 2008). Nevertheless, a larger sample for *I. piscatus* n. gen., n. sp. would be necessary to give a firmer interpretation for this observed variation.

FUNCTIONAL ANATOMY

From a functional point of view, bony crests, depressions, and prominences in the facial area of modern odontocetes are often demonstrated to be related to soft anatomy elements of the forehead (facial and rostral muscles, blowhole, melon, nasal passages, nasal sacs, and other structures associated with echolocation; see e.g.,

Cranford *et al.* 2008; Huguenberger *et al.* 2009). For example, the deep prenarial basin of adult males of *Ziphius cavirostris* contains a fat body usually identified as the melon (Heyning 1989a), but it has been recently differentiated from the melon as the anterior spermaceti organ (Cranford *et al.* 2008). Low maxillary crests in the supraorbital region of odontocetes correspond to areas of origin for facial muscles (Mead 1975; Heyning 1989a; Mead & Fordyce 2009), acting on the nasal passages, blowhole, and melon. In addition, the lateral and medial surfaces of the huge rostral maxillary crests of *Hyperoodon* spp. are areas of origin for several facial and rostral muscles (Schenkkan 1973), even if this is much likely not the unique function of the crests (see Mead 1989a; Gowans & Rendell 1999; Hardy 2005). The premaxillary eminences anterolateral to the bony nares of *Phocoena* bring the overlying premaxillary sac fossae, potential sound reflectors, closer to the acoustic pathway (Huguenberger *et al.* 2009).

ROSTRAL PREMAXILLARY THICKENING

Several functions have been proposed for the varied conditions of pachyosteosclerotic rostral bones in extinct and extant ziphiids (Heyning 1984; Buffrénil & Casinos 1995; Zioupos *et al.* 1997; MacLeod 2002). Until now, no single functional interpretation explains the whole diversity of morphologies observed (Buffrénil & Lambert 2011; Lambert *et al.* 2011). The spherical prominence of *Globicetus* n. gen. and the medial bulge of *Tusciziphius atlanticus* n. sp. are certainly some of the most bizarre rostral elements described to date for odontocetes, and the question of their potential function as well as the question of their influence on, or link with, the echolocation system are both difficult to answer.

In lateral view, the anterior margin of the spheroid in *Globicetus* n. gen. and of the bulge in *T. atlanticus* n. sp. occupies a position roughly similar to the anterior surface of the elevated rostral maxillary crests of extant *Hyperoodon*. In addition to being areas of origin for facial muscles (Heyning 1989a), the crests of *H. ampullatus* are thought to be used as weapons during head-butting

encounters between adult males; additionally, they might also provide a protection for the soft tissues located posterior and between them, mostly the melon, during impacts (Gowans & Rendell 1999; Hardy 2005).

A similar function could be proposed in *Globicetus* n. gen. and *T. atlanticus* n. sp. For the latter, it would be corroborated by the sexual dimorphism interpretation given above. However, contrasting with the spongy aspect of the bone in *Hyperoodon* (Hardy 2005; Lambert *et al.* 2011), the superficial layers of the spheroid of *Globicetus* n. gen. are made of very compact bone. Similarly, high compactness has been detected through preliminary macroscopic observations of transverse sections of the bulge in *T. atlanticus* n. sp., suggesting very different mechanical properties for this element (see discussion for *Mesoplodon densirostris* Blainville, 1817 in Buffrénil *et al.* 2000). Another type of function might be related to the deep-diving habit of extant ziphiids. Indeed, this voluminous element, made of compact bone, distinctly increases the weight of the skull, particularly in *Globicetus* n. gen. Such a feature has been proposed to help maintaining a vertical position in the water during descents towards feeding areas in other ziphiids (Buffrénil & Casinos 1995; Zioupos *et al.* 1997), but ecological data on extant ziphiids do not explain for now the observed sexual dimorphism. A combination of functions might likely better reflect the diversity of rostrum forms observed (Buffrénil *et al.* 2000; Lambert *et al.* 2011). It is clear that additional analyses will be necessary to continue the discussion of the potential function(s) of the spheroid and of the bulge. The examination of the inner bone organization, through Computed Tomography scanning (CT scan) or ground sections of more fragmentary specimens, will bring additional data about the compactness, mechanical properties, and growth process of these unusual bony structures.

