Systematics and phylogeny of the fossil beaked whales *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Mammalia, Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium)

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ABSTRACT

A systematic revision of the fossil beaked whales (Cetacea, Odontoceti, Ziphiidae) *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 from the Neogene of Antwerp (Belgium, southern margin of the North Sea Basin) is undertaken. It is based on several rostra and partial skulls from the collection of the Institut royal des Sciences naturelles de Belgique. From the previous conclusions about those taxa, dating from the beginning of the 20th century and suggesting only one species in each genus, *Mioziphius* (*Ziphirostrum*) *belgicus* and *Choneziphius planirostris*, the following modifications are proposed. The genus *Ziphirostrum* includes three species: *Z. marginatum*, *Z. turniense*, and *Z. recurvus* n. comb. Basicranial fragments and teeth of *Z. marginatum* are described for the first time. Besides the most common species *Choneziphius planirostris*, the species *C. macrops* is identified from Antwerp and the east coast of North America. A new genus and species *Beneziphius brevirostris* n. gen., n. sp. is described on the basis of two specimens characterized by a short and pointed rostrum. Two partial skulls are placed in Ziphiidae aff. *Eboroziphius*, a genus known from the east coast of North America. The genus name *Aporotus* is restored, with a large species *A. recurvirostris*, and a smaller species *A. dicyrtus*. A parsimony analysis including fossil and extant ziphiid taxa shows a sister-group relationship between *Choneziphius* + (*Tusciziphius* + *Ziphius*) and *Ziphirostrum* + *Beneziphius* n. gen. The poorly known *Aporotus* seems more closely related to *Choneziphius* + (*Tusciziphius* + *Ziphius*), but additional morphological information is needed.

KEY WORDS
Mammalia,
Cetacea,
Odontoceti,
Ziphiidae,
Ziphirostrum,
Choneziphius,
Miocene,
Pliocene,
Belgium,
fossil,
phylogeny,
new genus,
new species.

RÉSUMÉ

Systématique et phylogénie des baleines à bec fossiles Ziphirostrum *du Bus, 1868 et* Choneziphius *Duvernoy, 1851 (Mammalia, Cetacea, Odontoceti) du Néogène d'Anvers (nord de la Belgique).*

La révision des baleines à bec fossiles (Cetacea, Odontoceti, Ziphiidae) *Ziphirostrum* du Bus, 1868 et *Choneziphius* Duvernoy, 1851 du Néogène d'Anvers (Belgique, bord sud du Bassin de la mer du Nord) est basée sur une série de rostres et de crânes partiels de la collection de l'Institut royal des Sciences naturelles de Belgique. À partir des conclusions systématiques précédentes, datant du début du XXe siècle et suggérant une seule espèce dans chaque genre, *Mioziphius* (*Ziphirostrum*) *belgicus* et *Choneziphius planirostris*, les modifications suivantes sont proposées. Le genre *Ziphirostrum* inclut trois espèces : *Z. marginatum, Z. turniense* et *Z. recurvus* n. comb. Des fragments du basicrâne et des dents de *Z. marginatum* sont décrits pour la première fois. À côté de l'espèce la plus commune *Choneziphius planirostris*, *C. macrops* est identifié à Anvers et sur la côte est de l'Amérique du Nord. Le nouveau genre et espèce *Beneziphius brevirostris* n. gen., n. sp. est décrit sur la base de deux spécimens caractérisés par un rostre court et pointu. Deux crânes partiels sont considérés comme Ziphiidae aff. *Eboroziphius*, un genre connu de la côte est de l'Amérique du Nord. Le nom de genre *Aporotus* est rétabli, incluant une grande espèce, *A. recurvirostris*, et une plus petite, *A. dicyrtus*. Une analyse de parcimonie incluant des genres fossiles et actuels de ziphiidés montre un lien de groupes-frères entre *Choneziphius* + (*Tusciziphius* + *Ziphius*) et *Ziphirostrum* + *Beneziphius* n. gen. Le genre moins bien connu *Aporotus* semble plus proche de *Choneziphius* + (*Tusciziphius* + *Ziphius*), mais des informations morphologiques complémentaires seraient nécessaires.

INTRODUCTION

The extant beaked whales (family Ziphiidae), including 21 species in six genera, considered for at least a part of them as deep-diving feeders, are among the least known of all mammalian groups (Wilson 1992); some of the species are only known by several specimens. Well preserved fossil ziphiids are also rare. The Neogene of Antwerp (North of Belgium, southern part of the North Sea Basin) is probably the richest location where diagnostic specimens of ziphiids have been discovered, with several genera based on species from the sequence.

The first species described from Antwerp by Cuvier (1823) were *Choneziphius planirostris* and *Mesoplodon longirostris*. The original skulls were found between 1809 and 1812 during the excavation of docks (Van Beneden 1864), and are now preserved at the Muséum national d'Histoire naturelle, in Paris.

Most ziphiids were discovered in the second part of the 19th century, during the building of fortifications around Antwerp. In 1860, Van Beneden reported a head of "Cétacé ziphioïde", which he named *Dioplodon d'Hemixem*. This skull, with the posterior part detached but preserved, was probably lost before 1900 (Abel 1905). In 1864, Van

Beneden changed the genus name *Dioplodon* in *Ziphirostre*, again without descriptions or identification number. In his work of 1868, du Bus used the genus name *Ziphirostrum* for five poorly described species of ziphiids, without reference to the species named by Van Beneden. However, several labels of skulls, written by du Bus in the 1860s, bear the name "*Ziphirostrum hemixemii*, Van Ben." (Abel 1905). Du Bus (1868) also created several new ziphiid genera: *Aporotus* with three species, *Ziphiopsis* with two species, and *Rhinostodes* with one species. Further, he named a new species in *Belemnoziphius* Huxley, 1864. Several of these taxa were subsequently briefly discussed in Owen (1870).

Later, Abel (1905) reduced the many nominal species of *Ziphirostrum*, *Aporotus*, and *Ziphiopsis*, in a manner quite similar to his work on eurhinodelphinids, to one species in one genus, *Mioziphius belgicus* (except a skull of *Ziphiopsis phymatodes*, placed in *Choneziphius planirostris*). Abel considered the range of variation briefly described by du Bus (1868) to be intraspecific ontogenetic variation. He further included in *Mioziphius belgicus* the fragmentary mandibles of *Synostodon* sensu du Bus (in Vanden Broeck 1874: 147), totaling 49 partial skulls and mandibles for one species, *Mioziphius belgicus*. *Mioziphius* is a junior synonym of *Ziphirostrum* (e.g., Muizon 1984, 1991; Bianucci *et al.* 1992; McKenna & Bell 1998; Fordyce & Muizon 2001).

On the basis of a fragment of mandibular symphysis lacking teeth, du Bus (1872) proposed the species *Champsodelphis scaldensis*, identified as a ziphiid by Abel (1905), who named it *Palaeoziphius scaldensis*. Abel (1905) also placed another fragment of symphysis in *Cetorhynchus atavus*. Those species, based on isolated mandibles, will not be discussed here.

The subject of this paper is a systematic revision of the numerous specimens of *Ziphirostrum* and *Choneziphius* from the collections of the IRSNB, addressing the opinions of du Bus (1868) and Abel (1905) on that subject. This part is followed by a discussion of the phylogenetic relationships of the revised taxa with the other fossil and extant ziphiids.

ABBREVIATIONS

ED   Specimen given by E. Delheid to the IRSNB;
IRSNB   Institut royal des Sciences naturelles de Belgique, Brussels;
M   Collection of types and figured specimens of fossil mammals from the IRSNB;
MGPD   Museo di Geologia e Paleontologia dell'Università di Padova;
MNHN   Muséum national d'Histoire naturelle, Paris;
MP   Museo di Storia Naturale e del Territorio Certoso di Calci dell'Università di Pisa;
NMB   Natuurhistorisch Museum Boekenberg, Antwerp;
USNM   United States National Museum of Natural History, Washington DC;
ZMA   Zoölogisch Museum of Amsterdam.

MATERIAL AND METHODS

SPECIMENS. — Most of the specimens described or redescribed in this work are from the collection of the IRSNB. Some of them have never been figured and did not belong to the collection of types and figured specimens. Some of them were exhibited in the Museum of the IRSNB in the past, but most were not available for study since the time of Abel (around 1905). The lists of numbered specimens given by Abel (1905: 104, 109 and 116) were used to identify the specimens described by du Bus (1868) for which the labels were lost or not readable.

TERMINOLOGY. — The main anatomical terms designating the different bony and soft parts of the ziphiid head are taken from the review of Heyning (1989a).

DESCRIPTION OF THE MEASUREMENTS. — See Figure 1 and Tables 1-6.

SYSTEMATICS

Order CETACEA Brisson, 1762
Suborder ODONTOCETI Flower, 1867

Family ZIPHIIDAE Gray, 1865

TYPE GENUS. — *Ziphius* Cuvier, 1823.

INCLUDED GENERA. — The extant genera *Berardius* Duvernoy, 1851, *Hyperoodon* Lacépède, 1804, *Indopacetus* Moore, 1968, *Mesoplodon* Gervais, 1850, *Tasmacetus* Oliver, 1937, and *Ziphius*, the fossil genera
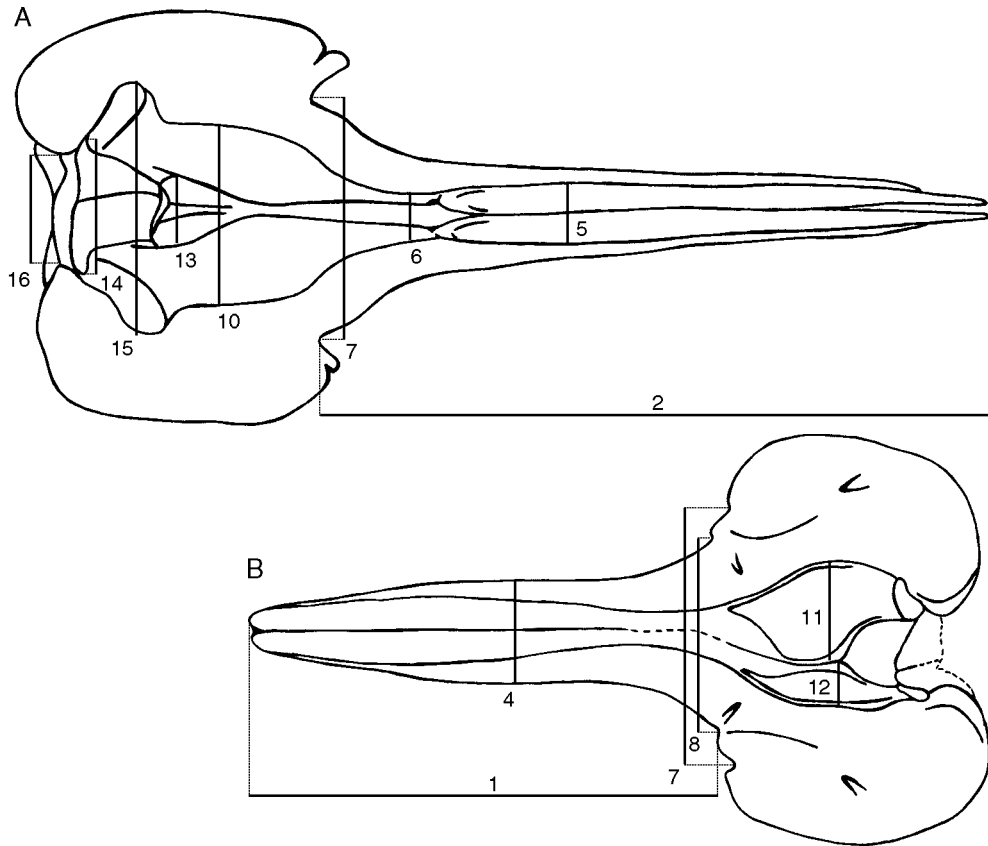
Fɪɢ. 1. — Line drawings showing the measurements used for the different ziphiid taxa in this work; **A**, *Ziphirostrum marginatum* du Bus, 1868 (combination of IRSNB 3845-M.536 and IRSNB 3847-M.537); **B**, *Choneziphius planirostris* (Cuvier, 1823) (reconstruction from IRSNB 3774-M.1881). For the values of each measurement, see Tables 1-4 and 6.

known by at least a partial skull *Aporotus* du Bus, 1868, *Choneziphius* Duvernoy, 1851, *Messapicetus* Bianucci, Landini & Varola, 1992, *Ninoziphius* Muizon, 1983, *Beneziphius* n. gen., *Tusciziphius* Bianucci, 1997, and *Ziphirostrum* du Bus, 1868, and the fossil genera only known by rostra: *Belemnoziphius* Huxley, 1864, *Eboroziphius* Leidy, 1877, *Pelycorhamphus* Cope, 1895, and *Proroziphius* Leidy, 1876, or fragments of mandible: *Anoplonossa* Cope, 1869 and *Cetorhynchus* Gervais, 1861. The systematic status of *Squaloziphius* Muizon, 1991 is discussed below, and this archaic genus is provisionally excluded from the family Ziphiidae. The fragment of mandibular symphysis of *Palaeoziphius scaldensis* Abel, 1905 is placed in Odontoceti *incertae sedis*.

EMENDED DIAGNOSIS. — A family of odontocetes with the following derived characters: elevated vertex with wide transverse premaxillary crests, and with medial edge of the maxillae and lateral edge of the premaxillae distinctly overhanging the maxillae laterally; strong development of the hamular lobe of the pterygoid sinus and enlargement of the hamular process of the pterygoid; enlargement of apical or subapical mandibular teeth (in some taxa, more developed in adult males); anterior process of the periotic transversely thickened at its base; enlarged posterior process of the tympanic bulla.

COMMENTS

Wide transverse premaxillary crests are also present on the delphinid *Australodelphis mirus* Fordyce, Quilty & Daniels, 2002. The posterior process of the tympanic bulla is also enlarged in physeteroids.

Genus *Ziphirostrum* du Bus, 1868

Ziphirostrum du Bus, 1868: 622.

Mioziphius Abel, 1905: 98, *partim*.

TYPE SPECIES. — *Ziphirostrum marginatum* du Bus, 1868 by present designation.

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

EMENDED DIAGNOSIS. — A fossil ziphiid genus differing from:
– *Choneziphius*, *Tusciziphius*, and *Ziphius* in: the absence of elevated longitudinal maxillary crest on the supraorbital process; less asymmetrical premaxillary sac fossae (ratio between maximum widths of left and right fossae higher or equal to 0.69); and anterodorsally shorter nasals;
– *Choneziphius* in: the excavation of a prenarial basin at the base of the rostrum margined by a wide strip of the maxillae elevated towards the antorbital notches; flat surface of the premaxillary sac fossa lacking a strong anterior concavity;
– *Aporotus* in: fused premaxillae above the mesorostral groove; strip of the maxilla limiting the prenarial basin anterolaterally, without valley along the lateral side of the elevated premaxilla on the rostrum;
– *Beneziphius* n. gen. in: a relatively longer and less pointed rostrum; a deeper prenarial basin; the lack of excrescences on the dorsal surface of the maxilla along the prenarial basin;
– other known ziphiids in the fusion of the thickened premaxillae above the mesorostral groove and the presence of a prenarial basin.
Most of the characters defining *Ziphirostrum* are present in *Messapicetus*, except the very dense rostrum, which is variable in *Ziphirostrum*. The prenarial basin is probably shallower in *Messapicetus*. Those two genera might therefore be more closely related than suggested by Bianucci *et al.* (1994) (see discussion below).

REMARK

When du Bus (1868) used for the first time the genus name *Ziphirostrum*, he intended to refer several new species to the same genus than *Dioplodon d'Hemixem* Van Beneden, 1860. However, the specimen on which Van Beneden (1860) based *Dioplodon d'Hemixem* (later renamed by Van Beneden [1864] *Ziphirostre d'Hemixem*) was lost, and Van Beneden (1860, 1864) did not provide any illustration. Abel (1905) therefore suggested a new genus name, *Mioziphius*, to clarify the situation, and he named a new single species, *M. belgicus*. However, more

recent authors always use the genus name *Ziphirostrum* (Mead 1975; Muizon 1984, 1991; Bianucci *et al.* 1992, 1994; McKenna & Bell 1998; Fordyce & Muizon 2001). Because there is no evidence to determine what specimen constitutes the species *Dioplodon d'Hemixem*, and because of the Principle of Priority (ICZN 1999: Art. 23), the genus name that should be used is *Ziphirostrum*. Within *Ziphirostrum*, the first species that can be identified from its original description is *Z. marginatum* du Bus, 1868. The single specimen included in this species by du Bus (1868: 624) was the partial skull IRSNB 3783-M.1878.

Ziphirostrum marginatum du Bus, 1868

Ziphirostrum marginatum du Bus, 1868: 624.

Ziphirostrum laevigatum du Bus, 1868: 624. — Van Beneden & Gervais 1880: pl. 27bis, fig. 5.

Ziphirostrum gracile du Bus, 1868: 625.

Mioziphius belgicus Abel, 1905: 99, *partim*, fig. 17, 101, fig. 18.

HOLOTYPE. — IRSNB 3783-M.1878, a partial rostrum with a part of the right premaxillary sac fossa and the right supraorbital process (single specimen of *Ziphirostrum marginatum* sensu du Bus, 1868).

REFERRED SPECIMENS. — 16 additional specimens: IRSNB 3845-M.536, partial skull (identified by du Bus as "*Ziphirostrum hemixemii* Van Ben." [label on the skull], described and figured as cotype of *Mioziphius belgicus* by Abel 1905: fig. 17); IRSNB 3847-M.537, partial skull (labelled "*Ziphirostrum hemixemii* Van Ben." by du Bus, described and figured as cotype of *Mioziphius belgicus* by Abel 1905: fig. 18); IRSNB 3820, partial rostrum; IRSNB 3828, partial rostrum; IRSNB 3829, partial skull; IRSNB 3833, partial rostrum; IRSNB 3839, partial skull (labelled "*Ziphirostrum hemixemii* Van Ben." by du Bus); IRSNB 3841, partial rostrum (labelled "*Ziphirostrum hemixemii* Van Ben." by du Bus); IRSNB 3842, partial skull (labelled "*Ziphirostrum hemixemii* Van Ben." by du Bus); IRSNB 3843-M.1876, partial skull; IRSNB 3844-M.1874, partial skull; IRSNB 3846-M.1875, partial skull (labelled "*Ziphirostrum hemixemii* Van Ben." by du Bus); IRSNB 3827-M.1879, fragment of rostrum (*Ziphirostrum gracile* sensu du Bus, 1868); IRSNB 3830-M.542, partial skull (*Ziphirostrum laevigatum* sensu du Bus, 1868, figured by Van Beneden & Gervais 1880: pl. 27bis, fig. 5); IRSNB IG.8638, partial skull (from Deurne, donated by Hasse, April 30,

1921); IRSNB M.1877, partial skull with four teeth (found by M. Bosselaers in April 2001, at Deurne, eastern suburbs of Antwerp, cited in Bosselaers *et al.* 2004).

TYPE HORIZON. — No information is available for the holotype. The skull IRSNB M.1877 was found in the Deurne Sands Member, Diest Formation, upper Miocene, middle to late Tortonian (Louwye 2002).

TYPE LOCALITY. — Area of Antwerp, Belgium, exact locality uncertain.

EMENDED DIAGNOSIS. — The species differs from *Ziphirostrum turniense* in: a deeper, longer and wider prenarial basin, bordered by relatively thicker and higher strips of the maxillae posterolaterally curving towards the antorbital notches; a more posterior position of the top of the premaxillae on the rostrum, at one quarter of its total length. It differs from the more-fragmentarily known *Z. recurvus* n. comb. in a relatively lower rostrum, wider than high in its anterior portion; the open mesorostral tunnel.

DESCRIPTION (FIGS 2-10)

General observations

This species was previously only known by the rostrum and the anterior part of the cranium; the basicranium and supraoccipital are usually lacking, as well as the teeth and ear bones. No mandible can be referred to this species; the mandibles described by Abel (1905) were found isolated (see below). The preserved parts are always robust and heavy, particularly the pachyosteosclerotic rostrum with the mesorostral groove dorsally closed by the thickened premaxillae. The skull is medium-sized, with a supraorbital width (see Table 1, measurement 6) intermediate between the smaller *Messapicetus* and the larger *Ziphius*. The relatively long roughly cylindrical rostrum is shorter than in *Messapicetus*, but more elongated than in *Ziphius*, proportionally closer to *Tasmacetus*. A deep prenarial basin (*sensu* Heyning 1989a) precedes the asymmetrical premaxillary sac fossae. The vertex is wide and high.

Several specimens – IRSNB 3845-M.536, IRSNB 3844-M.1874, IRSNB 3829, IRSNB 3841, and IRSNB 3842 – show rounded *postmortem* excavations of the surface of the bone with a more or less regular outline. Those depressions have a variable diameter: the small ones reach only 7 to 9 mm, while larger ones, more

TABLE 1. — Measurements (in mm) on skulls of *Ziphirostrum marginatum* du Bus, 1868 from the Neogene of Antwerp. **e**, estimate; **–**, no data. See Figure 1 for the description of the measurements.

	IRSNB 3845-M.536	IRSNB 3847-M.537	IRSNB 3846-M.1875	IRSNB 3844-M.1874	IRSNB 3843-M.1876	IRSNB 3842	IRSNB 3839	IRSNB 3833	IRSNB 3841	IRSNB 3830-M.542	IRSNB M.1877	IRSNB 3783-M.1878
2. length maxilla on rostrum	–	500	530	–	–	–	–	–	–	–	–	–
5. maximal width premaxillae on rostrum	51	75	?	55	57	66	52	62	–	71	60	50
6. minimal distance between maxillae at prenarial basin	34	33	27	25	46	36	33	–	25	55	e45	39
7. width base rostrum	192	–	–	e185	203	–	–	–	–	–	e210	–
9. width skull at supraorbital processes	334	–	–	–	–	–	–	–	–	–	–	–
10. width premaxillary sac fossae	142	139	e147	144	141	e138	–	–	–	–	–	–
11. width right premaxillary sac fossa	71	70	71	e65	65	65	59	–	–	–	–	–
12. width left premaxillary sac fossa	55	50	e50	e49	44	e46	–	–	–	–	–	–
13. width bony nares	53	57	–	59	–	–	–	–	–	–	–	–
14. width nasals	e60	72	–	–	–	75	–	–	–	–	–	–
15. width transverse premaxillary crests	168	158	–	–	–	134	–	–	–	–	–	–
16. minimal posterior distance between maxillae	80	76	–	e72	–	–	–	–	–	–	–	–

ellipsoidal, have a maximum diameter reaching 19-23 mm – with the largest reaching 33 mm. The depth is also variable: the depressions are sometimes very shallow (less than 1 mm) but some are deeper than 10 mm. The most excavated area of the skulls is the dorsal part of the maxillae and the premaxillae on the cranium, indicating that the large mass of facial muscles was already detached at the moment of the drillings. Some fossae also excavate the lateral and ventral surfaces of the rostrum. More than 25 fossae are counted on IRSNB 3845-M.536 (Fig. 2). Those shallow holes may be aborted drillings made by bivalves. Those molluscans tried to excavate the bone, but its high density and hardness might have precluded them to finish their work. Among the bivalves recorded in the upper Miocene of the region of Antwerp, species that are known to drill in harden substrates are *Hiatella arctica* (Linnaeus, 1758) and *Gastrochoena dubia* (Pennant, 1777) (R. Marquet pers. comm. 2004). Other organisms that could be responsible of those holes are bone-eating osteopeltid limpets, or even echinoids (R. E. Fordyce pers. comm. 2005).

Premaxilla

The premaxillae are thick and dense on the rostrum, making it strong and heavy. They dorsally close most of the mesorostral groove. On the nearly complete rostrum IRSNB 3847-M.537, the premaxillae are closely applied for 310 of the 550 preserved mm, with a dorsal median suture distinct as a thin groove (Fig. 5A). They are separated on the apical 140 mm, with a progressive forward opening, and on the prenarial basin. When dislocated, the surface of suture between the two premaxillae on the rostrum is planar, without vascular grooves, indicating a close contact. A central tunnel between the vomer and the premaxillae, remnant of the mesorostral groove, is retained. The premaxillae occupy a large part of the dorsal surface of the rostrum apically; they widen posteriorly, reaching their maximum width at 200-205 mm of the antorbital notch. Then their width slightly decreases until the prenarial basin. Along their descent in the basin, the
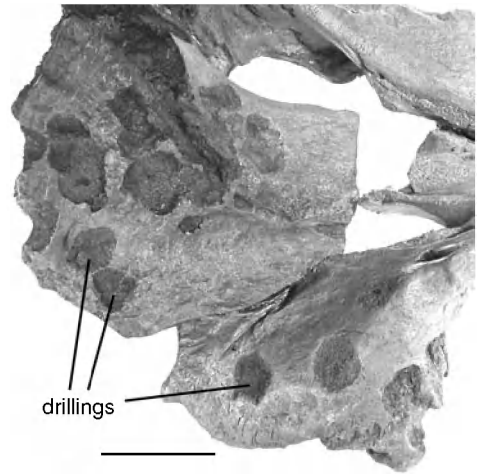

FIG. 2. — Skull of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3844-M.1874), from the Neogene of Antwerp, detail of the left part of the cranium in dorsal view showing aborted ?molluscan drillings. Scale bar: 50 mm.

premaxillae abruptly narrow, and nearly disappear from the dorsal view, the left one more distinctly than the right one, at the level of the premaxillary foramen. Seen in lateral view, the rostrum is roughly rectilinear. The premaxilla appears at the anterior limit of the prenarial basin; it thickens until a maximum height reached 60-80 mm forwards. Then, it progressively lowers, with a second less pronounced prominence, and tapers towards the apex.

On the skull IRSNB 3847-M.537, with a long portion of the rostrum preserved, the poorly marked lateral suture between maxilla and premaxilla is visible until the anterior end of the maxilla, 510 mm anterior to the antorbital notch and 45 mm before the apex of the incomplete rostrum (probably lacking some centimetres).

In *Ziphirostrum marginatum*, the prenarial basin is a deep and wide depression in the base of the rostrum, formed by nearly complete resorption of the premaxillae, and laterally limited by the maxillae. The basin extends from a level slightly anterior to the premaxillary foramina to the anterior of the premaxillary sac fossae (Fig. 4A). The floor of the basin is made of the vomer, which sends thin dorsomedial plates partially dorsally closing the mesorostral groove in the basin.

Fig. 3. — Skull of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3845-M.536); **A**, dorsal view; **B**, left lateral view. Scale bar: 100 mm.

The premaxillary sac fossae are distinctly asymmetrical: the right one is longer and wider than the left. On IRSNB 3845-M.536, the right fossa reaches a maximum width of 68 mm (taken perpendicular to the longitudinal axis of the skull), and the left one 54 mm. The premaxillae nearly contact each other immediately anterior to the bony nares (6 mm of separation on IRSNB 3845-M.536). More anteriorly, they are joined on IRSNB 3845-M.536 by an irregular mass of bone, probably the mesethmoid, closing the mesorostral groove for a short distance. The posterodorsal elevation of the premaxilla is progressive, with an inclination of more or less 45° for the main part of the ascending process. At the level of the narrowest portion of the premaxilla, the slope distinctly increases; on the last centimetres, the flat anteriorly-facing surface of the bone becomes vertical, with a distinct twisting giving that surface a more medioanterior orientation. The wide and thick dorsal extremity of the premaxilla forms the transverse premaxillary crest, a
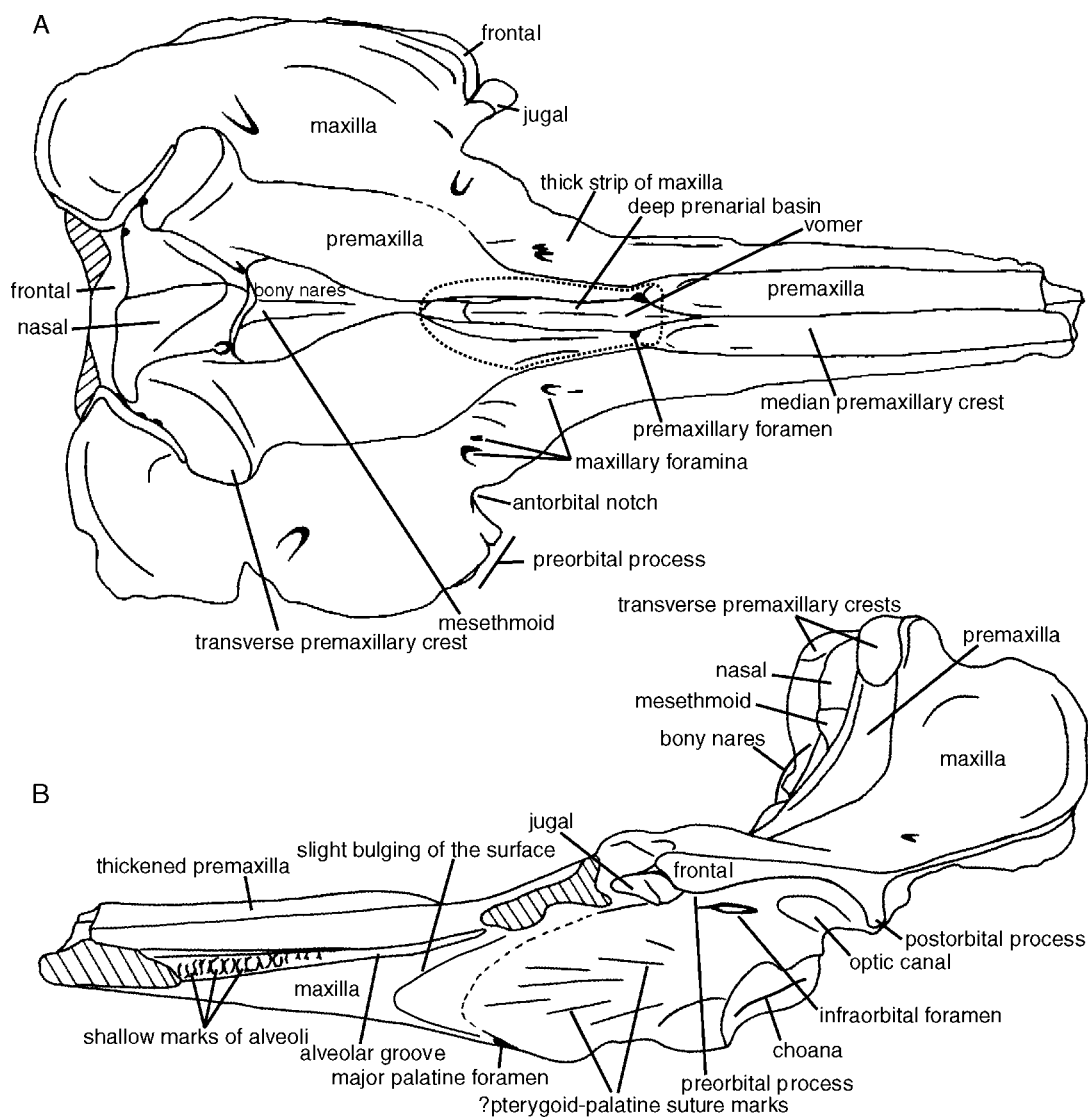
FIG. 4. — Line drawings of the skull of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3845-M.536); **A**, dorsal view, dotted line indicates limits of the prenarial basin; **B**, left lateral view, slightly anterior.

lateral part of the vertex. The medial part of the crest is anterolaterally directed, while the antero-lateral part is more laterally directed (Fig. 5D).

Maxilla

The prenarial basin is laterally margined by the thick, prominent and wide maxilla, sometimes slightly lower and flatter, rising towards the antorbital notch. This posterolaterally oriented thick strip of the maxilla at the base of the ros-trum is pierced by a series of dorsal infraorbital foramina until the level of the antorbital notch. The maxilla reaches a maximum dorsal height just before the notch, with a variably acute dorso-lateral edge (e.g., lower and more rounded on IRSNB 3845-M.536).

A

A-C

D

B

C

alveolar groove

slight bulge

vomer

major palatine foramina

palatine-maxilla suture

pterygoid sinus fossa
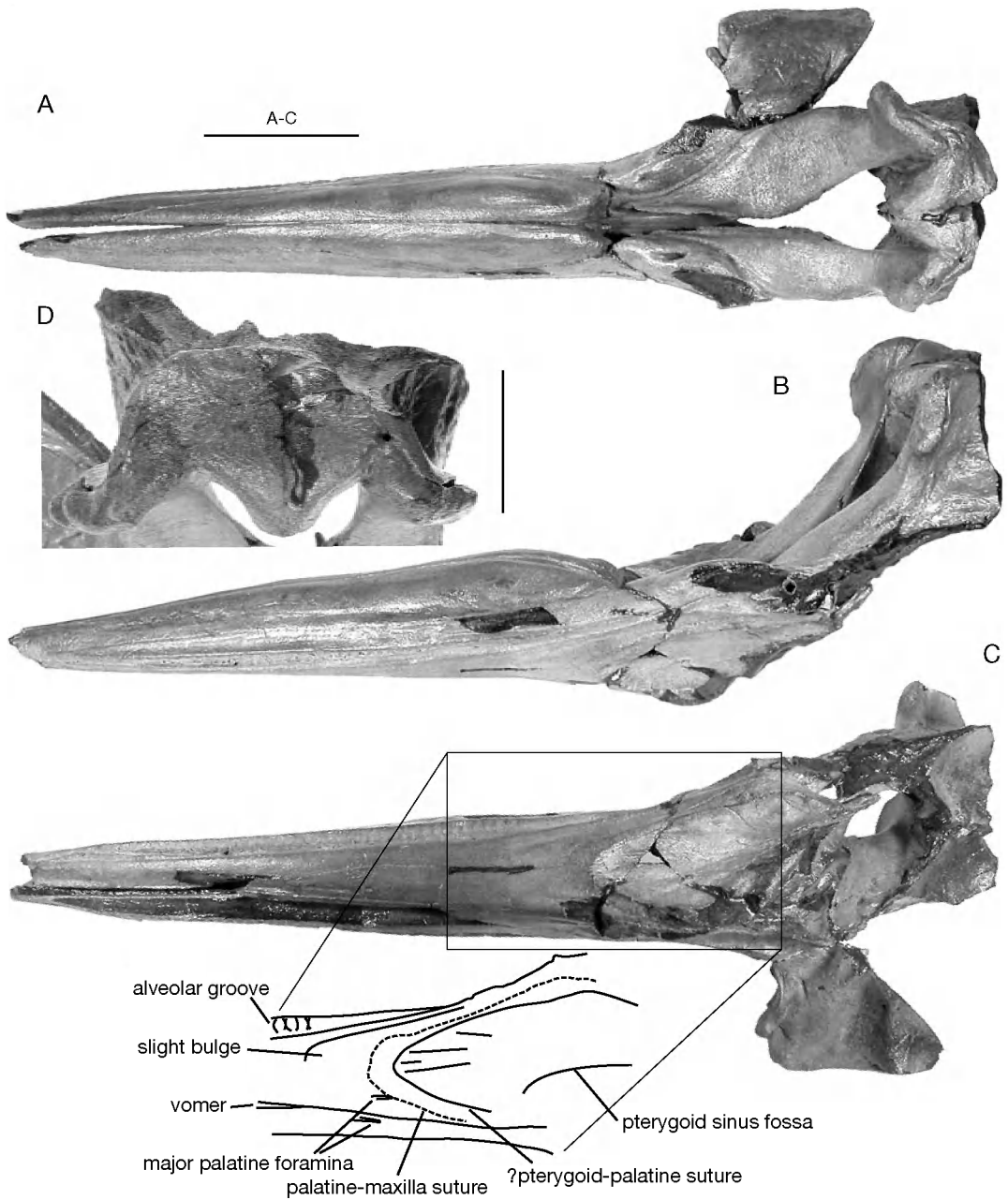
?pterygoid-palatine suture

FIG. 5. — Skull of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3847-M.537); **A**, dorsal view; **B**, left lateral view; **C**, left ventrolateral view and line drawing detailing the palate; **D**, detail of the vertex in dorsal view. Scale bars: A-C, 100 mm; D, 50 mm.

In lateral view, a longitudinal lateral groove appears below the maxilla-premaxilla suture 100-120 mm anterior to the antorbital notch; it quickly widens forward up to *c.* 15 mm width. The bottom of this groove is punctuated by a series of regularly spaced shallow depressions 6-7 mm in diameter, separated by transverse bridges 3-4 mm long (Figs 3B; 4B). These shallow vestigial alveoli could probably not effectively hold teeth; alternatively, perhaps teeth were mainly supported by the gum. The groove and alveoli disappear some centimetres before the anterior point of the maxilla, and do not mark the smooth lateral surface of the premaxilla. Forty-two alveoli are counted on the complete left maxilla of the skull IRSNB 3847-M.537.

The median ventral sutures are poorly discernable and the acute keel seen on the holotype medially to the anterior sinus fossa is at least partially made of the vomer. From 40 mm anteriorly to the palatines, the two maxillae are separated by a thin anteriorly widening ventral exposition of the vomer, for more than 190 mm on the skull IRSNB 3847-M.537. The maxillae are pierced along their median suture by pairs of palatine foramina opening forwards (more than three pairs on the incomplete IRSNB 3845-M.536). The most posterior pair is located along the median margins of the palatines (Figs 4B; 5C).

The antorbital notch is deep and wide. The anterior margin of the maxilla on the preorbital process curves anteroventrally around the jugal, forming a half cylinder anterolaterally directed, with a lateral extremity well demarcated from the preorbital process of the frontal. The thick strip of the maxilla medial to the antorbital notch extends for a short distance on the preorbital process, forming a shallow dome. The supraorbital process of the maxilla is pierced on IRSNB 3845-M.536 by one dorsal infraorbital foramen on the left, and one major and one smaller foramen on the right side. A plate of the maxilla totally covers the posterolateral edge of the transverse premaxillary crest, slightly overhanging the rest of the maxilla. The suture between this plate and the transverse premaxillary crest is pierced by a series of small vertical foramina (five major ones

are distinct on both sides on IRSNB 3845-M.536, with several smaller ones).

Nasal

Between the premaxillary crests, the triangular nasals, longer than wide, form an anterior rounded protuberance overhanging the bony nares; this prominent anterior angle reaches the anterior level of the premaxillary crests. The posterior margin of the nasals is rectilinear; their median suture is, anteriorly, distinctly deviated to the left side, so that it lies to the left relative to the median sutures of the rostrum and the inner sagittal crest of the cranium (Fig. 4A). The joined dorsal surfaces of the nasals are slightly medially depressed. Each nasal contacts the premaxillary crest only at the level of its posterolateral corner. In some specimens, the nasal sometimes contacts the median plate of the maxilla, preventing a suture between premaxilla and frontal, but the sutures are never clear on this area, and the character might even be variable on opposite sides of the same skull.

Mesethmoid

The dorsal margin of the posterior plate of the mesethmoid reaches a level 30 mm under the dorsal surface of the nasals. The triple point between nasal, premaxilla and mesethmoid is pierced on IRSNB 3845-M.536 by a vertical foramen, wider on the right side, probably corresponding to the additional exit from the infraorbital complex mentioned by Rommel (1990: 36) in *Tursiops*, and observed in several odontocetes, including extant ziphiids. This foramen is not always present (e.g., absent on IRSNB 3847-M.537). On IRSNB 3845-M.536, the mesethmoid is pierced by a terminal nerve foramen (see Rommel 1990 in *Tursiops*), at mid-height and on the two sides of the low and wide keel. This moderately large foramen is laterally prolonged by a short groove, and exits on the inner anterior face of the cranium cavity at the suture between frontal and mesethmoid.

Frontal

The lateral margin of the supraorbital process is horizontal and thin, with a moderate preorbital

thickening. The postorbital process is slender, probably originally more than 27 mm long. The frontals are poorly preserved on the vertex, forming a short strip along the posterior margin of the nasals and the posterior tip of the premaxillae. The right frontal of IRSNB 3847-M.537 is complete with a length of 20 mm (see Fig. 5D).

Palatine
The palatine is completely fused with the maxilla on IRSNB 3845-M.536; a slight bulging of the surface, going 165 mm anterior to the antorbital notch, probably corresponds to an area of muscle insertion. On the skull IRSNB 3847-M.537, the maxillopalatine suture is partly distinct, indicating a palatine reaching laterally close to the antorbital notch, and extending forward 135 mm anterior to the notch (Fig. 5C). Posteriorly, the lateral part of the bone goes beyond the anterior wall of the choana (incompletely preserved). The pterygoid is lost but a large portion of the palatine is excavated, either by the lost pterygoid, or by the pterygoid sinus fossa, only retaining a narrow unexcavated strip around the fossa. Grooves and ridges on the anterior margin of the fossa indicate the suture with the pterygoid. The remaining surface of the fossa is very smooth, the pterygoid being probably very thin or even absent there. The dorsolateral margin of the fossa is a low longitudinal ridge.

Lacrimal-jugal-optic groove
On the orbit roof, the lacrimal and the jugal are completely fused. The lacrimal-jugal complex is fused to the frontal and the anterior curved part of the maxilla. The optic groove is wide, with the anterior wall more elevated, separating it from the large infraorbital foramen. One or two small frontal foramina pierce the posterior wall of the groove. A foramen starting from the large infraorbital foramen in a posteromedial direction, presumably the sphenopalatine foramen, emerges on the lateral wall of the choana.