In addition to the question of its function, the spheroid of *Globicetus* n. gen., and in a lesser extent the narrower medial bulge of *T. atlanticus* n. sp., must obviously be considered in the framework of echolocation. Indeed, in odontocetes the echo-

location sounds are thought to be produced in the area of the forehead roughly vertical to the bony nares, and transmitted forwards via a low-density pathway including the melon (Cranford *et al.* 1996, 2008). If the lateral view of the skull of *Globicetus* is compared to a CT scan of the head of the extant *Ziphius* (see Cranford *et al.* 2008: fig. 6), the spheroid of *Globicetus* n. gen. is only slightly more anterior than the position of the melon in *Ziphius*, and it is nearly as high. Therefore, there is only little space for the melon in *Globicetus* n. gen., and this soft tissue was certainly located more posterodorsally than in other ziphiids. In *Hyperoodon*, the melon has been described as elongated, situated between the rostral maxillary crests (Schenkkan 1973), a condition impossible in *Globicetus* n. gen. In the latter, the only way for the transmission of sounds is dorsal to the spheroid, which must be considered as an unsurpassable obstacle, an acoustic reflector, considering its high compactness (acoustic impedance mismatch with surrounding soft tissues, including the phonic lips area, where the sounds are produced, and the melon, through which the sounds are transmitted). This implies that the sounds were produced at a level high enough above the level of the dorsal surface of the spheroid.

ROSTRAL MAXILLARY CREST

For the rostral maxillary eminences and crests of *Tusciziphius atlanticus* n. sp. and *Imocetus* n. gen., n. sp., a similar functional explanation might be proposed: protection of forehead soft tissues facing more lateral impacts. However, the supraorbital region and rostrum base of odontocetes is mainly an area of origin for facial and rostral muscles, acting on the air sac system, the blowhole, the nasal plugs, and the melon (Heyning 1989a). The development of high crests might provide surfaces for the attachment of muscles, with a different direction of action. Considering the posterodorsal direction of the pointed spur-like rostral maxillary crest in *Imocetus* n. gen., muscles originating there reached a relatively posterior region of the forehead, possibly the posterior part of the melon. In various odontocetes, rostral muscles have been proposed to

modulate the shape of the melon, influencing therefore the shape of the sound beam (Mead 1975; Au 1993; Huggenberger *et al.* 2009). In *T. atlanticus* n. sp., the asymmetry of the crests (right crest considerably larger than left crest) would mirror the asymmetry of the forehead soft tissues observed in extant ziphiids, as well as in other odontocetes (Heyning 1989a; Cranford *et al.* 1996). A similar argument was proposed to explain the asymmetry in the development of excrescencies on both sides of the rostrum base in *Choneziphius planirostris*, presumably for the attachment of rostral muscles (Lambert 2005).

FACIAL BASIN AND MAXILLARY CREST

By comparison with the odontocetes displaying the most developed facial basin (supracranial basin in the sperm whale *Physeter* and prenatal basin in adult males of *Ziphius*), the large facial depression of *Imocetus* n. gen. probably contained the main portion of the fat bodies of the forehead (anterior spermaceti organ and/or melon). The unusual length of the facial area, linked to the derived anterior shift of the preorbital process, might be an indication of an enlarged fat body. In modern odontocetes, melon and spermaceti organ are both considered as low density preferential acoustic pathways, for the transmission and shaping of echolocation sound beams (reviewed in Cranford *et al.* 1996; Cranford 1999). The lateral flank of the long and high maxillary crest on the supraorbital process of *Imocetus* was probably an important area of origin for facial muscles. In the modern *Mesoplodon carlhubbsi* Moore, 1963, Heyning (1989a: figs 6-8) describes two longitudinal ridges on the supraorbital process: the lateral ridge, ending anteriorly as the antorbital tubercle, and the maxillary ridge, ending anteriorly as the maxillary prominence (or maxillary tubercle). Possibly corresponding to the supraorbital crest of other odontocetes, the lateral ridge is the site of origin for the *pars anteroexternus* of the *m. maxillonasolabialis*, whereas the maxillary ridge (= maxillary crest) is the site of lateral origin of the much larger *pars anterointernus* (Heyning 1989a; synonyms in Mead & Fordyce 2009). It is more likely that