INTRASPECIFIC VARIATION
In *Ziphius cavirostris*, which is the only recent ziphiid possessing a prenarial basin, this structure is considered as extremely sexually dimorphic, only well developed in adult males (Heyning 1989a). While the prenarial basin roughly occupies the same position in *Ziphirostrum marginatum*, its morphology differs from *Ziphius cavirostris*: in the former, the basin is not laterally margined by the elevated lateral portion of the premaxilla, but by the thickened maxilla. Furthermore, the basin is observed in all the preserved specimens of *Ziphirostrum marginatum*, large and smaller ones, with a nearly total resorption of the premaxillae anterior to the premaxillary sac fossae (Fig. 6). The absence of resorption would give stronger skulls, more likely to be preserved; because this condition is not recorded in the collection of the IRSNB, the species *Z. marginatum* is probably characterized by the presence of a prenarial basin on specimens of both sexes and different ages. Width and length of the basin vary among the specimens – for instance, the distance between the posterior apex of the thickened premaxilla on the rostrum and the antorbital notch is greater on IRSNB 3845-M.536 relative to IRSNB 3847-M.537 (respectively 95 and 79 mm). However, it seems difficult to correlate this variation to ontogeny, contrary to *Ziphius cavirostris*: the larger skull IRSNB 3846-M.1875 has a minimum width between the thickened lateral strips of maxillae that is smaller than on IRSNB 3845-M.536 (respectively 27 and 34 mm). The premaxillary sac fossae of the skull IRSNB 3843-M.1876 are anteriorly longer in the basin than on IRSNB 3845-M.536, for a specimen similar in size. In *Z. cavirostris*, the variably developed resorption of the premaxillae is related to the more or less complete filling of the mesorostral gutter (Heyning 1989a), mainly by the vomer, while in *Ziphirostrum marginatum* the mesorostral gutter is not filled by the vomer, but is dorsally closed by the joined premaxillae on every specimen observed. The pattern of bones is therefore very different. Nevertheless, the filling of the prenarial basin with the enlarged right nasal plug, observed in the adult males of *Ziphius cavirostris* (Heyning 1989a), is suggested in *Ziphirostrum marginatum*, but without distinction of sex and age.
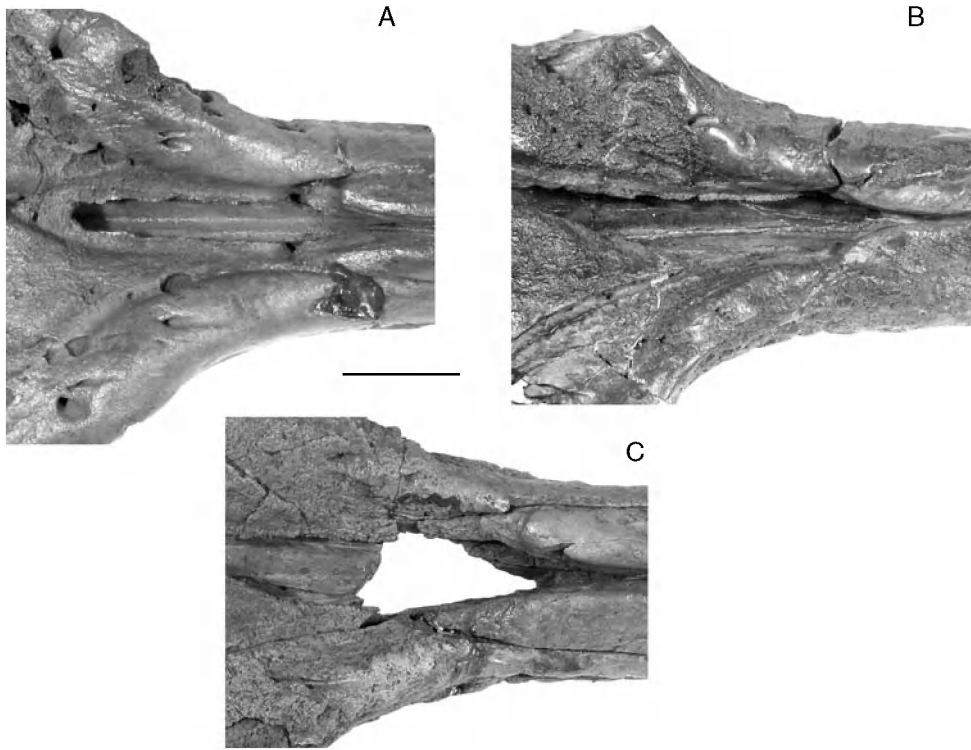
Fig. 6. — Detail of the prenarial basin in dorsal view for *Ziphirostrum marginatum* du Bus, 1868; **A**, IRSNB 3845-M.536; **B**, IRSNB 3846-M.1875; **C**, IRSNB 3843-M.1876. Scale bar: 50 mm.

The morphology of the premaxillae at the anterior limit of the prenarial basin is variable in *Z. marginatum*. On IRSNB 3845-M.536, the premaxillae are separated for a length of 30 mm. They are more closely appressed on the skull IRSNB 3847-M.537, but they present a narrow posterior projection towards the prenarial basin. The skulls IRSNB 3842, IRSNB 3843-M.1876, IRSNB 3844-M.1874, and IRSNB 3846-M.1875 show more posteriorly diverging lateral margins of the prenarial basin, with more elevated posterolateral crests compared to IRSNB 3845-M.536.

Height and width of the premaxillae anterior to the prenarial basin, are also variable (see Fig. 1A, Table 1, measurement 5 for the width). For instance, the premaxillae of IRSNB 3847-M.537 are wider and more elevated than in IRSNB 3845-M.536 and the large skull IRSNB 3846-M.1875. On

IRSNB 3847-M.537, the lateral margins of the enlarged premaxillary dome nearly reach the lateral edges of the rostrum, and, at the level of the maximum elevation, the rostrum is higher than wide, contrary to IRSNB 3845-M.536 and IRSNB 3846-M.1875.

The narrowing of the premaxillae just before the transverse premaxillary crests is more pronounced on IRSNB 3847-M.537 than on IRSNB 3845-M.536, with minimum widths of the left premaxilla respectively of 30 and 38 mm.

Taking into account this intraspecific variability, several species of the genus *Ziphirostrum* described by du Bus (1868) should be referred to *Z. marginatum*. Each of these species was based on fragmentary rostral material, lacking the vertex. Hereafter, several characters of these nominal species are briefly discussed to examine the variability and the anatomical data they add to *Z. marginatum*.
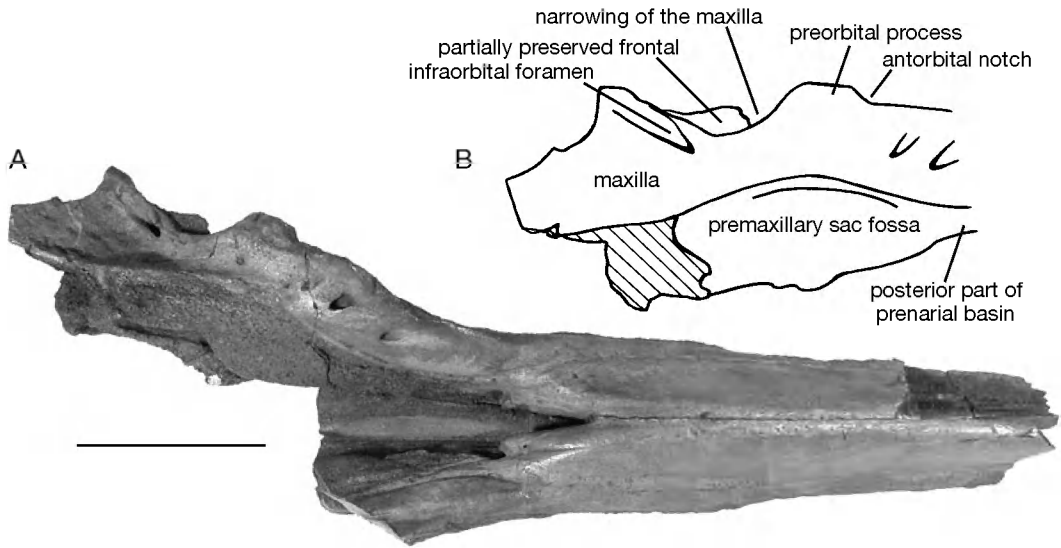
FIG. 7. — **A**, rostrum and left supraorbital process of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3830-M.542) (*Z. laevigatum* sensu du Bus, 1868) in dorsal view; **B**, line drawing of the left supraorbital process displaying an unusual narrowing of the maxilla posterior to the preorbital process. Scale bar: A, 100 mm.

ZIPHIROSTRUM LAEVIGATUM SENSU DU BUS, 1868

The species *Ziphirostrum laevigatum* sensu du Bus, 1868 was erected for the specimen IRSNB 3830-M.542, a partial skull figured by Van Beneden & Gervais (1880: pl. 27bis, fig. 5). The definition of the species was based on different proportions of the rostrum in general, on the thickness and the porosity of the maxillae, the size of the prenarial fossa, and the proportions and porosity of the premaxillae (du Bus 1868). Some of these characters were later used to suggest affinities with *Z. laevigatum* for the specimen IRSNB M.1877, a more complete skull collected in non-reworked deposits (Bosselaers *et al.* 2004). For these two skulls, the general morphology of the rostrum matches that described above, and the few differences observed – the anterior part of the rostrum wider than high, due to the poorly elevated premaxillae, the lateral part of the premaxillae forming with the lateral maxillae a concave dorso-lateral surface, and a longer separation between the premaxillae before the prenarial basin – are considered intraspecific variation. The density of the rostrum bones, used by du Bus (1868) to distinguish *Z. laevigatum*, will be discussed in

another work. The degree of rostral mineralization is far from consistent in *Z. marginatum*, and should not be used as a diagnostic character.

A strange characteristic of the skull IRSNB 3830-M.542 is the morphology of the left maxilla posteriorly to the antorbital notch (Fig. 7). Even if the notch is only partially preserved, the lateral margin of the maxilla, some centimetres posterior to the notch, extends no further laterally than just before the notch: the preorbital process forms a reduced lateral projection anterior to a strong narrowing of the maxilla with a deep inner curvature. The frontal being poorly preserved under the maxilla, this strange feature, not observed on other specimens of *Z. marginatum*, seems difficult to explain – very narrow supraorbital process or only resorption of the maxilla. The surface of the maxilla at that level is relatively smooth, and does not provide indications for a pathology derived from a trauma.

The specimen IRSNB M.1877, with more porous bone, has the left squamosal, fragments of the left exoccipital, the left occipital condyle, fragments of the basioccipital and supraoccipital, and four teeth preserved, parts never described
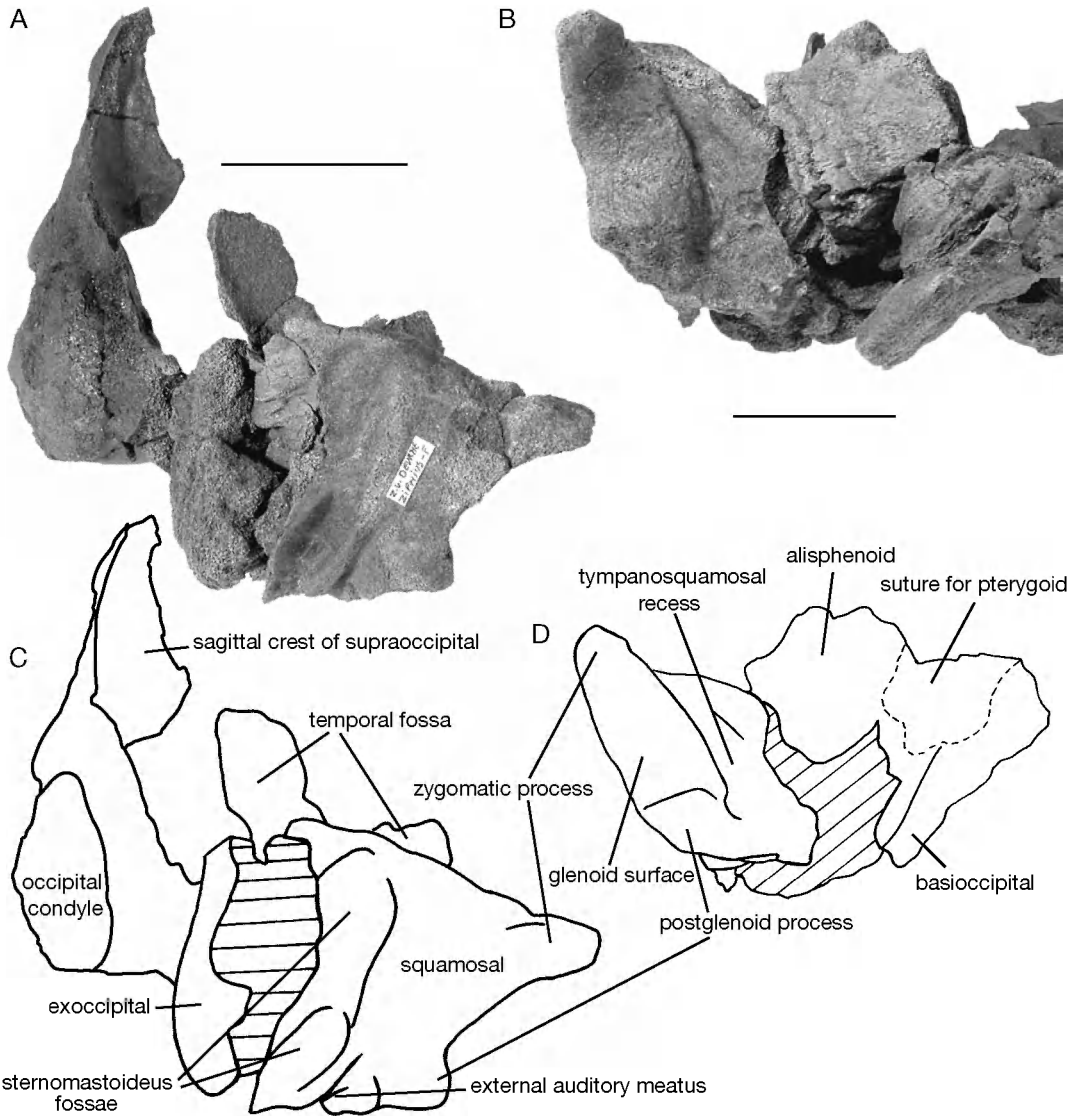
FIG. 8. — *Ziphirostrum marginatum* du Bus, 1868 (IRSNB M.1877) from the Deurne Sands Member, late Miocene, Deurne, Antwerp; **A**, right lateral view of the basicranium; **B**, ventral view of the right part of the basicranium; **C**, line drawing in right lateral view; **D**, line drawing in ventral view. Scale bars: 50 mm.

for the species. In lateral view, the squamosal (Fig. 8) shows a long and anterolaterally pointed zygomatic process, perpendicular to the wide and short postglenoid process. This articular part of the bone is separated from the post-tympanic process by a weakly marked oblique ridge, forming the anterior wall of the two sternomastoideus fossae; the lower fossa is deep and narrow and the upper one is wider. The glenoid surface occupies a large part of the ventral surface of the squamosal, laterally to a poorly excavated and narrow tympanosquamosal recess (compared to *Ziphius* for instance). The floor of the temporal fossa is a wide basin, more distinct than in *Ziphius*.
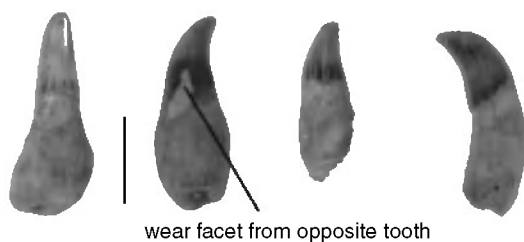
wear facet from opposite tooth

Fig. 9. — Four detached teeth of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB M.1877) from the Deurne Sands Member, late Miocene, Deurne, Antwerp. One of the teeth displays a wear facet from contact with an opposite tooth. Scale bar: 10 mm.

The four teeth (Fig. 9) were found detached near the skull IRSNB M.1877 on the field; whether upper or lower is uncertain. Their length ranges from 18 to 22 mm. All of them have a variously curved smoothly enamelled crown, slightly anteroposteriorly flattened, constituting less than half the total length of the tooth. The root is thick, wide (maximum diameter between 8 and 9 mm), nodulous, and rectilinear. The size of the root is too large for the shallow maxillary alveoli described on *Ziphirostrum marginatum* IRSNB 3847-M.537; this might suggest a dentary origin for those teeth. The apex of the root is hollowed by a circular pulp cavity variously filled (one of the teeth has a deep and narrow empty cavity, characteristic of younger individuals). Three of the teeth show an irregular apical wear of the crown. Additionally, one of them bears a smooth wear facet at the base of the crown, perfectly matching the shape of a crown. This feature probably indicates the presence of opposite functional teeth (lower and upper jaw teeth), a primitive character shared with the extant *Tasmacetus*, the Pliocene *Ninoziphius platyrostris* and the Miocene *Messapicetus longirostris*. On a specimen of *Tasmacetus shepherdi*, Oliver (1937) also noticed signs of wear on the crowns of the teeth, many truncated tips, and grooves where opposing teeth have worn against them; Oliver concluded that those teeth were functional. There is a great variation of size and shape for the teeth of extant ziphiids, partially due to ontogeny and sexual dimorphism (e.g., Mead 1989). The swelling of the root and the blunt proximal extremity in the

fossil teeth are reminiscent of the teeth of *Hyperoodon ampullatus* figured by Moore (1968: figs 4, 5) and *Tasmacetus shepherdi* figured by Oliver (1937: pl. 4, fig. 10). Similarly, *Ninoziphius platyrostris* has a wide tooth root, but the crown is too worn to be compared (see Muizon 1984). Furthermore, the teeth of *N. platyrostris* are larger, with a width of the roots reaching 12 mm. On the holotype of that species, the long roots are only partially inserted in the alveolar groove, a feature that could be partially due to a *post-mortem* shifting; it is, however, likely that a portion of the root was included in the gum.

ZIPHIROSTRUM MARGINATUM SENSU DU BUS, 1868
The holotype, IRSNB 3783-M.1878 (Fig. 10), was originally the only specimen referred to *Ziphirostrum marginatum* by du Bus (1868). That species was defined by the relative width and shape of the premaxillae and maxillae in dorsal view of the rostrum, and the size of the prenarial fossa; the premaxillae are a little bit narrower on the rostrum and the maxillae flatter and wider with a more acute lateral margin than in most of the other specimens of *Z. marginatum*. From the premaxillary foramen, an anteromedial sulcus excavates the thickened premaxilla on a short distance; anteriorly, the sulcus divides in a series of narrow and shallow sulci spreading on the surface of the premaxilla. A deep (more than 8 mm) and wide posterior sulcus connects the premaxillary foramen to the anterior of the premaxillary sac fossa, where it divides in short posteromedial and posterolateral sulci, vanishing before the level of the antorbital notch. On the other specimens of *Ziphirostrum marginatum*, this fragile structure is either broken, or resorbed by deepening of the prenarial basin; the morphology described here indicates how the prenarial basin develops in *Z. marginatum*, by deepening of a sulcus consisting in the joined anterior portions of the posteromedial and posterolateral sulci.
The holotype shows interesting similarities with *Messapicetus longirostris*, from the late Miocene of Italy (Bianucci *et al.* 1992), including the narrow and moderately high premaxillae anteriorly to the prenarial basin, median to wide and flat maxillae,
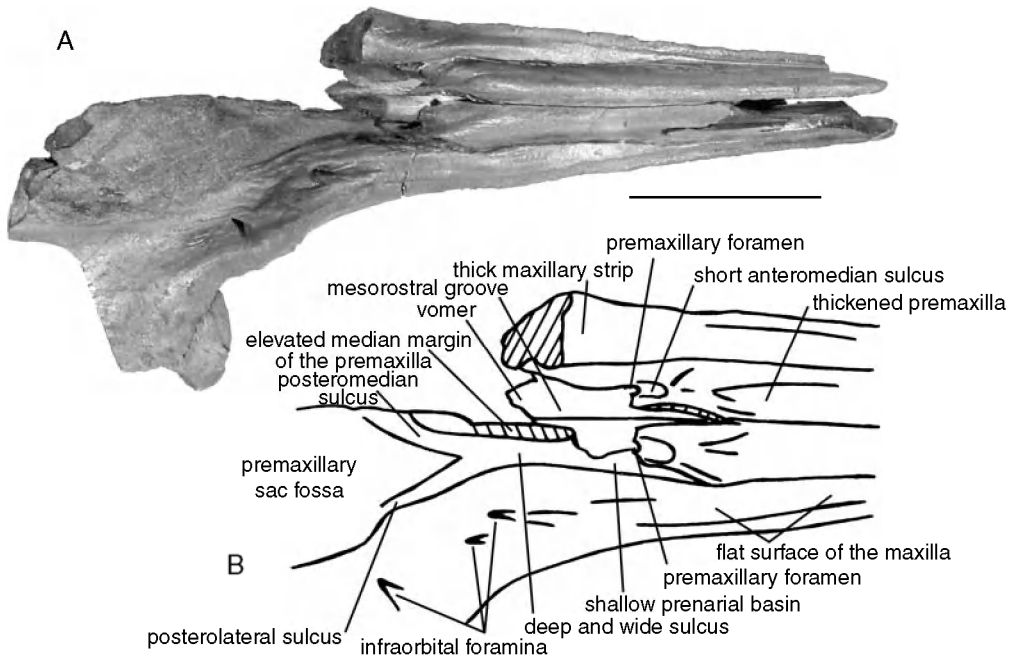
FIG. 10. — **A**, rostrum and right supraorbital process of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3783-M.1878, holotype) in dorsal view; **B**, line drawing of the base of the rostrum, showing the shallow prenarial basin between the thick maxillary strips. Scale bar: A, 100 mm.

and the poorly excavated prenarial basin with a pair of wide longitudinal sulci bordered medially by a prominent ridge of the premaxilla and laterally by the thick maxilla. However, *Messapicetus* has more distinct and ventrally oriented maxillary alveoli, and the rostrum is longer. *Messapicetus longirostris* might nevertheless be closer to *Ziphirostrum marginatum* than previously thought (see Bianucci *et al.* 1992, 1994, and phylogenetic discussion below).

ZIPHIROSTRUM GRACILE SENSU DU BUS, 1868
The fragmentary rostrum IRSNB 3827-M.1879 is the only specimen of *Ziphirostrum gracile* sensu du Bus, 1868 found in the collection. The two others cited by Abel (1905), including the one on which du Bus (1868) noticed several deeper alveoli, are lost. This specimen is composed of fused rostral portions of the premaxillae with applied fragments of maxillae (Fig. 11). The dorsolateral surfaces of the rostrum are concave, as in IRSNB
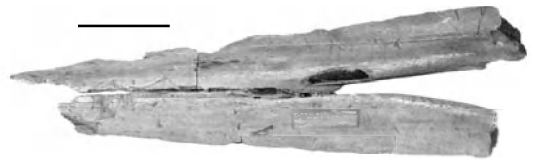

FIG. 11. — Fragment of rostrum of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3827-M.1879) (*Z. gracile* sensu du Bus, 1868) in dorsal view. Scale bar: 50 mm.