the maxillary crest of n. gen., much higher than the ridges described in *M. carlhubbsi*, was the site of origin for the *pars anterointernus*. In modern ziphiids, fibers of this muscle insert on the nasal passages (Heyning 1989a).

PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY

The 18 diagnostic partial skulls recovered from the Atlantic Ocean floor off the coasts of Spain and Portugal are referred to the six genera (two of them are new) and four species (all of them are new) listed below.

- *Choneziphius leidy* n. sp. (three specimens from Galicia, 2 from Portugal);
- *Tusciziphius atlanticus* n. sp. (four from Galicia, one from Portugal);
- *Globicetus hiberus* n. gen., n. sp. (two from Galicia, one from Portugal);
- *Imocetus piscatus* n. gen., n. sp. (three from Portugal);
- aff. *Caviziphius* sp. (one from Galicia);
- aff. *Ziphirostrum* sp. (one from Galicia).

Several other ziphiid skulls, including two specimens trawled off the Galician coast and identified by us as belonging to *I. piscatus* n. gen., n. sp., are not described here in detail because they are kept in private collections.

In addition to the fossil ziphiids, the following fragmentary remains were also collected: five isolated teeth of stem physeteroids; three periotics, eight tympanic bullae, and a skull fragment all belonging to mysticetes (Balaenidae, Balaenopteridae and Cetotheriidae); and several vertebrae and teeth of sharks (some belonging to *Cosmopolitodus hastalis* and *Carcharocles megalodon*).

On the whole, the fossil ziphiid associations of Galicia and Portugal show the same composition, with the exception of two fragmentary skulls collected off the Galician coast and referred to aff. *Caviziphius* sp. and aff. *Ziphirostrum* sp. A similar condition is present today as the ziphiid communities, and more generally the cetacean assemblages, off Galicia and Portugal are substantially similar (Covelo & Martínez 2001). Even if

we cannot demonstrate that all these taxa lived at the same time, this past ziphiid diversity is roughly similar to the present diversity; six extant species have been recorded by strandings and/or sightings off the Atlantic coast of the Iberian Peninsula: *Hyperoodon ampullatus*, *Mesoplodon bidens* (Sowerby, 1804), *M. densirostris*, *M. europaeus* (Gervais, 1855), *M. mirus* True, 1913, and *Ziphius cavirostris* (see Reiner 1979; Valverde & Galan 1996; Valverde 1997; López *et al.* 2002; Kiszka *et al.* 2007; Smith 2010). The geographic distribution of at least a part of these extant taxa being strongly related to topographic parameters (depth and slope) (Smith, 2010), we think that the concentration of large and heavy, not easily transported, fossil specimens at important depths in the proximity of local topographic features (e.g., Nazaré Canyon off Portugal or Ortegal Spur off Galicia) might reflect roughly similar ecological preferences.

Acknowledging the lack of precise stratigraphic data (see below), a comparison between the fossil ziphiid association of the Iberian Atlantic coast and those of other areas (see the systematic paragraph below) reveals that: 1) *Tusciziphius atlanticus* n. sp. is also recorded in South Carolina (USA), whereas another species of *Tusciziphius* (*T. crispus*) was found in Tuscany (Italy); 2) *Choneziphius* is also reported in South Carolina and in the North Sea (Belgium and The Netherlands), with a few large indeterminate specimens (roughly similar to *C. leidy* n. sp.) and smaller specimens (referred to *C. planirostris* in the North Sea); and 3) *Caviziphius* and *Ziphirostrum* are recorded in the area of Antwerp (Belgium). The fossil record of *Globicetus* n. gen. and *Imocetus* n. gen. is instead restricted for now to the Iberian Atlantic coast. Unfortunately the fossil ziphiid samples from eastern North America and Mediterranean are still too fragmentary for a comprehensive comparison between these associations. The fossil ziphiid record outside the North Atlantic Ocean and Mediterranean Sea is even more fragmentary, with two major exceptions: Peru and South Africa.

From the middle Miocene-Pliocene Pisco Formation of Peru, *Messapicetus gregarius* Bianucci, Lambert & Post, 2010, *Ninoziphius platyrostris*

Muizon, 1983, and *Nazcacetus urbinai* Lambert, Bianucci & Post, 2009 are recorded. None of these three genera is present in the Atlantic Iberian fossil association, but *Messapicetus* is reported in Italy with a different species (*M. longirostris* Bianucci, Landini & Varola, 1992; see Bianucci *et al.* 1992) and is tentatively reported from Maryland, east coast of USA (Fuller & Godfrey 2007), whereas *Ninoziphius* Muizon, 1983 is also recorded, based on a fragmentary specimen, from the east coast of USA (Muizon & DeVries 1985; Morgan 1994).

The fossil ziphiid association recovered by trawling from the sea floor off the South African coast, also characterized by a low stratigraphic resolution, is very diversified, being represented by at least 11 species and 9 genera (Bianucci *et al.* 2007, 2008). Surprisingly, none of the taxa recorded in South Africa is listed in the Atlantic Iberian fossil association or any other North Atlantic realm assemblages, possibly evidencing an ecological and/or physical barrier between North and South Atlantic, in addition to expected temporal gaps between different communities (and between species from a same region). An analysis of the extant ziphiid community reveals substantial differences, even if less pronounced, between the beaked whales off the Iberian Peninsula and South African coasts (Ross 1984; Mead 1989b; López *et al.* 2002; Dalebout *et al.* 2003; Kiszka *et al.* 2007; Smith 2010). At the genus level the widely ranging *Hyperoodon*, *Mesoplodon*, and *Ziphius* are recorded in both areas, whereas *Berardius* Duvernoy, 1851 and *Indopacetus* Moore, 1968 are not recorded in the North Atlantic. At the species level, among the eight ziphiid species living off the South African coasts, only the widely ranging *Mesoplodon densirostris*, *M. mirus* and *Ziphius cavirostris* are also recorded off the Atlantic coast of the Iberian Peninsula.

The different modern cetacean compositions of the northern and southern hemispheres are directly related to the presence of an equatorial warm water mass, representing an efficient barrier to dispersal, but also generating vicariant speciation (e.g., in the genera *Berardius* and *Hyperoodon*, both containing antitropical spe-

cies) during temporary cooling event(s) of the oceanic waters (Davies 1963; Hare *et al.* 2002). It is possible that most of the fossil ziphiids of Iberia and South Africa were restricted to cold and/or temperate waters and consequently were not able to cross the warm equatorial barrier, as today for species of *Berardius* and *Hyperoodon*.

GEOLOGICAL SETTING AND AGE OF THE SPECIMENS

On the Ortegal Spur, off the northwestern corner of the Iberian Peninsula, one of the areas where fossil ziphiids were found (Fig. 1), the Neogene sedimentary succession lies above about 1200 m of Late Jurassic-Eocene deposits and is represented by Oligo-Miocene silty marl and foraminiferal ooze, associated with slope breccias or conglomerates, indicating a relatively deep-water depositional environment (Wallrabe-Adams *et al.* 2005; Jané *et al.* 2010). It is probable that the fossil ziphiids originate from one or more phosphorite episodes within this succession (see below). The Miocene sediments are irregularly covered by Plio-Quaternary deposits consisting of alternated silt and clay laminae interbedded with coarse sediments (Jané *et al.* 2010).