3830-M.542; the premaxillae are posteriorly separated on more than 90 mm, a character also present on the specimens IRSNB 3820 and IRSNB 3828, and considered as an individual variation in the species *Ziphirostrum marginatum*. "More porous maxillae" is the only character used by du Bus (1868) to define *Z. gracile*, a character unreliable in *Z. marginatum*. The maximum width of the premaxillae on the rostrum (50 mm) matches the variability observed in *Z. marginatum*.
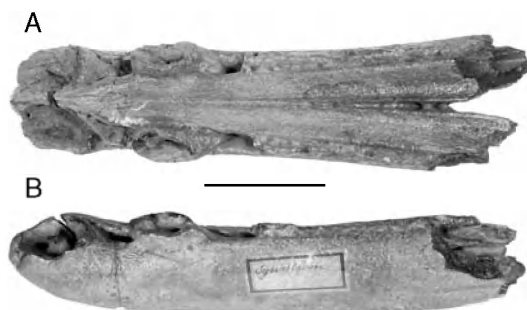
Fig. 12. — Symphyseal part of a mandible of Ziphiidae *incertae sedis* (IRSNB 3854-M.538) (*Synostodon* sp. *sensu* du Bus in Vanden Broeck 1874); **A**, dorsal view; **B**, left lateral view. Scale bar: 50 mm.

MANDIBLES PREVIOUSLY REFERRED TO
MIOZIPHIUS BELGICUS

In 1905, Abel placed in his carryall species *Mioziphius belgicus* several isolated symphyses and partial rami of mandibles. The best-preserved specimen, IRSNB 3854-M.538 (named *Synostodon* sp. by du Bus [in Vanden Broeck 1874], and identified by Abel [1905: fig. 19] as a cotype of *Mioziphius belgicus*), is mainly composed of a fused symphysis (177 of the 215 mm of the fragment), hollowed by two pairs of prominent alveoli for enlarged apical teeth (Fig. 12). The first anterior pair is the largest, constituting the anterior rounded margin of the mandible. Those alveoli are slightly longitudinally elongated, with a maximum length of 28 mm. The alveoli of the second pair, separated from the first by 15-20 mm, are distinctly narrower and have a length of 25 mm. A pointed anterodorsally directed peg is present at the centrum of the first and near the anterior wall of the second of these cylindrical depressions. The alveoli are inserted in a wide groove (8-9 mm wide between the first and second alveoli). 6-7 mm posteriorly to the second alveolus, the groove is filled by a continuous series of small rounded bony pegs. The external aspect of those pegs is reminiscent of the alveolar groove of the mandible of a fetus of *Physeter macrocephalus* (ZMA 12.810, total length of the body = 2540 mm), with the prominent but unerupted teeth still embedded in the bone of the alveolar groove. A lateral longitudinal

groove is present on the posterior few centimetres. Ventrally, the joined acute medioventral edges of the rami progressively diverge, opening a long triangular depression which opens dorsally only after 60 mm. Five pairs of small foramina pierce the mandible on both sides of the ventral symphysis, on the apical 25 mm. Width and height of the mandible at the level of the posterior wall of the first alveolus are respectively of 44 and 37 mm, and at the posterior end of the symphysis of 53 and 36 mm.

Following the interpretation of Abel (1905), the pointed pegs on the enlarged alveoli are probably a center of fixation for the root of poorly-inserted large apical teeth. A reduction of the number of mandibular teeth and the development of a few pairs of apical enlarged teeth is one of the main characteristics of the ziphiids. Among extant ziphiids, the genera *Hyperoodon*, *Ziphius* and *Mesoplodon* only keep one pair of apical (or subapical) mandibular teeth, two pairs are present in *Berardius*, with some variation, and about 48 pairs occur in *Tasmacetus* (with one apical pair of slightly greater size) (Moore 1968). The teeth of *Indopacetus* are not known. The shallow protruding alveoli of this specimen, partially filled with porous bone, can be compared to the platforms of dendritic or spongiform bone in *Tasmacetus*, or to the spongiform pads in *Berardius* (Moore 1968). They also fit the description made by True (1910) in *Ziphius*: "[…] in adult males the teeth are almost entirely protruded from the alveoli, which are filled with a coarse bony network". In *Ziphius*, the filling of the alveoli forces the teeth up and causes them to erupt in adult males (Heyning 1989b). Moore (1968) suggested that the same process happens in males of *Hyperoodon* but not in *Mesoplodon*. The mandible of *Ninoziphius* (early Pliocene, Peru) bears three apical and subapical pairs of "exostoses", also suggested as the support of enlarged teeth (Muizon 1984). The similarities of the smaller posterior pegs in the alveolar groove with the situation in fetal *Physeter* might provide an idea of the way the reduction of the number of teeth occurs in the ziphiids, by retention of a juvenile condition for a large part of the teeth in

adults, and an "extra" growth of only a small number of them.

The more eroded symphyses IRSNB 3848 and IRSNB 3855, even if smaller, do not show strong differences with IRSNB 3854-M.538; they might belong to the same taxon. Nevertheless, all these specimens are isolated, and their size and characters might correspond equally to *Ziphirostrum* sp., *Choneziphius* sp. or *Aporotus* sp. (see below). Accordingly, these symphyses are considered as Ziphiidae *incertae sedis*.

For two isolated fragments of left ramus IRSNB 3851 and IRSNB 3852 referred to *Mioziphius belgicus* by Abel (1905), few characters are comparable to the above symphyses; on both specimens, the preserved symphyseal portion does not seem to be tightly fused, and the dorsal groove is hollowed by shallow and poorly distinct alveoli. Because no clear ziphiid characters are apparent, these undiagnostic fragments are placed in Odontoceti *incertae sedis*.

Ziphirostrum turniense du Bus, 1868

Ziphirostrum turniense du Bus, 1868: 622, 623. — Van Beneden & Gervais 1880: pl. 27bis, fig. 6.

Mioziphius belgicus Abel, 1905: 104, *partim*.

LECTOTYPE. — IRSNB 3785-M.539, a partial skull (identified by du Bus [1868] as *Ziphirostrum turniense*, figured by Van Beneden & Gervais [1880: pl. 27bis, fig. 6, reversed], and placed in *Mioziphius belgicus* by Abel [1905]).

PARALECTOTYPE. — IRSNB 3784-M.1880, a partial skull (also referred to *Ziphirostrum turniense* by du Bus [1868] and placed in *Mioziphius belgicus* by Abel [1905]).

TYPE HORIZON. — "Crag gris" (du Bus 1868). Following Misonne (1958), the subdivisions "crag gris", "crag rouge" and "crag jaune" in the lower Pliocene of Antwerp indicate types of alteration more than stratigraphic levels. Furthermore, some levels in the upper Miocene have a similar colour. This species might therefore be late Miocene or early Pliocene. Several circular holes, with a diameter of approximately 14 mm and a depth less than 5 mm, pierce the premaxillary sac fossae of the holotype, in a way identical to the excavations on several specimens of *Z. marginatum* interpreted as bivalve drillings. This feature, added to the similar external aspect of the bones in specimens of the two species, might indicate an origin in the same stratigraphic unit.

TYPE LOCALITY. — Antwerp, Belgium, exact locality uncertain.

EMENDED DIAGNOSIS. — Species of the genus *Ziphirostrum* with a size of the skull close to *Z. marginatum*, differing from that species in: most elevated point of the premaxillae on the rostrum more anteriorly positioned, roughly at mid-length of the rostrum; posterior branch of the premaxillary longitudinal ridge on the rostrum laterally divergent with a small median depressed surface, indicating a less excavated and shorter prenarial basin laterally margined by the premaxilla (and not the maxilla as in *Z. marginatum*); wider and flatter dorsal exposure of the maxilla lateral to the premaxilla at the base of the rostrum and for some distance anteriorly. *Z. turniense* differs from *Z. recurvus* n. comb. in its less massive and lower rostrum, and an anteriorly open mesorostral groove.

DESCRIPTION (FIGS 13; 14)

Only one of the two known rostra of the species is associated with the anterior part of the cranium. The vertex is therefore unknown, but the preserved parts provide enough information to separate this species from *Ziphirostrum marginatum*, contrary to the assertion of Abel (1905).

The bones of the straight rostrum are dense and thick. The rostrum of the lectotype is roughly complete anteriorly: its total length is estimated at 550 mm, which is close to that inferred for *Z. marginatum*.

Premaxilla

The premaxillae compose the main part of the dorsal view of the rostrum. They are closely sutured on their dorsomedian margin until a progressive anterior separation, 200 mm before the apex (Fig. 13A). The maximum width of the premaxillae occurs at mid-length of the rostrum, more anteriorly than in *Z. marginatum*, and at the level of maximum elevation. The height of this prominence progressively reduces posteriorly, with a separation of the premaxillae forming thick diverging crests. These crests reach the anterior margin of the premaxillary sac fossae, with posterior extremities separated on the lectotype by 60 mm. Medially to the low crest, each premaxilla shows an elongated triangular and
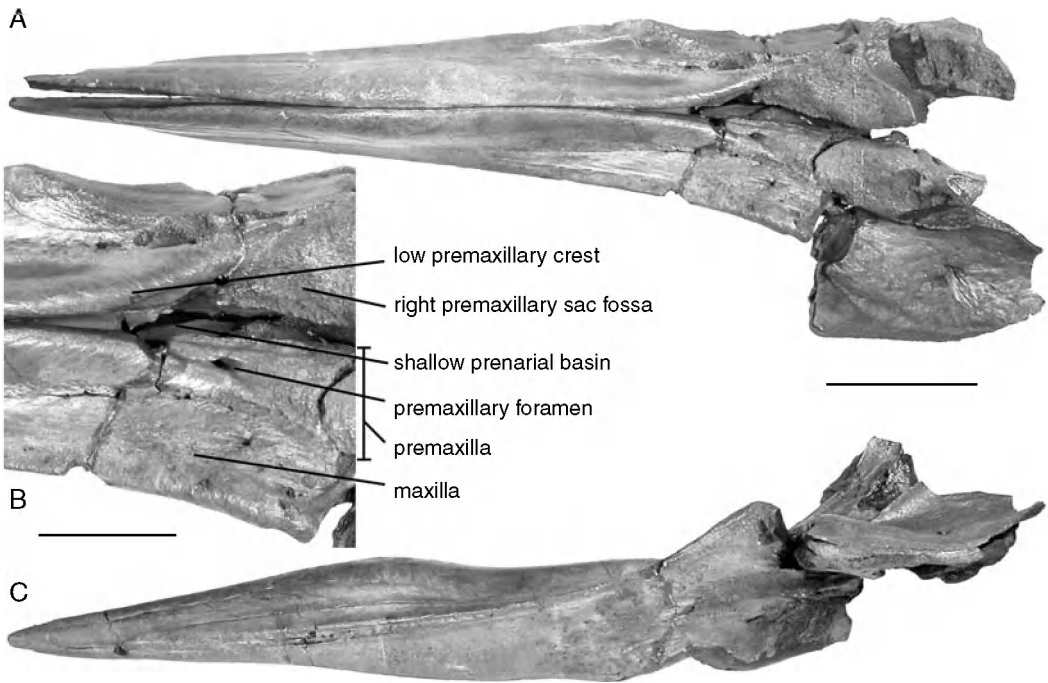
FIG. 13. — Rostrum and anterior part of the cranium of *Ziphirostrum turniense* du Bus, 1868 (IRSNB 3785-M.539, lectotype); **A**, dorsal view; **B**, detail of the base of the rostrum in dorsal view; **C**, left lateral view. Scale bars: A, C, 100 mm; B, 50 mm.

depressed surface pierced by a large premaxillary foramen. The foramen extends posterolaterally in a short posterolateral sulcus, and anteriorly in a longer anteromedian sulcus on the median edge of the crest, until the level of the median junction of the two premaxillae. Numerous thin anastomosed vascular grooves run anterolaterally from the sulcus, on the dorsal surface of the premaxilla. The grooves spread on the whole surface; a major groove runs posteriorly from the anterior opening of the mesorostral groove. The left premaxilla is somewhat narrower than the right at the level of the premaxillary sac fossa (respectively 50 and 55 mm for the maximum width).

Maxilla
Lateral to the premaxilla, the maxilla is nearly invisible in dorsal view on most of the length of the rostrum. Posteriorly, it widens to form a dorsally exposed platform, better developed on the lectotype. The posterior part of the platform, at the base of the rostrum, slopes medially from a high and prominent lateral edge (Fig. 13B). This structure limits laterally the shallow prenarial basin, characterized by a weaker premaxillary resorption than in *Ziphirostrum marginatum*. The supraorbital process is similar to *Z. marginatum*.

In lateral view, the left maxilla ends 92 mm before the apex of the rostrum on the lectotype (Fig. 13C). On the lateral side of the maxilla, the surface is excavated by a shallow vestigial alveolar groove beginning 120-130 mm anteriorly to the antorbital notch. On the paralectotype, the groove is almost totally filled by irregular bone (Fig. 14B); the alveoli are weakly excavated on the lectotype and only recognizable on the median portion. This groove continues anteriorly on the premaxilla and divides into two sulci for the last 25 mm.

In ventral view, a large foramen is anteriorly extended by a long and distinct sulcus along the median suture of the maxilla, 250 mm before the
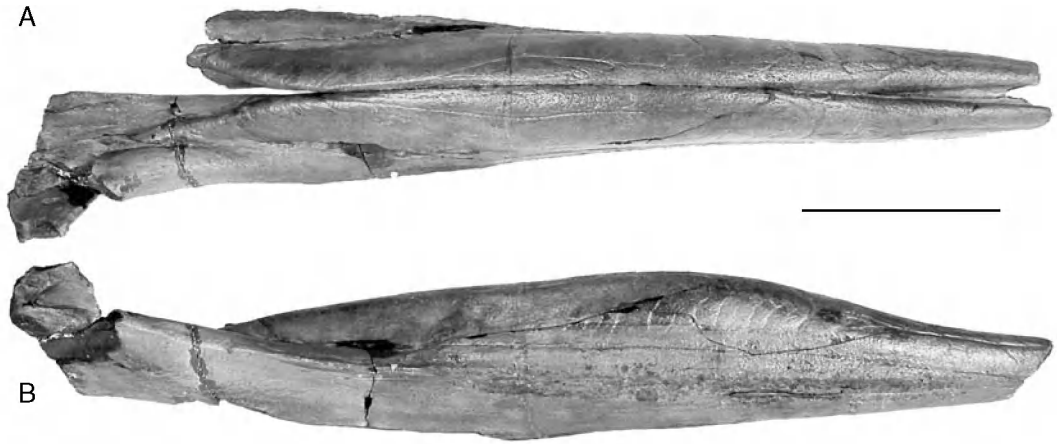
FIG. 14. — Rostrum of *Ziphirostrum turniense* du Bus, 1868 (IRSNB 3784-M.1880, paralectotype); **A**, dorsal view; **B**, right lateral view. Scale bar: 100 mm.

apex of the rostrum. An additional smaller foramen is present more posteriorly. The vomer appears between the maxillae for 190 mm on the lectotype, but not on the paralectotype.

Palatine
The palatine is not preserved anteriorly, but the marks of the foliated suture with the maxilla reach forward more than 150 mm anterior to the antorbital notch. Small lateral portions of the palatine are present, with a morphology similar to *Ziphirostrum marginatum*.

SYSTEMATIC DISCUSSION
These two skulls differ from *Ziphirostrum marginatum* in: more anterior position of the prominence of the premaxillae on the rostrum, roughly at mid-length of the rostrum; the poorly developed prenarial basin, with longer posterior extremity of the dense premaxilla contacting the premaxillary sac fossa; the wider flat dorsal surface of the maxilla at the base of the rostrum; the thinner lateral maxillary wall of the prenarial basin.

The most significant differences between *Ziphirostrum marginatum* and these specimens are therefore related to the shape and development of the prenarial basin and of the thickened premaxillae on the rostrum. As discussed above,

the prenarial basin is subject to a strong sexual dimorphism in the extant *Ziphius*, and the protuberances on the dorsal face of the rostrum are also sexually dimorphic in extant ziphiids (e.g., the maxillary crests much more developed in the adult males of *Hyperoodon* sp.). However, this sexual dimorphism is often based on the size of the structures: width and depth of the prenarial basin in *Ziphius*, height of the protuberances in *Hyperoodon*. What is observed here is also shape differences: the elevation of the premaxillae on the rostrum occupies a different position and has a different shape from *Ziphirostrum marginatum*, and the margins of the reduced prenarial basin are occupied by the premaxillae, not the maxillae (which is the case for *Z. marginatum*). Even if those specimens are fragmentary, the characters discussed above are regarded here as sufficiently diagnostic to support the species *Z. turniense*.

Ziphirostrum recurvus (du Bus, 1868) n. comb.

Belemnoziphius recurvus du Bus, 1868: 630. — Van Beneden & Gervais 1880: pl. 27bis, fig. 2.

Mesoplodon longirostris Abel, 1905: 113, *partim*.

HOLOTYPE. — IRSNB 3805-M.544, incomplete rostrum (single specimen of *Belemnoziphius recurvus* sensu du Bus, 1868, and referred to *Mesoplodon longirostris* by Abel [1905]).
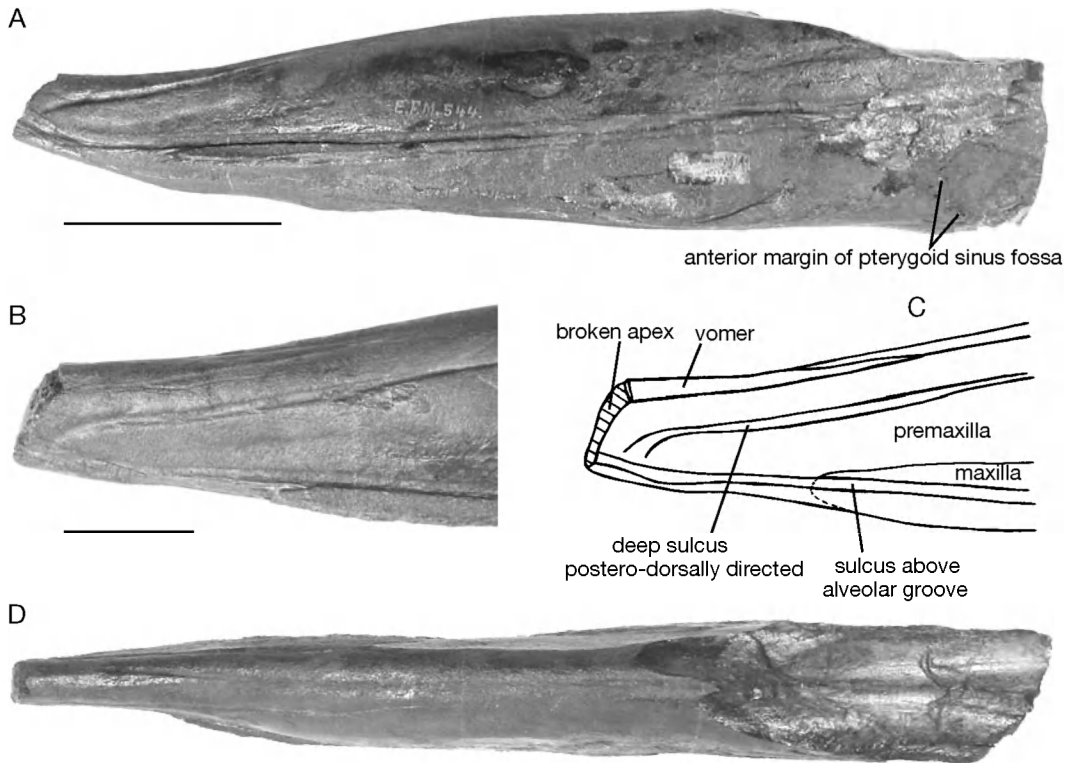
FIG. 15. — Rostrum of *Ziphirostrum recurvus* (du Bus, 1868) n. comb. (IRSNB 3805-M.544, holotype); **A**, left lateral view; **B**, detail of the apex in dorsolateral view; **C**, line drawing of the apex in dorsolateral view, indicating the filling of the mesorostral groove by the dense vomer; **D**, dorsal view. Scale bars: A, D, 100 mm; B, C, 50 mm.

TYPE HORIZON. — No data available, probably Miocene or early Pliocene.

TYPE LOCALITY. — Antwerp, Belgium, exact locality uncertain.

EMENDED DIAGNOSIS. — A large species of the genus *Ziphirostrum* characterized by: a very massive rostrum, higher and relatively narrower than in *Z. marginatum* and *Z. turniense*; a mesorostral groove dorsally closed by the premaxillae, as in the two other species of the genus, but completely filled by the dense vomer.

DESCRIPTION (FIG. 15)

IRSNB 3805-M.544 is a massive rostrum, lacking the apex, the base, and fragments of the right side. It is much higher than wide; the maximum posterior height is 113 mm for a width of 69 mm at the same level. The tapering towards the apex is associated with a distinct dorsal curvature (Fig. 15A). At the apex, the height is 41 mm, and the width, 24 mm.

This rostrum has a mesorostral gutter completely filled with dense bone, without an anterior opening. The placement of this specimen in the species *Mesoplodon longirostris* by Abel (1905) implied that the gutter was filled by the vomer only, as it is the case in several fossil and extant species of *Mesoplodon*. The sutures of the different bones are difficult to distinguish, because of the strong ossification. However, a V-shaped suture is clearly present on the apical portion of the dorsal surface (Fig. 15B, D). By comparison with *Ziphirostrum turniense* and *Z. marginatum*, this suture can be related to the dorsomedian margins of the thickened premaxillae, anteriorly diverging in *Ziphirostrum*. This suture is interpreted here as the premaxillary-vomer contact.

This implies that at least the most apical part of the mesorostral groove is filled by the vomer, and that the rest of the groove is roofed by the joined dense premaxillae. This last feature is characteristic of the genera *Ziphirostrum* and *Choneziphius*. The premaxillary eminences are, however, closer to *Ziphirostrum* than to *Choneziphius*, and even more similar in size and position to *Z. turniense*: on the rostrum of *Z. turniense* IRSNB 3784-M.1880, the dorsal margin of the apex exhibits the same kind of curvature, even if less pronounced. On both skulls of *Z. turniense*, a sulcus starts on the lateral side of the apex, runs posterodorsally, and divides in smaller branches; this kind of sulcus is present, even deeper and longer on the rostrum IRSNB 3805-M.544. By comparison with *Z. turniense*, it is possible to establish the path of the indistinct lateral suture between maxilla and premaxilla. This confirms the above hypothesis of the roofing of the mesorostral groove by the premaxillae. Ventrally to this suture, the alveolar groove is only slightly visible under a deep longitudinal sulcus, lacking alveoli.