The Nazaré Canyon, in the area where the fossil ziphiids from Portugal were found, represents one of the late Variscan faults that cut transversally the Mesozoic rifted Iberian margin (Pinheiro *et al.* 1996). At the end of Mesozoic the rifting ended; during Eocene and Miocene this area suffered a compressional episode that reactivated the old Variscan structures (Pinheiro *et al.* 1996). Published studies on the sediments outcropping on the sea bottom of the Nazaré Canyon report that a large portion is covered with Holocene mud (Koho *et al.* 2007; Masson *et al.* 2011). The age of rocks of the area where the fossil ziphiids were found include Miocene and Pliocene (Badagola 2008; LNEG-LGM 2001). According to the geological map of the continental platform, the only Miocene rocks that might have been the source of the skulls here described are in an area around 39°18'N and 9°47'W and about 160 m of depth, in the Mar da Ericeira, which has

been dated as Aquitanian to Langhian, early to middle Miocene (Badagola 2008).

Although we have not found data about the presence of phosphorite levels in the specific areas where the fossil ziphiids were collected, North Atlantic phosphorite deposits dated to Cenozoic are reported both off Spain and Portugal (Riggs & Sheldon 1990). These sediments are related to the Upper Early Miocene-Middle Miocene (20-14 Ma) episode of phosphogenesis associated with the TB2 second-order eustatic sea-level fluctuation (Haq *et al.* 1987; Riggs & Sheldon 1990). This interval of age is compatible with those of the fossil ziphiids examined, considering that the oldest unquestionable records of this family are from late early Miocene-middle Miocene (Bianucci *et al.* 2005; Lambert & Louwye 2006). Unfortunately precise ages are not available for most of the fossil ziphiids from other localities in the world that are related to those examined here. Indeed, most of these fossil ziphiids are from phosphorite deposits and/or their precise stratigraphical position is unknown. Moreover, since only one Iberian species (*Tusciziphius atlanticus* n. sp.) is also reported from a locality outside Iberia, faunal correlations remain difficult. As mentioned above, *T. atlanticus* n. sp. was found reworked on the bottom of Morgan River (South Carolina, USA), and a late Miocene-Pliocene age can only be proposed (Post *et al.* 2008). *Tusciziphius* is also recorded from Italy, with a more precise early Pliocene age (Bianucci 1997; Bianucci *et al.* 2001), but with a different species (*T. crispus*). A precise dating is not available for most of the Neogene ziphiids of the North Sea (Belgium and the Netherlands) (Bianucci & Post 2005; Lambert 2005; Lambert & Louwye 2006). This is unfortunately especially true for genera also reported (*Choneziphius*), or tentatively reported (*Caviziphius* and *Ziphirostrum*), from Iberian Peninsula. Nevertheless Lambert (2005) mentioned a skull of *Ziphirostrum marginatum* and a skull of *Choneziphius planirostris*, both collected from the Tortonian (late Miocene) Deurne Sands Member of the Diest Formation (Antwerp, Belgium). The genus *Choneziphius* is also reported from Phosphate Beds of South Car-