The anterior margin of the pterygoid sinus fossa reaches a level 475 mm posteriorly to the incomplete apex (lacking at least 50 mm). This indicates a rostrum longer than in *Z. turniense*; the holotype of *Z. turniense* IRSNB 3785-M.539 has a distance between the pterygoid sinus fossa and the nearly complete apex of 440 mm.

The keeled vomer wedges between the maxillae on the ventral side for at least 242 mm, a feature present in the lectotype but not the paralectotype of *Z. turniense*.

DISCUSSION

This rostrum probably belongs to a distinct species of the genus *Ziphirostrum*, *Z. recurvus* (du Bus, 1868) n. comb., closer to *Z. turniense* than to *Z. marginatum*. The complete filling of the mesorostral groove is an interesting combination of a dorsal covering by the joined thickened premaxillae, as in *Ziphirostrum*, associated with the filling of the remaining aperture by the dense vomer, in a way reminiscent of *Mesoplodon*.

Genus *Choneziphius* Duvernoy, 1851

Choneziphius Duvernoy, 1851: 63.

Belemnoziphius Huxley, 1864: 395, *partim*.

Ziphius Owen, 1870: pl. 2, fig. 1, *partim*.

Proroziphius Leidy, 1876: 87; 1877: pl. 32, figs 1-4.

TYPE SPECIES. — *Ziphius planirostris* Cuvier, 1823 by present designation.

OTHER INCLUDED SPECIES. — *Choneziphius macrops* (Leidy, 1876) and *C. liops* Leidy, 1876 (figured in Leidy 1877).

EMENDED DIAGNOSIS. — This fossil ziphiid genus differs from all the other known living and fossil ziphiids in: the mesorostral groove dorsally closed at the level of the antorbital noches by the joined medial margins of the premaxillary sac fossae, forming a prominent ridge posteriorly deviated on the left, and separating deeply concave anterior portions of the premaxillary sac fossae. It further differs from:
– *Ziphirostrum* and *Messapicetus* in: flatter and lower maxillary surface at the dorsal base of the rostrum; more asymmetrical premaxillary sac fossae (ratio between maximum widths of left and right premaxillae at the level of the fossae lower or equal to 0.65); elevated longitudinal maxillary crest on the supraorbital process;
– *Aporotus* in: fusion of the elevated premaxillae over the mesorostral groove;
– *Ziphius* in: dorsal roofing of the mesorostral groove by the premaxillae; less elevated vertex not overhanging the bony nares as clearly as in *Ziphius*;
– *Tusciziphius* in: concavity of the surface of the premaxillary sac fossa anteriorly followed by a deep longitudinal foramen; much narrower transverse premaxillary crests on the vertex.
The vertex is only known from the species *C. planirostris*.

DISCUSSION

The drawing of the partial rostrum from Suffolk, identified by Lankester (1870: pl. 33, figs 1-4) as *Choneziphius packardi* is not detailed enough and the fragment is probably too eroded to allow a specific or even generic determination.

The fragmentary *C. trachops* is similar to *C. planirostris*; the only difference clearly noted by Leidy (1877) is the less excavated premaxillary sac fossae. However, this character is demonstrated here as variable in *C. planirostris*.

C. liops might represent a different species, given its relatively shorter rostrum, with a stronger anterior narrowing.

The holotype of *Proroziphius macrops* sensu Leidy, 1876, from the Phosphate Beds of South

Carolina, is discussed below, and is considered as a member of the genus *Choneziphius, C. macrops*. In the same way, the poorly preserved holotype of *Proroziphius chonops* Leidy, 1877 (USNM 16689) should probably be included in the genus *Choneziphius*: it shows premaxillary sac fossae separated by a deviated crest, the complete dorsal roofing of the mesorostral groove, and the roughly horizontal dorsal surface of the maxillae at the base of the rostrum, typical of *Choneziphius*.

Choneziphius planirostris (Cuvier, 1823)

Ziphius planirostris Cuvier, 1823: 352-356, pl. 27, figs 4-8. — Owen 1870: 5, fig. 2. — Van Beneden & Gervais 1880: pl. 27, figs 4, 5.

Choneziphius planirostris Duvernoy, 1851: pl. 2, fig. 5. — Gervais 1859: pl. 40, fig. 2. — Abel 1919: figs 575, 576. — Bianucci 1997: pl. 2, fig. 1, pl. 3, fig. 1.

Ziphius cuvieri Owen, 1870: 6, fig. 3.

Choneziphius trachops Leidy, 1877: pl. 30, fig. 2, pl. 31, fig. 1.

LECTOTYPE. — The best preserved of the two originals of Cuvier (1823), the anterior part of a skull (found on July 23, 1812, figured in Cuvier [1823: pl. 27, figs 5, 6], and housed at the MNHN).

PARALECTOTYPE. — The second original from Cuvier (1823), a rostrum and the anterior part of the cranium (figured in Cuvier [1823: pl. 27, figs 8, 9] and housed at the MNHN).

REFERRED SPECIMENS FROM ANTWERP. — 14 partial skulls and rostra from the IRSNB referred to *Choneziphius planirostris* by Abel (1905): IRSNB 3774-M.1881 (partial skull including the rostrum and the anterior of the cranium); IRSNB 3767 (rostrum and anterior of the cranium); IRSNB 3768 (rostrum and anterior of the cranium); IRSNB 3769 (rostrum and anterior of the cranium, except the left supraorbital process); IRSNB 3770 (rostrum and anterior part of the premaxillary sac fossae); IRSNB 3771 (rostrum); IRSNB 3772 (rostrum and anterior of the cranium); IRSNB 3773 (rostrum and anterior of the cranium); IRSNB 3775-M.1883 (rostrum and anterior of the cranium, except the left supraorbital process); IRSNB 3776 (rostrum and anterior of the cranium, except the left supraorbital process); IRSNB 3777-M.1882 (rostrum and anterior of the cranium); IRSNB 3779 (fragment of rostrum and anterior part of the premaxillary sac fossae); IRSNB 3780 (left part of rostrum); IRSNB 3790 (right fragment of rostrum); and four additional undescribed skulls found in the collections of the

IRSNB: IRSNB 1719a (rostrum and anterior of the cranium, except the left supraorbital process); IRSNB 1719b (rostrum and anterior of the cranium, except the two supraorbital processes); IRSNB 1719c (rostrum and anterior of the cranium, except the left supraorbital process); IRSNB ED001 (rostrum and anterior of the cranium, found in a box with the skull IRSNB ED002-M.1885 and with a common label: "*Choneziphius planirostris* – Et. : Anversien – Loc. : Steendorp – Don Delheid – Reg. I.G. 8289". One of these two skulls was cited in Delheid [1896] and was found in 1888 near Rupelmonde – this is probably the skull of *C. planirostris* IRSNB ED001, judging by the presence of fragments of the label's rope on this skull).

TYPE HORIZON. — The remarks of M. de la Jonkaire cited in Cuvier (1823: 352, 353) are not clear enough to identify a precise stratigraphic level. However, a specimen from the private collection of P. Gigase was found in the upper Miocene Deurne Sands (P. Gigase pers. comm. 2002).

TYPE LOCALITY. — Antwerp, "bassin du port, [...] à quatre cents mètres de la rive droite de l'Escaut, [...]" (Cuvier 1823: 353).

EMENDED DIAGNOSIS. — A species-level diagnosis seems difficult to obtain, because the only well known species of the genus is *Choneziphius planirostris*. Few differential characters are therefore available. This ziphiid species of moderate size is smaller than *Ziphius cavirostris*. It differs from *C. liops* in a more elongated, less pointed rostrum, with the lateral margins roughly parallel on most of its length. It differs from *C. macrops* in its smaller size and a rostrum relatively higher and narrower (see Table 2).

DISCUSSION

The rostrum from the Red Crag of Suffolk named *Ziphius planus* by Owen (1870: pl. 2, fig. 1) is referred to *Choneziphius planirostris*, as suggested by Abel (1905). This fragment has the large asymmetrical excavation of the premaxillary sac fossae and is similar to the specimens of Antwerp IRSNB ED001 and IRSNB 1719b.

An isolated periotic from Suffolk was placed by Lydekker (1887: pl. 2, fig. 7) in *C. planirostris*, but no ear bone-skull association is known for the genus, while several species of ziphiids are present in the Red Crag. This periotic is therefore placed in Ziphiidae *incertae sedis*.

DESCRIPTION (FIGS 16-19)

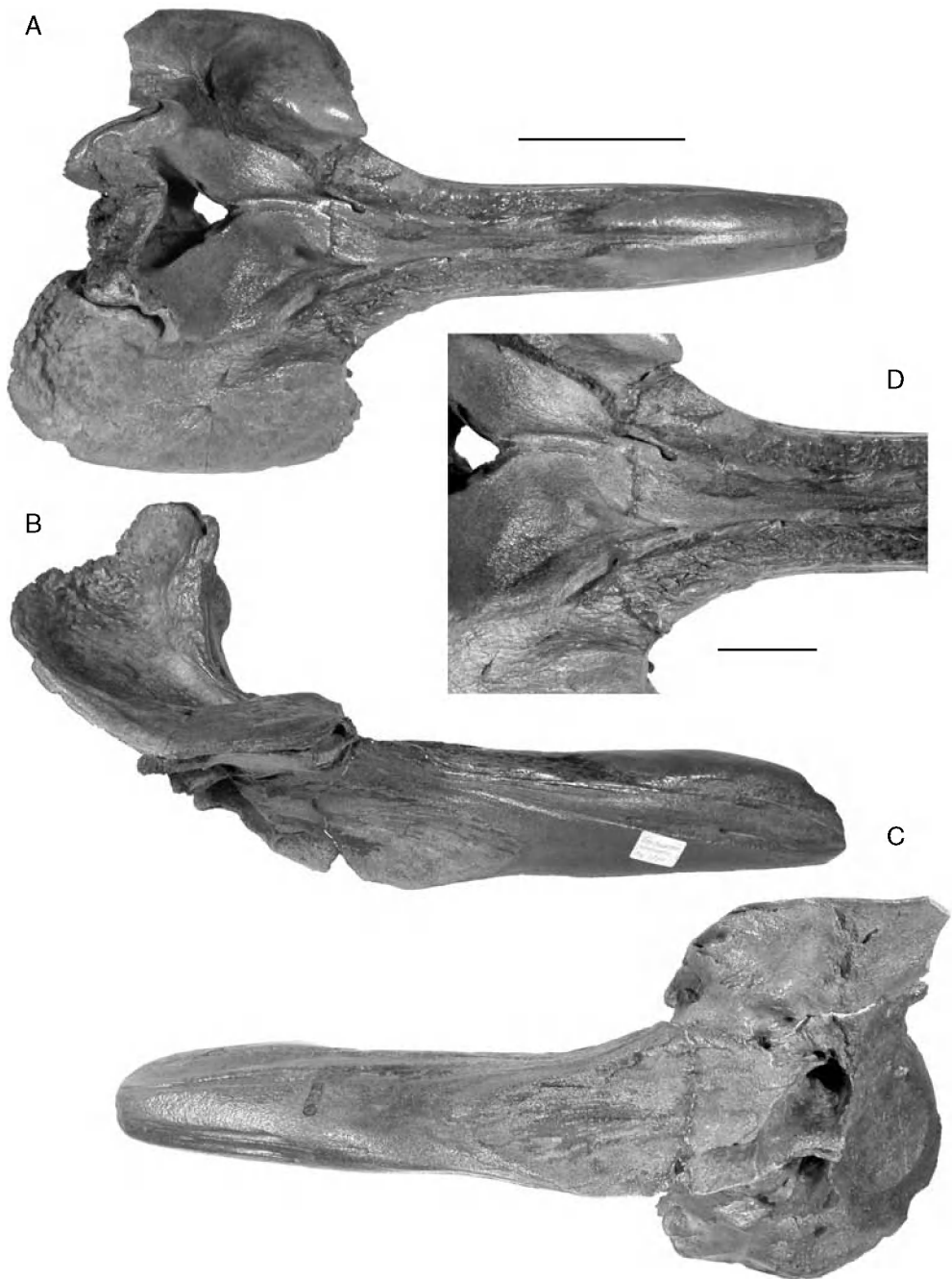This species is only known by anterior parts of skulls, usually including the complete dense

Fig. 16. — Skull of *Choneziphius planirostris* (Cuvier, 1823) (IRSNB 3774-M.1881); **A**, dorsal view; **B**, right lateral view; **C**, left ventro-lateral view; **D**, detail of the base of the rostrum in dorsal view. Scale bars: A-C, 100 mm; D, 50 mm.
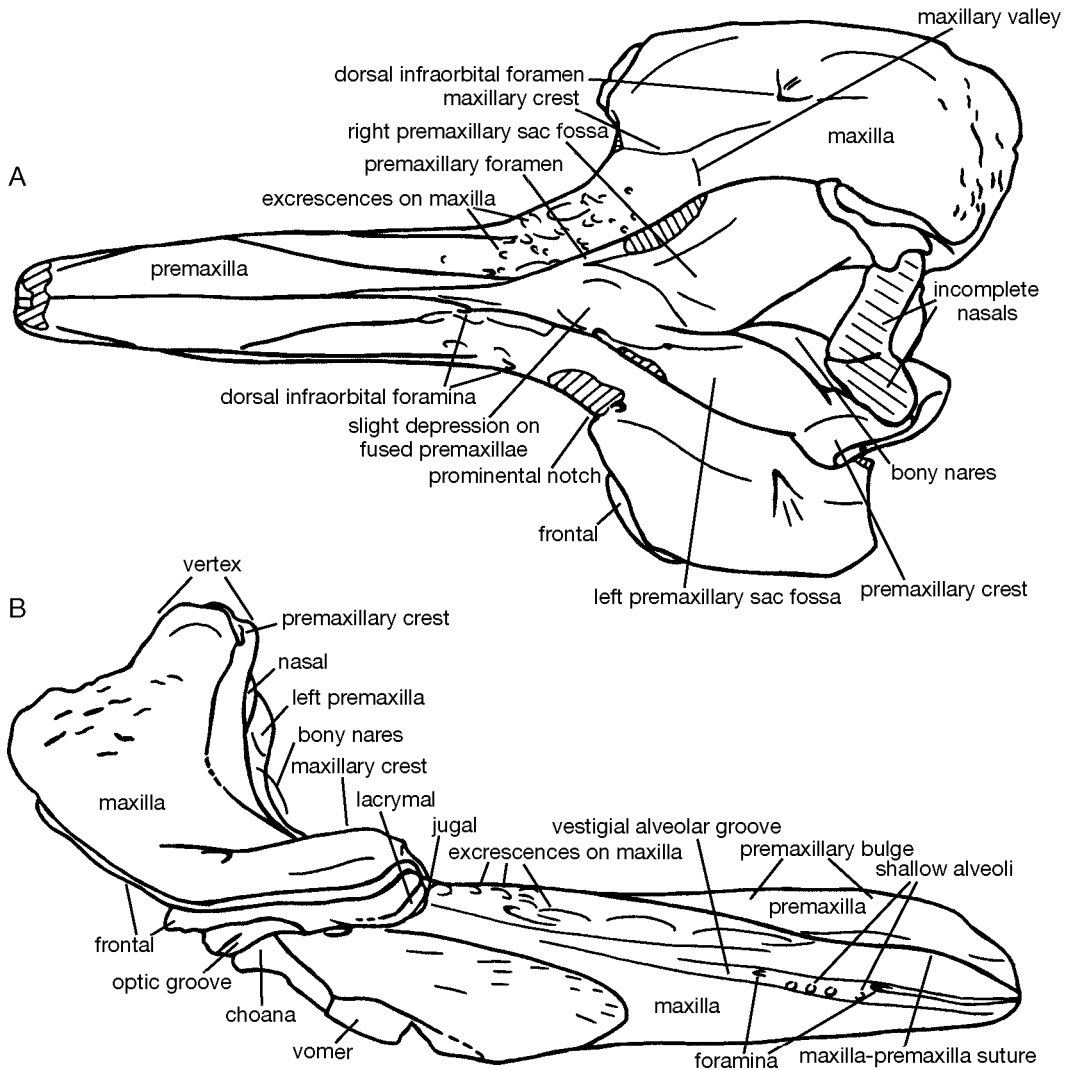
Fɪɢ. 17. — Line drawings of the skull of *Choneziphius planirostris* (Cuvier, 1823) (IRSNB 3774-M.1881); **A**, dorsal view; **B**, right lateral view.

rostrum and the anterior of the cranium, with the elevated vertex. No basicranial parts, teeth, mandibles or ear bones are known. Abel (1919: figs 575, 576) provided a reconstruction of the skull, including the unknown basicranium and pterygoids, probably inspired from the extant *Ziphius* morphology.

The rectilinear rostrum has a length ranging from 297 to 415 mm (Fig. 21) and is either roughly as

high as wide or slightly higher; the width of the cranium at the level of the postorbital processes ranges from 310 to 324 mm (only four skulls of the IRSNB measured) (see Table 2).

Premaxilla

The premaxillae occupy the dorsal face of the rostrum on the first third of its length. They are dense, dorsally thickened (pachy-osteosclerotic),

TABLE 2. — Measurements (in mm) on the main skulls of *Choneziphius planirostris* (Cuvier, 1823) and *C . macrops* (Leidy, 1876) (= IRSNB 3778-M.1884) from the Neogene of Antwerp. **e**, estimate; **+**, nearly complete; **–**, no data. See Figure 1 for the description of the measurements.

	Lectotype MNHN	IRSNB 3767	IRSNB 3768	IRSNB 3769	IRSNB 3773	IRSNB 3774-M.1881	IRSNB 3775-M.1883	IRSNB 3776	IRSNB 3777-M.1882	IRSNB 3778-M.1884	IRSNB 1719a	IRSNB 1719b	IRSNB 1719c	IRSNB ED001
1. length rostrum	+358	347	415	325	350	361	297	329	385	495	352	–	342	351
3. maximal anterior height rostrum	89	79	85	73	75	90	71	71	99	e80	83	–	68	80
4. maximal anterior width rostrum	83	68	87	65	75	76	60	71	e88	e113	72	78	72	77
7. width base rostrum level antorbital notches	195	–	187	–	180	–	–	–	197	–	–	–	–	192
8. width base rostrum level prominental notches	140	117	e134	99	136	e153	+100	–	151	e151	121	–	–	e132
9. width skull level postorbital processes	–	–	312	–	312	324	–	–	–	–	–	–	–	e310
10. width premaxillary sac fossae	e134	–	132	113	129	138	110	129	141	–	129	135	+120	121
11. width right premaxillary sac fossa	84	78	74	69	e84	83	70	78	82	e88	76	85	e69	64
12. width left premaxillary sac fossa	e45	+32	48	40	42	47	36	42	51	e56	49	45	e46	40
13. width bony nares	60	–	62	53	59	66	51	–	–	–	65	62	–	56
14. width nasals	64	–	69	–	76	86	+65	64	–	–	e69	78	–	–
15. width transverse premaxillary crests	–	–	137	–	+129	144	118	–	–	–	+127	137	–	–
16. minimal posterior distance between maxillae	58	–	90	–	–	67	68	–	–	–	e65	81	–	–

and medially fused, dorsally closing the mesorostral groove (Figs 16A; 17A). A reduced longitudinal tunnel is maintained, with a transverse diameter at apex of 10-11 mm. The rostral prominence of the premaxillae narrows posteriorly, and, at the two-thirds of the rostrum length, the closely joined premaxillae only occupy the median third of the rostrum width, as a slightly depressed surface between the maxillae. The longitudinal position of the highest point of the premaxillary prominence, usually close to the apex, is sometimes more posterior, for instance on IRSNB 3777-M.1882 or IRSNB 3773, with a variable width. The surface of this area is often worn (*post-mortem*). Nevertheless, on the left side of the rostrum IRSNB 3777-M.1882 at least five distinct laminae, roughly horizontal, demonstrate the growth process of this portion of the premaxilla (see Fig. 18A). A similar periodical laminar growth pattern is noticed on the vomer of the fossil *Mesoplodon longirostris* (pers. obs.) and the extant *M. carlhubbsi* (Heyning 1984). The laminae are not visible on the other skulls of *Choneziphius planirostris*, but the smallest rostrum of the collection, 118 mm shorter than the largest, has already well developed thickened premaxillae. This might indicate that the development of this thickening starts early in the life of the individual – even if the relative age of the different specimens is difficult to assert because of the usually strong osteosclerosis, closing the sutures.

The premaxillary sac fossae are characteristic: the right fossa is much wider than the left, with a ratio between the maximum widths ranging from 0.5 to 0.66 (Table 2; Fig. 25). The two fossae, strongly concave, are anteriorly hollowed by a deep canal, wider on the right fossa, leading to a large anteriorly directed foramen, at the level of the prominental notches (*sensu* Heyning 1989a, medial to the antorbital notches; = inner notches
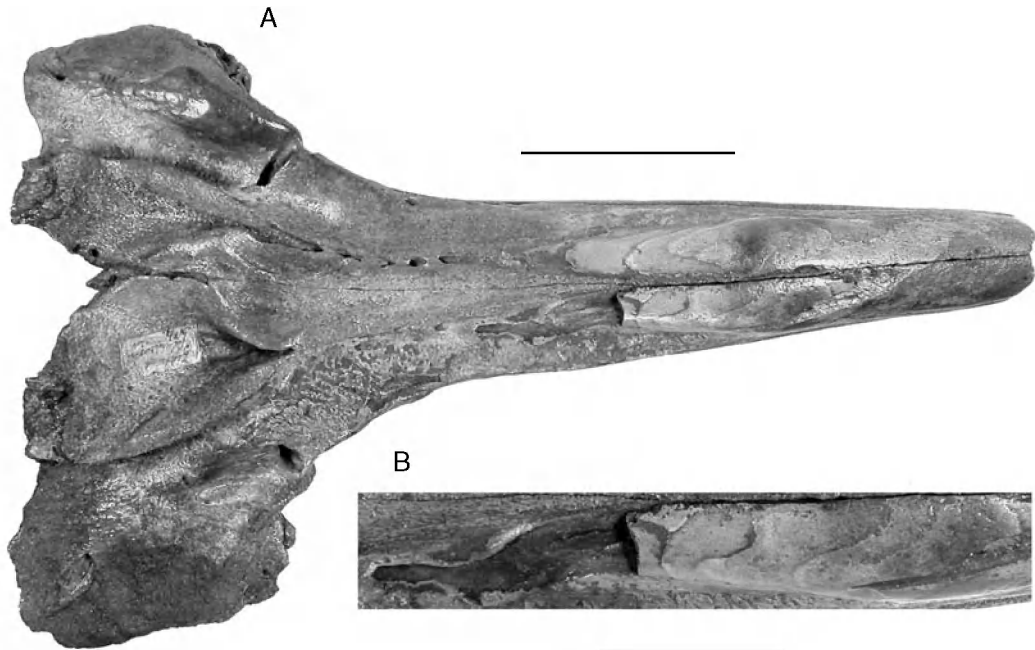
Fig. 18. — Rostrum and anterior part of the cranium of *Choneziphius planirostris* (Cuvier, 1823) (IRSNB 3777-M.1882); **A**, general dorsal view; **B**, detail of the laminar deposits on the dorsal surface of the rostrum (right side). Scale bars: A, 50 mm; B, 100 mm.

sensu Harmer 1924) (Figs 16D; 17A). The roofing of this foramen is variable: several rostra (e.g., IRSNB 3776) show a dorsally open sulcus for more than 70 mm anteriorly. The two deep premaxillary sac fossae are separated by a prominent asymmetrical platform of the joined premaxillae, posteriorly narrowing with a strong deviation towards the left side. This platform, sometimes narrow and acute can also be wider and lower, with a depressed anterior part, at the level of the prominental notches. This shallow median depression might be interpreted as equivalent to the prenarial basin of the adult males of *Ziphius*, essentially filled with the right nasal plug (Heyning 1989a). The dorsal elevation of the premaxilla to the vertex is strong from the premaxillary foramen towards the vertical transverse premaxillary crest. The crest is moderately thickened, rectilinear and anterolaterally directed (by twisting of the narrowest portion of the ascending process of the premaxilla). The dorsal portion of the anterior surface of the

left ascending process, much narrower than the right, shows a clear corner with the medioanterior surface of the bone. The anterior surface, corresponding in extant ziphiids to the support of the left posterior nasal sac (Heyning 1989a), is therefore reduced relatively to the right side, as in *Ziphius*. The bony nares are triangular and asymmetric, with a longer and more oblique right side of the triangle.

Maxilla
Posterolaterally to the rostral prominence of the premaxillae, the maxilla forms a roughly horizontal surface, sometimes laterally twisted on its anterior portion. A main characteristic of *Choneziphius planirostris* is the covering of that surface by series of dorsoanteriorly directed prominent excrescences and irregularities. However, this character is far from consistent within the species: these structures are sometimes completely absent as on the lectotype, reduced as on the skull IRSNB 3773, or much developed,

on both sides of the paralectotype (Cuvier 1823: pl. 27, fig. 7) for example. They can also be asymmetric, and in this case they are always better developed on the right side (e.g., only present on the right maxilla of IRSNB 3777-M.1882, Fig. 18A), and this asymmetry is more pronounced posteriorly, in front of the antorbital notches. No relation with the ontogeny could be found for this variability. In extant ziphiids, such as *Ziphius* and *Mesoplodon*, the dorsal surface of the maxilla on the rostrum corresponds to the main area of insertion for the rostral muscles, extending partially dorsally and medially onto the melon (see Heyning 1989a: fig. 8). The irregularities in *Choneziphius planirostris* might be linked to a more efficient fixation of the muscles on the surface. Furthermore, more developed excrescences on the right side of several skulls might well indicate more powerful muscles compared to the left. In extant odontocetes, the melon is usually set asymmetrically, slightly off to the right side; the fatty core of the melon extends posteriorly into the right nasal plug, more than into the left, and, in the adult males of *Ziphius* – the closest extant genus to *Choneziphius*, the right nasal plug is much enlarged (Heyning 1989a).

In lateral view, the rostral lateral suture between maxilla and premaxilla is visible along most of its path, reaching or closely approaching the apex of the rostrum, going distinctly downwards for the last centimetres. The alveolar groove is sometimes shallow, with weak marks of small alveoli still visible in several places and with anterior foramina opening forward into narrow grooves (e.g., IRSNB 3774-M.1881). On other specimens, the alveolar groove is closed at some levels and presents a deep narrow furrow at others (e.g., IRSNB 3773).

The ventral surface of the rostrum is strongly ossified, with poorly visible sutures. The vomer appears between the maxillae some centimetres anteriorly to the palatines and vanishes before the apex of the rostrum. Several pairs of foramina are present along the median sutures from the median margins of the palatines until the anterior surface of the rostrum, where a pair of longitudinal larger foramina is present, ventrolaterally to the anterior opening of the mesorostral tunnel.

The anterior margin of the supraorbital process is incised by two notches: the prominental notch and the more lateral and slightly posterior antorbital notch, often more distinct. Those two notches are separated by a maxillary tubercule (*sensu* Heyning 1989a). The latter is followed posteriorly by a high and wide longitudinal crest, sometimes present almost until the posterior border of the maxilla (e.g., IRSNB 3773), but generally quickly lowering and vanishing, before (or at the level of) the postorbital process. The left crest is slightly more developed than the right. When one of the supraorbital processes is lost by *postmortem* damage, this is always the left. The medial slope of the crest is much steeper than the lateral, forming the lateral wall of a deep and wide valley (Figs 16A; 17A). This maxillary valley, separating the crest from the premaxillary sac fossa, is partially roofed by the overhanging acute outer margin of the premaxilla. The anterior part of the valley is pierced by a medium-size foramen anterolaterally followed by a sulcus towards the prominental notch. A large posterior dorsal infraorbital foramen, sometimes coupled with a smaller, pierces the supraorbital process of the maxilla into or in the prolongation of the maxillary crest.

In lateral view, the roughly horizontal supraorbital process presents a thin maxillary plate, anteroventrally curving around the thicker frontal, and contacting the only partially fused jugal and lacrimal on the anterior margin. At the level of the preorbital process, the differentiated erosion of the bone due to the inclusion of more porous bone between osteosclerotic layers sometimes preserves upper and lower thin plates of the frontal separated by a deep excavation. The same structure is observed on the underlying lacrimal, giving this area a multi-folded pattern.

The frontals are always lost on the vertex, by *postmortem* damage. The contact between maxilla and premaxilla on the vertex is folded and pierced by a series of vertical foramina.

Nasal

The nine skulls of the IRSNB for which the vertex is partially preserved show an identical type of break for the nasals: those bones are only preserved
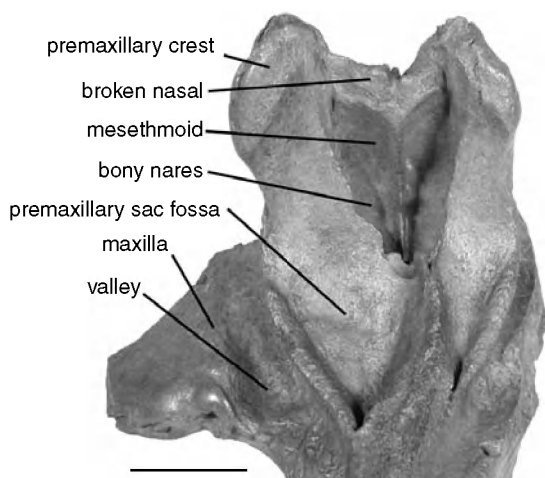
FIG. 19. — Detail of the premaxillary sac fossae and the vertex of *Choneziphius planirostris* (Cuvier, 1823) (IRSNB 3775-M.1883) in anterodorsal view. Scale bar: 50 mm.

for a short distance dorsally to the upper limit of the mesethmoid (Fig. 19). This common feature, contrasting with the usually completely preserved nasals of *Ziphirostrum marginatum*, implies a different morphology of the nasals. One possibility is that the dorsal part of the nasals was less dense in *Choneziphius*, and therefore more easily eroded. Another hypothesis, when comparing *Choneziphius* to *Ziphius*, is that the nasals of *Choneziphius* were dorsoanteriorly elongated, overhanging the external nares in a way similar to *Ziphius*. On such eroded skulls, such nasals are more likely to have been broken before burial than are the short nasals of *Ziphirostrum*, which are somewhat protected between the premaxillary crests. If this is the case, *Choneziphius* might also possess a cartilage filling the cleft between the premaxillary crest and the nasal, as in *Ziphius* (see Heyning 1989a: fig. 20). In *Ziphius*, the surface where the cartilage contacts the nasal and the premaxilla is rough, excavated by small grooves and pits. Even if on several individuals of *Choneziphius planirostris* the corresponding surface is also irregular (e.g., IRSNB 3774-M.1881), those irregularities could clearly be related to the structure seen in *Ziphius*; the premaxilla is usually too worn at that level to allow a description of the surface.

Mesethmoid
The sides of the sagittal keel of the mesethmoid are pierced at mid-height by one or two pairs of small olfactory foramina.

Palatine
The palatine is not always distinct; it reaches an anterior level at least 130 mm anterior to the antorbital notch. While the pterygoid is totally lost, the shape of the large anterior pterygoid sinus fossa can be seen, hollowing most of the surface of the palatine.
At the junction between the rostrum and the roof of the orbit, the infraorbital foramen is a shallow fossa pierced by a posterolateral foramen (= sphenopalatine foramen) and a slightly larger anteromedian foramen. A sulcus starts from the fossa towards the antorbital notch, and another leads to a vertical foramen emerging in the lateral wall of the choana.

COMMENTS ON THE SKULL IRSNB 3778-M.1884 REFERRED HERE TO *CHONEZIPHIUS MACROPS* (LEIDY, 1876)
The large and robust partial skull IRSNB 3778-M.1884 (Fig. 20), placed in *Choneziphius planirostris* by Abel (1905), has a rostrum more than 80 mm longer than the largest *C. planirostris* of the IRSNB (Fig. 21). Moreover, this specimen differs from members of *C. planirostris* by the following characters: the much flatter and wider rostrum, especially at its base with more acute laterodorsal edges; the more pronounced median separation between the premaxillary sac fossae; the relatively lower anterior thickening of the premaxillae; and the median margins of the premaxillae separated on the apical 80 mm. The *Choneziphius* characters of this specimen are: the excavation of the premaxillary sac fossa anteriorly extended by a partially roofed sulcus; the irregular subhorizontal dorsal surface of the maxilla on the proximal part of the rostrum; and the anterior thickening of the premaxilla, dorsally roofing the mesorostral groove. This rostrum shows interesting similarities with the holotype of *Proroziphius macrops* sensu Leidy, 1876 (figured in Leidy 1877: pl. 32, figs 1, 2), from the Phosphate Beds

Fig. 20. — Rostrum and premaxillary sac fossae of *Choneziphius macrops* (Leidy, 1876) (IRSNB 3778-M.1884); **A**, dorsal view; **B**, left lateral view. Scale bar: 100 mm.

of South Carolina. Those two specimens (holo-type of *P. macrops* and IRSNB 3778-M.1884) exhibit roughly the same kind of preservation and their proportions are more similar to each other than to *Choneziphius planirostris*. A comparison of the measurements provided by Leidy (1877) for the holotype of *Proroziphius macrops* (trans-formed from inches to millimetres) with IRSNB 3778-M.1884 is given here (Table 3). The rostrum of IRSNB 3778-M.1884 is somewhat flatter at every level but this difference is not suf-ficient to separate the two skulls; both of them are therefore included in a same species of the genus *Choneziphius*, *C. macrops* (Leidy, 1876). That species differs from *C. planirostris* by the larger size of the relatively wider and flatter ros-trum.

The second specimen of *Choneziphius planirostris* described by Cuvier (1823: pl. 27, figs 7, 8) is also larger, with a rostrum longer than 400 mm. The rostrum is somewhat wider and flatter than on the other specimens, with the subhorizontal irregular surfaces of the maxillae roughly covering three quarters of the length of the rostrum, and a narrower median elevation of the premaxillae. However, this skull shares the morphology of the premaxillary sac fossae of the species *C. pla-nirostris* (even if the right plate is deep and wide) and is maintained in that species. This might give an ontogenetic direction to the intraspecific vari-ation of several features, for instance the anterior spreading of the subhorizontal irregular surface of the maxilla and the excavation of the right pre-maxillary sac fossa. This argument is however not so clear among smaller individuals.

Genus *Beneziphius* n. gen.

TYPE AND ONLY SPECIES. — *Beneziphius brevirostris* n. sp.

ETYMOLOGY. — From "*Bene*" in honour of the Belgian naturalist Pierre-Joseph Van Beneden (1809-1894), whose work at the Catholic University of Louvain lead to major advances in the knowledge of the anatomy of extant and fossil cetaceans; and "*ziphius*": name of the type genus of the family Ziphiidae.

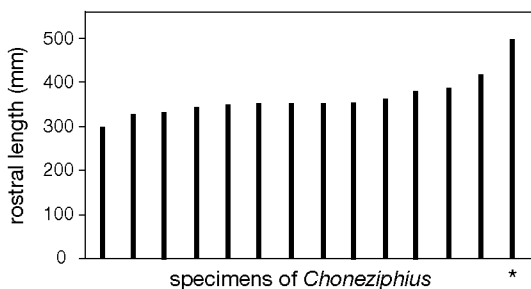DIAGNOSIS. — The same as for the only species *B. bre-virostris* n. sp.

FIG. 21. — Total length of the rostrum (in mm) for specimens of *Choneziphius* from MNHN and IRSNB. All the specimens belong to *C. planirostris* (Cuvier, 1823) except the one marked by *, which is referred to *C. macrops* (Leidy, 1876).

TABLE 3. — Measurements (in mm) on the holotype of *Choneziphius macrops* (Leidy, 1876) from the Ashley Phosphate Beds, South Carolina, USA, and *C. macrops* from the Neogene of Antwerp (IRSNB 3778-M.1884). The measurements of the holotype are taken from Leidy (1877: 229, transformed from inches to millimetres). +, not complete.

	holotype	IRSNB 3778-M.1884
1. width rostrum 1/2 length	106	107
2. height rostrum 1/2 length	86	75
3. width rostrum ant. 1/4 length	79	76
4. height rostrum ant. 1/4 length	76	67
5. width rostrum 3/4 length	108	117
6. height rostrum 3/4 length	89	+76

Beneziphius brevirostris n. sp.

HOLOTYPE. — IRSNB ED002-M.1885, a partial skull including the anterior part of the vertex, the anterior of the cranium, and the rostrum.

ETYMOLOGY. — "*brevi*" from Latin brevis: short, "*rostris*" from Latin rostrum: bill, beak. "*brevirostris*" because of the short and pointed rostrum characterizing this new species.

REFERRED SPECIMEN. — IRSNB 3782-M.1886, a partial skull including the anterior of the cranium and the nearly complete rostrum (syntype of *Ziphiopsis phymatodes* du Bus, 1868, and referred to *Choneziphius planirostris* by Abel [1905]).

TYPE HORIZON. — No data available, Neogene. Judging from the worn aspect of the holotype, it might have been reworked and found in a base gravel (for example the gravel at the base of the Kattendijk Formation, lower Pliocene). The referred specimen IRSNB 3782-M.1886 was found close to the first specimen of *Ziphiopsis phymatodes* sensu du Bus, 1868, IRSNB 3781-M.543, probably in the same stratigraphic unit (du Bus 1868).

TYPE LOCALITY. — Antwerp area, Belgium, exact locality uncertain.

DIAGNOSIS. — Small ziphiid species with a skull smaller than *Ziphirostrum marginatum* or *Choneziphius planirostris*, differing from:
– *Choneziphius* in: a more pointed rostrum in lateral and dorsal views; a distinct prenarial basin; a flat surface of the premaxillary sac fossae; a space between the less asymmetrical premaxillary sac fossae (ratio between maximum widths of left and right premaxillae at the level of the fossae of 0.69 on the holotype, Fig. 25); the less abrupt elevation of the premaxillae towards the vertex, not reaching a vertical position; less anteriorly directed transverse premaxillary crests;

– *Ziphirostrum* and *Messapicetus* in: a shorter and more pointed rostrum; the premaxillae shorter than the maxillae on the apex of the rostrum; joined thickened premaxillae anteriorly limiting the prenarial basin; the subhorizontal surface of the maxilla lateral to the prenarial basin covered by small excrescences;
– *Aporotus* in: fusion of the premaxillae above the mesorostral groove; flat maxilla medially to the antorbital notch;
– all the other known ziphiids in the dorsal roofing of the mesorostral groove by the premaxillae.

DESCRIPTION (FIGS 22-24)
The fragmentary skulls both lack the supraorbital processes and the basicranium. The length of the rostrum is estimated at 295 mm for the holotype IRSNB ED002-M.1885, close to the smallest individual of *Choneziphius planirostris*, and much shorter than in *Ziphirostrum marginatum*. The second rostrum IRSNB 3782-M.1886 was probably slightly shorter than the holotype. By comparing the width of the rostrum at its base, IRSNB 3782-M.1886 is smaller than *Z. marginatum* (Table 4).

Premaxillae
The pachy-osteosclerotic premaxillae dorsally close the mesorostral groove until 60 mm before the preserved apex of the rostrum on the holotype (Fig. 22). The joined premaxillae are spindle-shaped, with a median maximum width, and strong forwards and backwards tapering. Between the flattened maxillae, the premaxillae
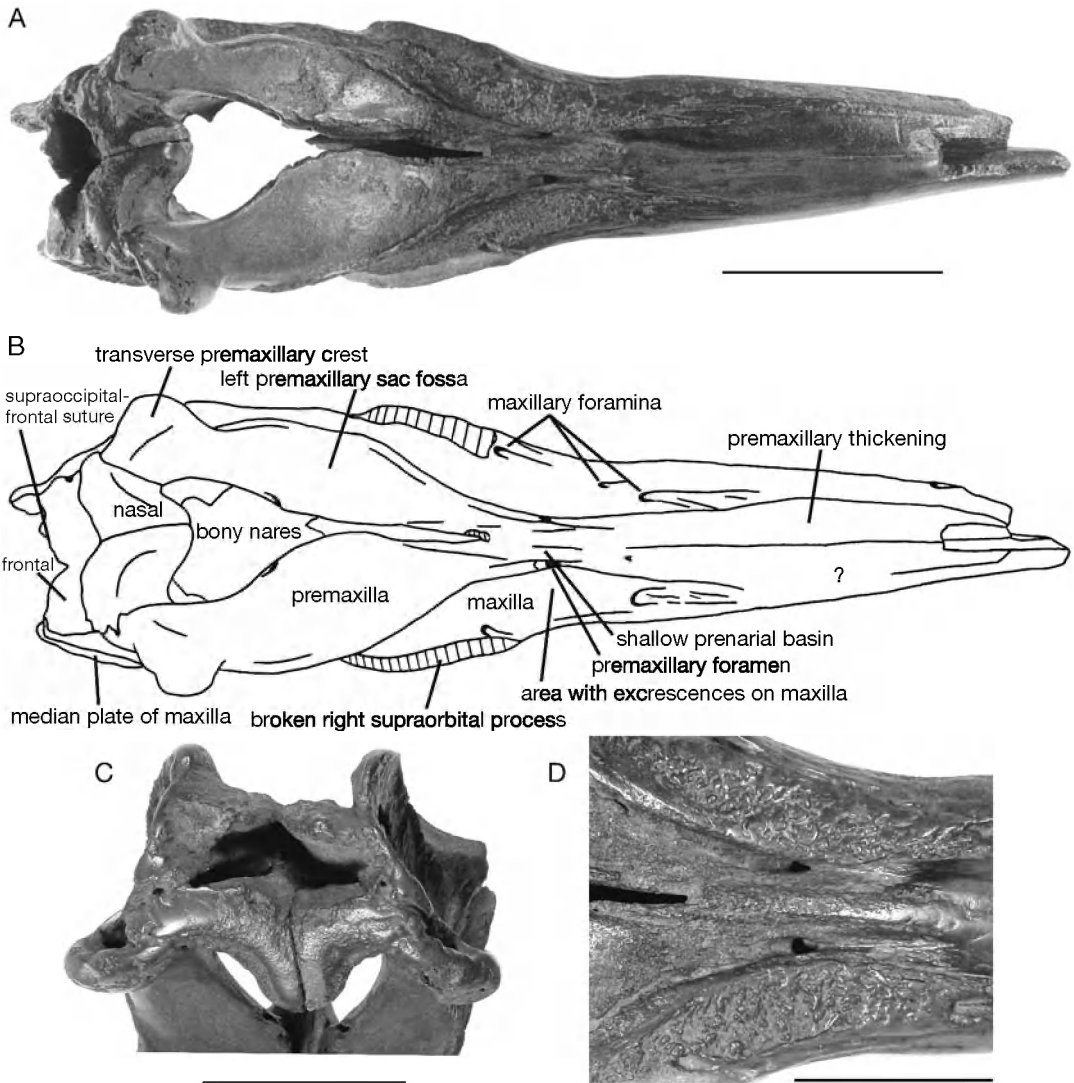
FIG. 22. — Skull of *Beneziphius brevirostris* n. gen., n. sp. (IRSNB ED002-M.1885, holotype); **A**, dorsal view; **B**, line drawing of the dorsal view; **C**, detail of the vertex in dorsal view; **D**, detail of the prenarial basin in dorsal view. Scale bars: A, 100 mm; C, D, 50 mm.

are distinctly depressed, as a fossa pierced by a pair of premaxillary foramina. This area is homologous to the prenarial basin present in *Ziphirostrum marginatum*, but less excavated, with a convex floor only 7-8 mm deep.