olina, USA, and from reworked sediments of the Lee Creek Mine, North Carolina (Whitmore & Kaltenbach 2008), with fragmentary skulls that, based on their large size, could be conspecific with *C. leidy* n. sp. Interestingly, even if the age of these Northern American ziphiids is not well defined (see Post *et al.* 2008), Riggs & Sheldon (1990: table 18.1) refer the South and North Carolina phosphorites to the same episode (TB2) than the Iberian phosphorites. In conclusion, the comparison with fossil ziphiids from other localities only provides minor clues for the definition of the age of the phosphoritized Iberian ziphiids. A late early Miocene-middle Miocene age, as suggested by TB2 phosphorites, is probable, even if the few well-dated extra-Iberian ziphiids (belonging to different species) are younger (late Miocene or early Pliocene). However, we cannot exclude a priori that all or part of these fossil ziphiids were collected from younger phosphorite episodes (e.g., the TB3, Late Miocene-Pliocene), for now not documented from the sea floor off the Atlantic coasts of Spain and Portugal. New data on the local geology and stratigraphy and the dating of associated phosphorites through radiometric methods are needed to better define the very approximative ages provided here for these specimens. Such additional data would be crucial to further support the palaeobiogeographic and palaeoecological hypotheses discussed above (see Pyenson *et al.* 2009 for an example of the importance of a detailed sedimentological and stratigraphical analysis for the understanding of fossil marine mammal localities).

CONCLUSION

The systematic study of 40 partial fossil ziphiid skulls dredged from the Atlantic Ocean floor off Portugal and Spain lead to the description of two new genera, *Globicetus* n. gen. and *Imocetus* n. gen., and four new species, *G. hiberus* n. gen., n. sp., *I. piscatus* n. gen., n. sp., *Choneziphius leidy* n. sp., and *Tusciziphius atlanticus* n. sp. In addition, members of the genera *Caviziphius* and *Ziphirostrum* are tentatively reported.

The phylogenetic analysis of the new taxa places them in the subfamily Ziphiinae here redefined, also including *Choneziphius planirostris*, *Tusciziphius crispus*, and the genera *Izikoziphius* and *Ziphius*.

Bizarre elements observed on the skull of *Globicetus* n. gen. (large premaxillary spheroid) and *T. atlanticus* n. sp. (medial premaxillary bulge, likely sexually dimorphic), are commented from a functional point of view; these structures are confronted to various hypotheses proposed for the function of pachyosteosclerotic parts of the rostrum in several ziphiid lineages.

Other peculiar features of the skull of *Imocetus* (spur-like rostral maxillary crests and long maxillary crests limiting a large facial basin) and *Choneziphius* spp. (excrescences on the maxilla at the rostrum base) are interpreted as areas of origin for rostral and facial muscles.

The palaeobiogeography of Neogene ziphiids is discussed in the light of the new discoveries. Differences in the composition of cold to temperate northern and southern hemisphere ziphiid communities might be explained by a warm equatorial barrier.

Finally, by comparison with other fossil ziphiid assemblages in the world and on the basis of a few geological and stratigraphic data for the Atlantic Ocean floor off Portugal and Spain, a late early to middle Miocene age is very tentatively proposed for the studied specimens. However, this hypothesis should be considered cautiously; a younger age cannot be excluded for part or all of these specimens.

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APPENDIX 1

Coding of the characters for taxa not considered in the previous analysis (Bianucci *et al.* 2010). **0**, primitive state; **1, 2, 3**, derived states; **a**, variable between 0 and 1; **?**, missing character.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
<i>Choneziphius planirostris</i>	2	0	3	0	1	1	2	a	1	1	1	0	1	?	0	1	0	2	?	?	?	?	?	?	?	?	1	?	?
<i>Choneziphius leidy</i>	1	0	3	0	1	1	3	0	1	1	1	0	1	?	0	1	0	2	?	?	?	?	?	?	?	?	1	?	?
<i>Tuscziphius crispus</i>	?	0	3	0	1	0	3	2	?	1	1	0	2	1	0	0	0	2	1	?	?	?	?	?	?	?	1	?	?
<i>Tuscziphius atlanticus</i>	1	0	3	0	1	0	3	2	?	1	1	0	2	1	0	0	0	2	1	?	?	?	?	?	?	?	1	?	?
<i>Globicetus</i>	1	0	3	0	1	0	3	2	?	3	1	1	2	1	0	0	0	2	?	?	?	?	?	?	?	?	1	?	?
<i>Imocetus</i>	2	0	3	1	0	0	3	2	?	3	1	0	1	1	?	0	0	2	?	?	?	?	?	?	?	?	1	?	?