In lateral view, the rostrum slopes steeply from 20 mm anterior to the palatine to the apex, with a short dorsal elevation of the premaxillae in front of the prenarial basin (Fig. 23).

The premaxillary sac fossae are not excavated, in contrast to *Choneziphius planirostris* and as in *Ziphirostrum* sp. The right fossa is wider than the left (respective maximum widths of the premaxillae at that level are 56 and 39 mm on the holotype), and there is no median contact between their rounded median margins, similarly to *Z. marginatum*, with a space between them of 5 mm for the holotype. The ascending process of

TABLE 4. — Measurements (in mm) on the two skulls of *Beneziphius brevirostris* n. gen., n. sp. from the Neogene of Antwerp. **e**, estimate; **–**, no data. See Figure 1 for the description of the measurements.

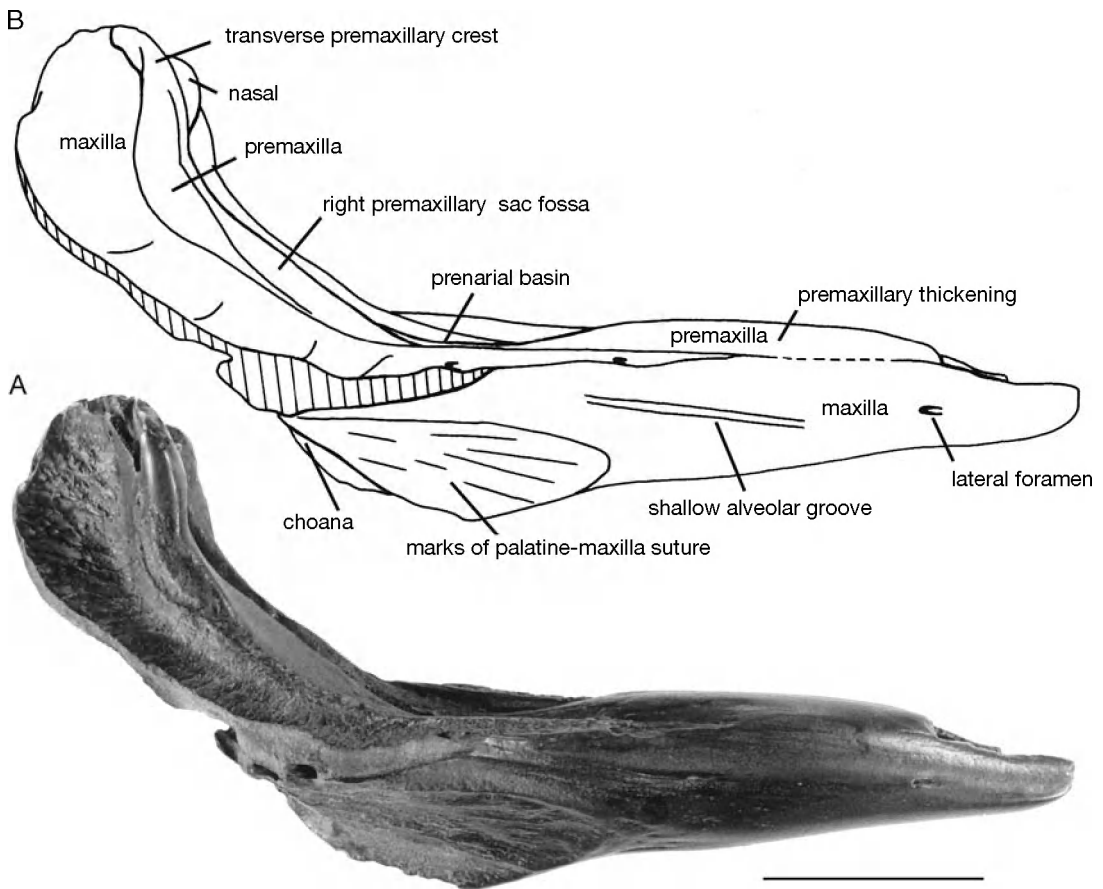|		IRSNB ED002-M.1885	IRSNB 3782-M.1886
2.	length maxilla on rostrum	e295	–
3.	maximal anterior height rostrum	71	66
4.	maximal anterior width rostrum	74	74
5.	maximal width premaxillae on rostrum	e40	43
6.	minimal distance between maxillae at prenarial basin	24	21
7.	width base rostrum	–	e140
10.	width premaxillary sac fossae	111	–
11.	width right premaxillary sac fossae	56	–
12.	width left premaxillary sac fossae	39	38
13.	width bony nares	53	–
14.	width nasals	71	–
15.	width transverse premaxillary crests	122	–
16.	minimal posterior distance between maxillae	57	–

FIG. 23. — **A**, skull of *Beneziphius brevirostris* n. gen., n. sp. (IRSNB ED002-M.1885, holotype) in right lateral view; **B**, line drawing. Scale bar: **A**, 100 mm.

Fig. 24. — Rostrum and premaxillary sac fossae of *Beneziphius brevirostris* n. gen., n. sp. (IRSNB 3782-M.1886) in dorsal view. Scale bar: 100 mm.

the premaxilla is nearly vertical, less elevated than in *Choneziphius planirostris*. The transverse premaxillary crest is closer to *Ziphirostrum marginatum*, more laterally directed than in *Choneziphius planirostris* or *Ziphius* (Fig. 22C).

Maxillae
The extremity of the rostrum is likely formed solely by the maxillae, with shorter premaxillae and a mesorostral groove dorsally open at its apex. However, the bone is too dense, worn, and incomplete to be certain of structure. The progressive posterior widening of the maxilla, with the development of excrescences on its horizontal surface, is comparable to the condition in *Choneziphius planirostris*, although the bone is relatively shorter. This surface of the maxilla bearing excrescences is anteriorly preceded by a foramen followed by a series of sulci forwards. A second foramen pierces the lateral margin of the surface at the level of the apex of the premaxillary sac fossa. The maxilla is excavated laterally to the premaxillary sac fossa; this excavation, not as deep as in *Choneziphius planirostris*, is slightly overhung by the premaxilla medially. The transverse compression of the vertical medial plates of the maxillae behind the vertex is pronounced, and the now-lost frontals were narrower than the nasals.
In lateral view, the alveolar groove is shallow with weakly marked alveoli on less than 100 mm.

These rounded excavations (less than 1-2 mm deep) have an approximate diameter of 3 mm and interalveolar septa of 2 mm. Fourteen alveoli are counted on the left side of the holotype. A posteriorly directed foramen pierces the maxilla just above the alveolar groove, at the same level in the two skulls, 72 mm before the preserved apex of the rostrum on the right side of the holotype.

Nasal
The nasals form an anteromedian rounded projection overhanging the bony nares, only differing from *Ziphirostrum marginatum* in more concave anterolateral margins, resembling the condition of *Aporotus recurvirostris* (see below). The suture between nasals and frontals slightly projects anteromedially.

Vomer-palatine
The features of the palate and the ventral face of the rostrum are similar to *Choneziphius planirostris* and *Ziphirostrum marginatum*: large palatines and pairs of foramina along the median maxillary suture. The vomer is ventrally visible between the maxillae for 100 mm, until 30 mm before the apex of the rostrum.

SYSTEMATIC DISCUSSION
The referred specimen IRSNB 3782-M.1886 was attributed by du Bus (1868) to the species *Ziphiopsis phymatodes* (second individual),
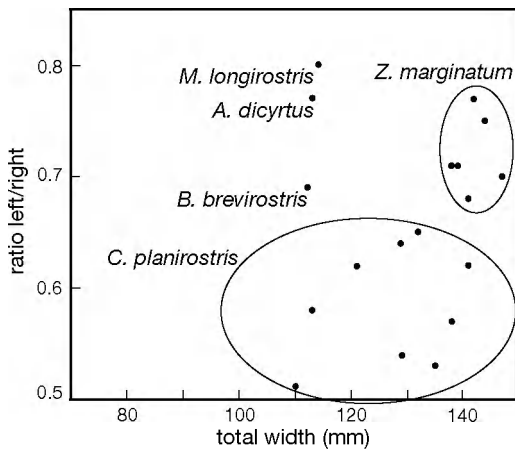
FIG. 25. — Diagram giving the ratio between maximum widths of left and right premaxillae at the level of the premaxillary sac fossae against the total width of the two premaxillae at that level (in mm), for specimens of fossil ziphiid taxa from the area of Antwerp: *Aporotus dicyrtus* du Bus, 1868, *Choneziphius planirostris* (Cuvier, 1823), *Mesoplodon longirostris* (Cuvier, 1823), *Beneziphius brevirostris* n. gen., n. sp., and *Ziphirostrum marginatum* du Bus, 1868.

together with the skull IRSNB 3781-M.543 (see discussion below), and by Abel (1905) to *Choneziphius planirostris*, probably because of the presence of moderately developed excrescences on the platform of the maxillae at the base of the rostrum. Those irregularities on the maxillae were shown above as highly variable in *C. planirostris*. Other similarities of *Beneziphius brevirostris* n. gen., n. sp. with that species are: dense, dorsally fused premaxillae, forming a prominence anteromedially to the platform of the maxillae; and excavation of the maxillae along the lateral margins of the premaxillary sac fossae. However, several putative derived characters of *Choneziphius planirostris* are absent in *Beneziphius brevirostris* n. gen., n. sp.: the premaxillary sac fossae are unexcavated, less asymmetrical (see Fig. 25) and medially separated; the premaxillary crests are more laterally directed and, in lateral view, the rostrum quickly narrows anteriorly, a feature different from the roughly parallel dorsal and ventral margins of the rostrum on most of its length in *C. planirostris*. Furthermore, the nasals of *Beneziphius brevirostris* n. gen., n. sp. are preserved in a way different from the dorsally broken

nasals of *Choneziphius planirostris*. Perhaps, as above, the nasals in *C. planirostris* were antero-dorsally elongated as in *Ziphius cavirostris*. If this hypothesis is correct, the morphology of the nasals of *Beneziphius brevirostris* n. gen., n. sp. might also be considered as primitive.

These differences with *Choneziphius planirostris* are also observed in *Ziphirostrum marginatum*. Another common character between *Z. marginatum* and *Beneziphius brevirostris* n. gen., n. sp. is the presence of a prenarial basin: it is shallower in *B. brevirostris* n. gen., n. sp., but likely homologous. Indeed, the basin is formed in both taxa by the deepening of the joined posteromedial and posterolateral sulci, and it is laterally margined by thick and wide posterolaterally curving strips of the maxillae. This condition is different from the completely filled space between the maxillae in *Choneziphius planirostris* (infilled by the premaxillae) and might be used as a synapomorphy of *Ziphirostrum marginatum* and *Beneziphius brevirostris* n. gen., n. sp. However, it is also possible that the prenarial basin was secondarily lost in *C. planirostris*.

REVISION OF *ZIPHIOPSIS PHYMATODES* DU BUS, 1868
The specimen IRSNB 3781-M.543, a partial rostrum with the left premaxillary sac fossa (Fig. 26), syntype of *Ziphiopsis phymatodes* by du Bus (1868, first of two individuals), and figured by Van Beneden & Gervais (1880: pl. 27bis, fig. 1, reversed), was referred to *Choneziphius planirostris* by Abel (1905), here again probably because of the presence of high excrescences on the dorsal surface of the maxillae at the base of the rostrum. As discussed above, the second individual of *Ziphiopsis phymatodes* sensu du Bus, 1868, IRSNB 3782-M.1886, is referred to a new genus and species, *Beneziphius brevirostris* n. gen., n. sp. du Bus (1868) already noticed several differences at the level of the premaxillae, the excrescences on the maxillae and the size between these two specimens. Indeed, the thickened premaxillae are narrower on the rostrum of IRSNB 3781-M.543, and the premaxillae diverge for more than 40 mm before the deeper prenarial basin.
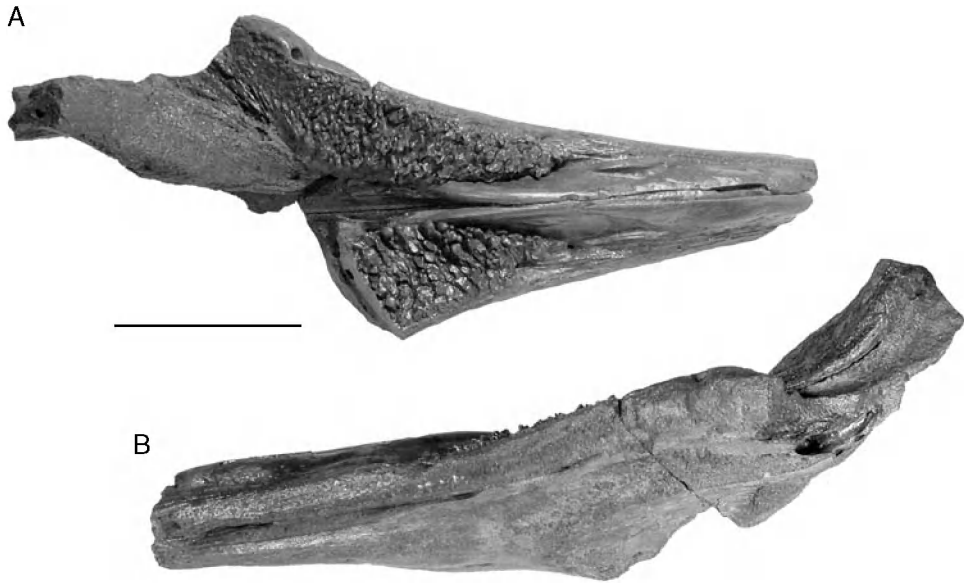
Fig. 26. — Rostrum and left premaxillary sac fossa (IRSNB 3781-M.543), Ziphiidae *incertae sedis* (*Ziphiopsis phymatodes* sensu du Bus, 1868); **A**, dorsal view; **B**, left lateral view. Scale bar: 100 mm.

The excrescences on the maxilla are much developed (some of them are longer than 8 mm, see Fig. 26A) and occupy a much wider medially sloping maxillary surface. IRSNB 3781-M.543 is also larger than IRSNB 3782-M.1886. Even if the size of the excrescences was demonstrated to be variable in *Choneziphius planirostris*, and in spite of the similar kind of abrupt anterior narrowing of the rostrum, this list of differences indicates that IRSNB 3781-M.543 is not referable to *Beneziphius brevirostris* n. gen., n. sp. Conversely, this skull lacks important apomorphies of *Choneziphius*: the mesorostral groove is still posteriorly open; the premaxillary sac fossae are unexcavated and probably separated; in lateral view, the rostrum is more quickly anteriorly lowering.

The morphology of the maxillae and the premaxillae around the prenarial basin is comparable to the condition in *Ziphirostrum turniense*, specially the holotype IRSNB 3785-M.539. The rostrum of *Z. turniense* is however much longer (550 mm for IRSNB 3785-M.539, and more or less 400 mm for IRSNB 3781-M.543) and less pointed.

The specimen IRSNB 3781-M.543, identified here as the holotype of *Ziphiopsis phymatodes* du Bus, 1868, lacks sufficient features to diagnose the species, which is thus a *nomen dubium*. The holotype is therefore classified Ziphiidae *incertae sedis*. Similarities with *Ziphirostrum turniense* and *Beneziphius brevirostris* n. gen., n. sp. were demonstrated, but the absence of information about the vertex precludes a better systematic resolution.

Therefore, if considered separately, the character "presence of excrescences on the dorsal face of the maxillae at the base of the rostrum" appears to be poorly diagnostic at the species level, being present in three different taxa and highly variable in *Choneziphius planirostris* – even bilaterally on one specimen.

REVISION OF *ZIPHIOPSIS SERVATUS* DU BUS, 1868
The rostrum IRSNB 3806-M.540, holotype and only specimen of the species *Ziphiopsis servatus* sensu du Bus, 1868, was figured by Van Beneden & Gervais (1880: pl. 27bis, fig. 8), and later referred by Abel (1905) to *Mioziphius belgicus*.

This incomplete rostrum is 450 mm long, but some centimetres are probably missing posteriorly (Fig. 27D-F). At the base of the rostrum, the lateral margin of the dorsal surface is elevated relatively to a shallow longitudinal depression, mainly marking the premaxilla. This concave area is medially followed by a slope towards a median elevation of the premaxillae, partly missing on the specimen but originally closing the mesorostral groove. Therefore, no prenarial basin could be present. Anteriorly, the margins of the broken area diverge, reaching a maximum width of 48 mm 270 mm before the apex. This morphology is probably related to a median crest of the joined premaxillae, which, because of its prominence, could have been easily broken.

Such a structure is observed on a large and robust rostrum found recently in Antwerp (no precise locality), NMB 002 (Fig. 27A-C). This specimen (preserved length 700 mm), includes most of the rostrum and the anterior portion of the cranium. The anterior 290 mm of the rostrum are marked by a high longitudinal median premaxillary crest, narrowing and slightly increasing in height posteriorly. The maximum height of the rostrum is near the posterior limit of the crest (120 mm high and 80 mm wide). The posterior margin of the crest is abrupt, posteriorly extended by a lower and narrower crest, nearly reaching the premaxillary sac fossae. This lower crest is margined by a shallow longitudinal depression on the premaxilla, laterally limited by a low elevation of the maxilla, similar to IRSNB 3806-M.540. This allows one to interpret the dorsal break of the premaxillae in IRSNB 3806-M.540 as the base of a lost median crest probably resembling the condition of NMB 002. The only difference between the two specimens which might be significant at a specific level is the shorter and more pointed rostrum in IRSNB 3806-M.540. However, IRSNB 3806-M.540 is too fragmentary to allow more precise taxonomic determination.

The anterior part of the cranium of NMB 002 shows interesting features, never previously observed in Belgian specimens: the closely appressed and deeply excavated premaxillary sac fossae are strongly asymmetric, with a much wider right premaxillary sac fossa nearly occupying the same surface on the left side of the median plane of the skull as on the right (Fig. 27B, C). The fossae are anteriorly limited by a high elevation of the bone, in continuity with their lateral ridge. The right fossa is pierced in its anteromedian portion by three foramina; in that area, the surface is marked by irregular depressions.

Anterolaterally to the premaxillary sac fossa, the right maxilla supports a crest-like elevation, longitudinally elongated and medially overhanging the depressed suture between maxilla and premaxilla. This medially directed maxillary crest, with a maximum height of 20 mm roughly at the level of the unpreserved antorbital notch, is reminiscent, although smaller, of the crest in several platanistoids, in particular *Zarhachis*. The depressed surface between this crest and the premaxillary sac fossa is pierced by a large dorsal infraorbital foramen (diameter of 12 mm); this foramen sends several posterolateral, lateral and anterior sulci. A second smaller foramen (5 mm), piercing the maxilla posterolaterally to the crest, also sends posterior and anterolateral sulci, and five additional tiny foramina are present on the lateral flank of the crest, coupled with short anteriorly directed sulci. Posteriorly to the crest, the surface of the maxilla is posterolaterally sloping, and is not overhung by the lateral margin of the premaxillary sac fossa.

The morphology of the strongly asymmetric premaxillary sac fossae, anteriorly enclosed, shows similarities with *Tusciziphius* Bianucci, 1997, from the Italian Pliocene, but no rostrum is known for that genus. More striking similarities are shared with *Eboroziphius coelops* Leidy, 1876, from the Phosphate Beds of South Carolina (figured by Leidy 1877: pls 30, 31), again at the level of the premaxillary sac fossae, but also on the rostrum: the dorsal face of the rostrum of the holotype of *E. coelops* is marked by a median broken area separating two low depressions, as in IRSNB 3806-M.540 and probably related to a median longitudinal premaxillary crest. Furthermore, the maxilla of the holotype of *E. coelops* is elevated anterolaterally to the premaxillary sac fossa. The maxillary crest is poorly preserved, but it could be
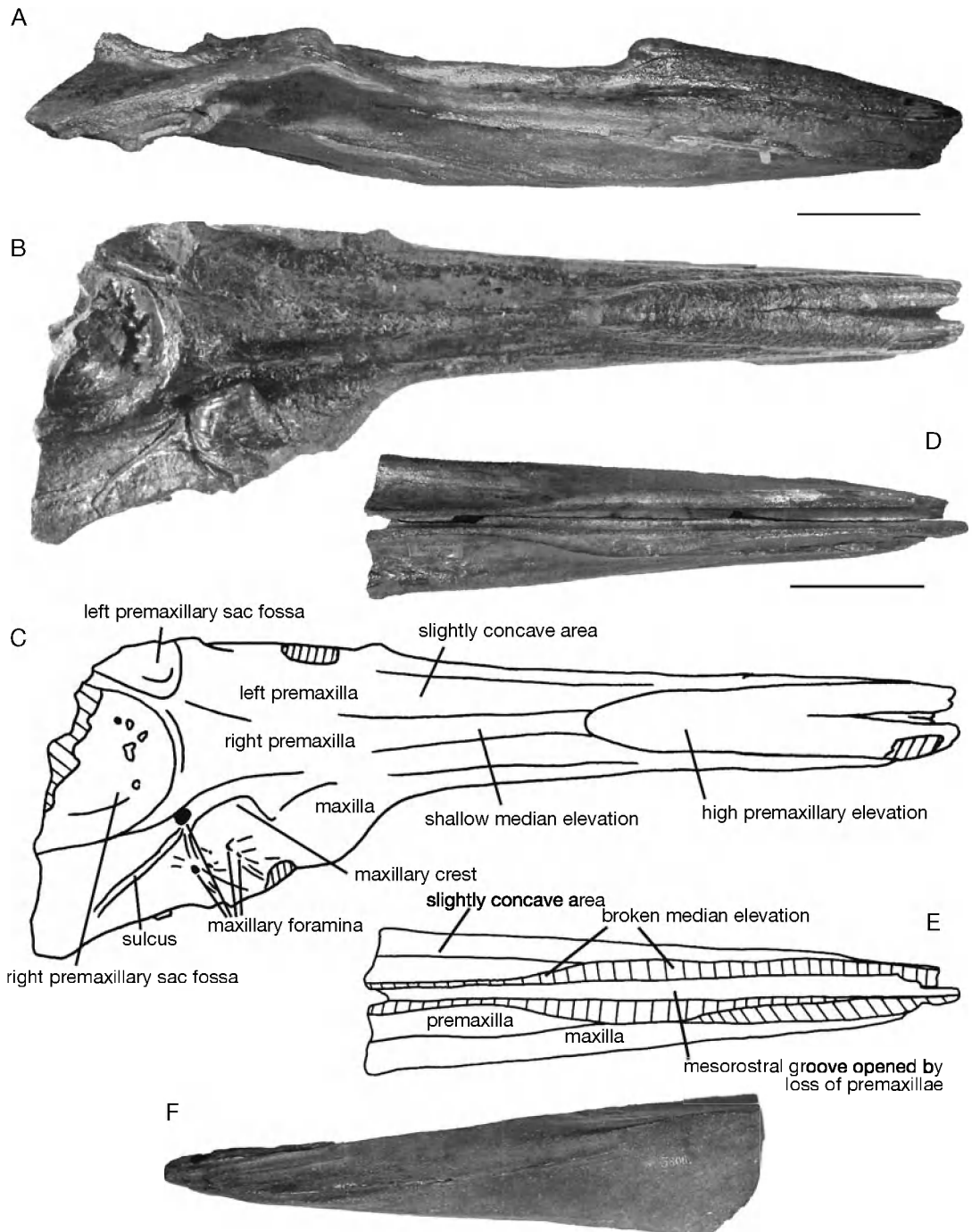
FIG. 27. — **A-C**, rostrum and right supraorbital process referred to Ziphiidae aff. *Eboroziphius* (NMB 002); **A**, dorsal view; **B**, right lateral view; **C**, line drawing of the dorsal view; **D-F**, rostrum referred to Ziphiidae aff. *Eboroziphius* (*Ziphiopsis servatus* sensu du Bus, 1868) (IRSNB 3806-M.540). The median portion of the premaxillary elevation and the premaxillary crest, present on NMB 002, are broken on this specimen; **D**, dorsal view; **E**, line drawing of the dorsal view; **F**, left lateral view. Scale bars: A, B, D, F, 100 mm.

Fig. 28. — *Pelycorhamphus pertortus* Cope, 1895, right premaxillary sac fossa and base of the rostrum (USNM 13796, holotype), from the Miocene of the Chesapeake Group (east coast of the USA), dorsal view. Scale bar: 100 mm.

more dorsally and anteriorly developed than in NMB 002. A large foramen is also present between this elevation and the premaxillary sac fossa. This brief comparison between fragmentary specimens is not enough detailed to discriminate inter- and intraspecific differences. *E. coelops* was referred to Ziphiidae *incertae sedis* by Fordyce & Muizon (2001), because of a non-diagnostic holotype. NMB 002 is only slightly more complete, and is considered here, together with IRSNB 3806-M.540, as Ziphiidae aff. *Eboroziphius*. The interest of NMB 002 is then more anatomical than taxonomic: the elevated premaxillary crest on the anterior part of the rostrum tentatively explains the break observed in the holotype of *E. coelops* and in IRSNB 3806-M.540; it represents an alternative way for a fossil ziphiid to increase the mass of the apical part of its rostrum.

The extreme asymmetry of the premaxillary sac fossae and the abrupt anterior wall of the right fossa, characteristic of NMB 002, are present in USNM 13796, the holotype of *Pelycorhamphus pertortus* Cope, 1895 (exact locality unknown, Miocene of the Chesapeake Group). The fossil includes the right premaxillary sac fossa and a short portion of the right premaxilla on the rostrum (Fig. 28). The wide and deeply excavated premaxillary sac fossa is similar to NMB 002, and although the premaxilla is more elevated anterior to the fossa, the two specimens are probably related. The fragment of skull USNM 360081 (location uncertain, North or South Carolina, ?Pliocene), with a label *Choneziphius trachops* cf., is nearly identical to the holotype of *Pelycorhamphus pertortus*.

Genus *Aporotus* du Bus, 1868

Mioziphius Abel, 1905: 98, *partim.*

TYPE SPECIES. — *Aporotus recurvirostris* du Bus, 1868 by subsequent designation.

OTHER INCLUDED SPECIES. — *Aporotus dicyrtus* du Bus, 1868. The specimens of the species *A. affinis* sensu du Bus, 1868 (including IRSNB 3819, referred to *Mioziphius belgicus* by Abel 1905), were not found in the collection. They consist in rostral fragments of maxillae and premaxillae, and their brief description by du Bus (1868) places them comparable to *Aporotus recurvirostris*.

EMENDED DIAGNOSIS. — Fossil ziphiid differing from *Ziphirostrum*, *Messapicetus*, *Choneziphius*, and *Beneziphius* n. gen. in the unfused elevated premaxillae covering the mesorostral groove. It further differs from:
– *Ziphirostrum* and *Messapicetus* in: longer and higher longitudinal maxillary crest on the preorbital process; a longitudinal wide valley between this maxillary crest and the more elevated premaxilla on the rostrum;
– *Choneziphius* in: excavation of a prenarial basin at the base of the rostrum; flat surface of the premaxillary sac fossae;
– *Tusciziphius* in: flat surface of the premaxillary sac fossae; thinner transverse premaxillary crests;
– all the other known ziphiid genera by the dorsal roofing of the mesorostral groove by the thickened premaxillae.

Because of the scarcity and incompleteness of the specimens referred to it, the genus *Aporotus* is poorly defined and the polarity of its characters is difficult to establish (see phylogenetic discussion).

Aporotus recurvirostris du Bus, 1868

Aporotus recurvirostris du Bus, 1868: 626.

HOLOTYPE. — IRSNB 3812-M.1887, partial skull (single specimen placed in *Aporotus recurvirostris* by du Bus [1868], included in the species *Mioziphius belgicus* by Abel [1905]).

REFERRED SPECIMENS. — Partial rostra IRSNB 3810, IRSNB 3811, IRSNB 3813, IRSNB 3814, IRSNB 3815, IRSNB 3816-M.1888, and IRSNB 3817, found in Antwerp without precise location, and two isolated fragments of rostra IRSNB 8243d and IRSNB 8243g, both found in October 1909 in Kessel, 18 km south-east of Antwerp.

TYPE HORIZON. — There are no data available for most of the specimens. The fragments of premaxillae found in Kessel might originate from the Antwerp Sands, late early to middle Miocene (Louwye *et al.* 2000), but this kind of dense fragment is strong enough to undergo one or more phases of reworking (Glaessner 1947).

TYPE LOCALITY. — Antwerp, Belgium, exact locality uncertain.

DIAGNOSIS. — Species larger than *Aporotus dicyrtus*, *Ziphirostrum marginatum* and *Choneziphius planirostris*, with a size of the skull close to adult *Ziphius cavirostris* (more than 380 mm in preorbital width). This species differs from *Aporotus dicyrtus* in: the longer, slightly anterodorsally curved rostrum; more elevated premaxilla on the rostrum forming a high longitudinal crest with a top more posteriorly positioned and a steeper posterior slope; the deeper and wider prenarial basin; the more elevated vertex with transverse premaxillary crests more anteriorly directed and overhanging the premaxillary sac fossae. This species appears to be more derived than *A. dicyrtus* for most of the given characters.

DESCRIPTION (FIGS 29; 30)

The description is essentially based on the holotype, which is much better preserved than the referred specimens, which only consist in rostrum fragments. The holotype is a large skull including the nearly complete rostrum, the anterior of the cranium, and the anterior of the vertex. The basicranium is lacking, as well as the supraoccipital and the frontals on the vertex and the supraorbital processes. The rostrum has a total length estimated at 570 mm, close to *Ziphirostrum marginatum*, but it is clearly curving upwards. The cranium is larger and the vertex is higher than for the latter species. Only a few additional measurements could be taken on that skull, because of the absence of a clear contact between the two halves: the width of the rostrum at the base is estimated at 270 mm, and the width of the skull at the level of the preorbital processes at 380 mm. The measurements on the rostral longitudinal premaxillary crests are given below (Table 5).

Premaxilla

The development of elevated longitudinal premaxillary crests makes the rostrum very high, with a maximum height posteriorly positioned (Fig. 29C). The posterior lowering is abrupt and steep, while the anterior lowering is progressive and accompanied by a narrowing. The right and left crests match very well, although there is no sutural contact between the median surfaces; in fact these surfaces show numerous anastomosed vascular sulci, which indicate the absence of a fused suture (Fig. 29D). The most ventral major sulcus originates at the large premaxillary foramen, located on an elongated depressed surface posteromedian to the crest, at the contact with the premaxillary sac fossa. The lateral surface of the crest is also covered by sulci.

The prenarial basin is wide and deep between the two maxillary crests, but the medial resorption of the premaxillae seems little pronounced (not totally preserved): there is no interruption between the high longitudinal premaxillary crest and the premaxillary sac fossa.

The posterior portion of the premaxillae, including the premaxillary sac fossae and the transverse premaxillary crests, is poorly preserved. The remaining fragments and the underlying maxillae allow a general description of the area: the premaxillary sac fossa is strongly tilted, anteromedially facing (seen on the right side), and the curvature continues on the ascending process of the bone, so that the roughly rectilinear transverse premaxillary crest is anterolaterally directed (Figs 29A; 30A).
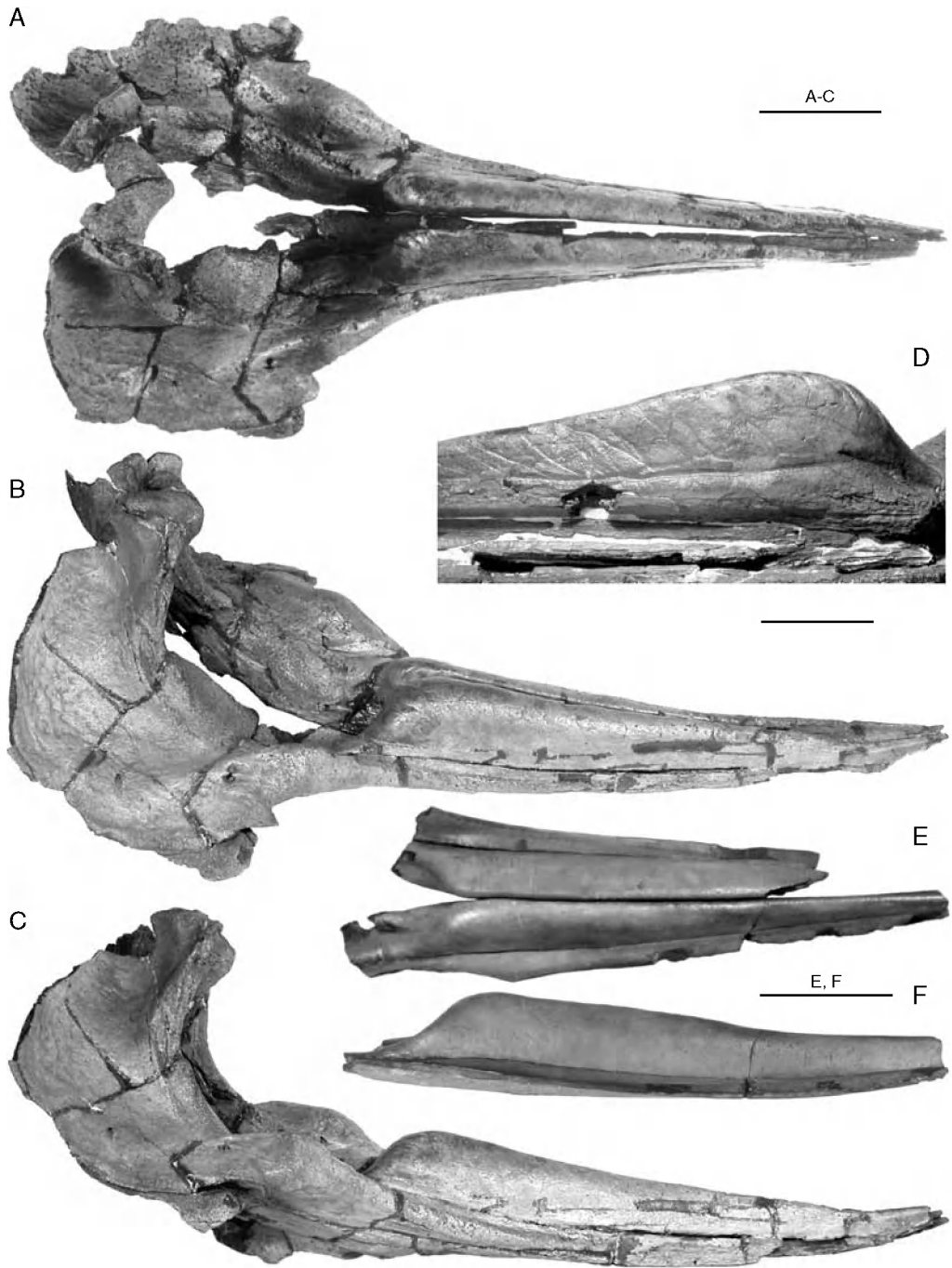
FIG. 29. — **A-D**, skull of *Aporotus recurvirostris* du Bus, 1868 (IRSNB 3812-M.1887, holotype); **A**, dorsal view; **B**, right dorsolateral view; **C**, right lateral view; **D**, medial view of the right rostral premaxillary crest showing the numerous sulci on the unfused surface; **E**, **F**, partial rostrum of *Aporotus recurvirostrus* du Bus, 1868 (IRSNB 3816-M.1888); **E**, dorsal view; **F**, right lateral view. Scale bars: A-C, E, F, 100 mm; D, 50 mm.
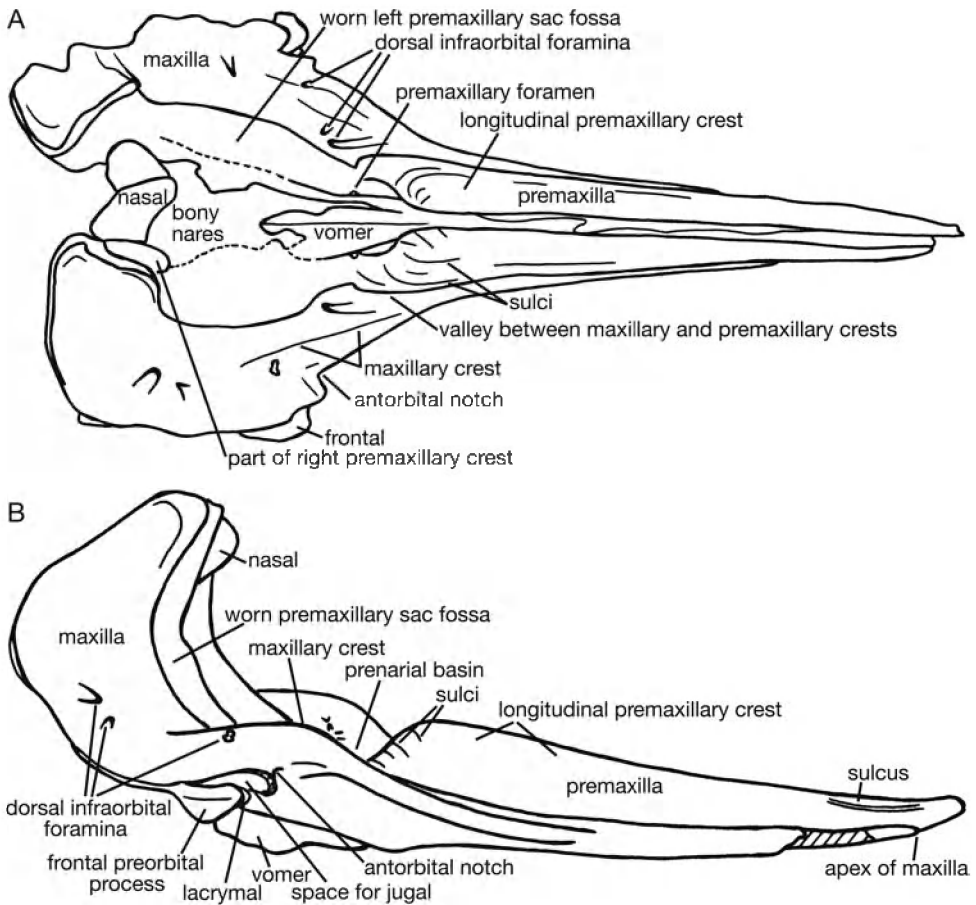
FIG. 30. — Line drawings of the skull of *Aporotus recurvirostris* du Bus, 1868 (IRSNB 3812-M.1887, holotype); **A**, dorsal view; **B**, right lateral view.

Maxilla

Laterally to the longitudinal crest of the premaxilla, the maxilla is little exposed on the rostrum, widening backwards without distinct horizontal surface. At a level posterior to the end of the premaxillary crest, the lateral margin of the maxilla strongly elevates to form an elongated longitudinal crest, more acute and higher on the right side, with a maximum height just before the antorbital notch. The posterior part of the crest, lowering on the preorbital process, is excavated by a dorsal infraorbital foramen (with a double exit on the right side), and a posteriorly directed foramen is present at the base of the inner slope

of the crest, along the suture with the premaxilla. A wide valley separates the maxillary crest from the rostral longitudinal crest of the premaxilla, anterolaterally directed from the prenarial basin.

In lateral view, the curvature of the rostrum is distinct at the level of the lateral suture between maxilla and premaxilla. The maxilla finishes anteriorly at least 60 mm before the apex of the rostrum. The latter is formed only of the premaxilla, laterally hollowed by a deep sulcus anteriorly following a foramen located at the apex of the maxilla. The lateral margin of the maxilla is less dense and more eroded than the premaxilla;

TABLE 5. — Measurements (in mm) on the rostral premaxillary crests of *Aporotus recurvirostris* du Bus, 1868, from the Neogene of Antwerp. –, no data. See Figure 1 for the description of the measurements.

	IRSNB 3810	IRSNB 3811	IRSNB 3812-M. 1887 (type)	IRSNB 3813	IRSNB 3814	IRSNB 3815	IRSNB 3816-M. 1888	IRSNB 3817	IRSNB 8243g	IRSNB 8243d
1. maximal height left	–	–	52	49	44	42	45	43	42	–
2. maximal height right	69	51	63	53	54	48	50	49	–	46
3. maximal width left	–	–	45	–	39	33	34	27	34	–
4. maximal width right	45	34	47	44	38	34	38	28	–	32

instead of an alveolar groove, there is a shallow depression with an irregular surface, lacking alveoli.

The maxilla is thin on the supraorbital process compared to the thick preorbital process of the frontal. A large dorsal infraorbital foramen pierces the supraorbital process of the maxilla near the posterolateral edge, accompanied by a more anterior smaller foramen.

The erect medial plate of the maxilla at the vertex extends medially beyond the level of the lateral margin of the nasal.

Nasal

The nasals, slightly longer than wide, are antero-medially pointed, with a concave posterior margin. The left nasal is shorter and narrower than the right, and the median suture is anterolaterally deflected on the left side. The mesethmoid is lost.

Palatine-vomer-lacrimal-jugal

The median sutures of the rostrum are totally eroded, the palatine is poorly delimited, the pterygoid is lost, and the vomer is preserved as a high keel in front of the choanae. The suture of the lacrimal with the frontal is not completely fused, allowing a good correlation with the morphology of *Ziphius*. The jugal is lost.

ADDITIONAL SPECIMENS

Several paired (six) and isolated (four) rostral longitudinal premaxillary crests similar to those of the holotype of *Aporotus recurvirostris* were found

at Antwerp and Kessel. Surprisingly, the pairs, always clearly belonging to a same individual (Fig. 29E, F), never show a bony suture, even ventrally. They were thus probably transported with other parts of the rostrum, which were destroyed after deposition and before burial, maybe because of their higher porosity. The right crest is in each case higher than the left (see Table 5), with a difference of 8 to 17%, but not clearly wider. There is no good correlation between the degree of asymmetry and the height of the crest. The maximum elevation is sometimes located somewhat more anteriorly than on the holotype.

Aporotus dicyrtus du Bus, 1868

Aporotus dicyrtus du Bus, 1868: 627. — Van Beneden & Gervais 1880: pl. 27bis, fig. 6.

HOLOTYPE AND ONLY REFERRED SPECIMEN. — IRSNB 3808-M.541, partial skull, single specimen of *Aporotus dicyrtus* du Bus, 1868, and referred to *Mioziphius belgicus* by Abel (1905).

TYPE HORIZON. — No data available, probably Miocene or lower Pliocene.

TYPE LOCALITY. — Antwerp, Belgium, exact locality uncertain.

EMENDED DIAGNOSIS. — Smaller than *Aporotus recurvirostris*, with a skull size close to *Choneziphius planirostris*. It differs from *Aporotus recurvirostris* in: the shorter and rectilinear rostrum; the lower premaxillae on the rostrum, with the top of the longitudinal crests more anteriorly located and the posterior slope less steep; the reduced prenarial basin; the lower vertex with transverse premaxillary crests more laterally directed.
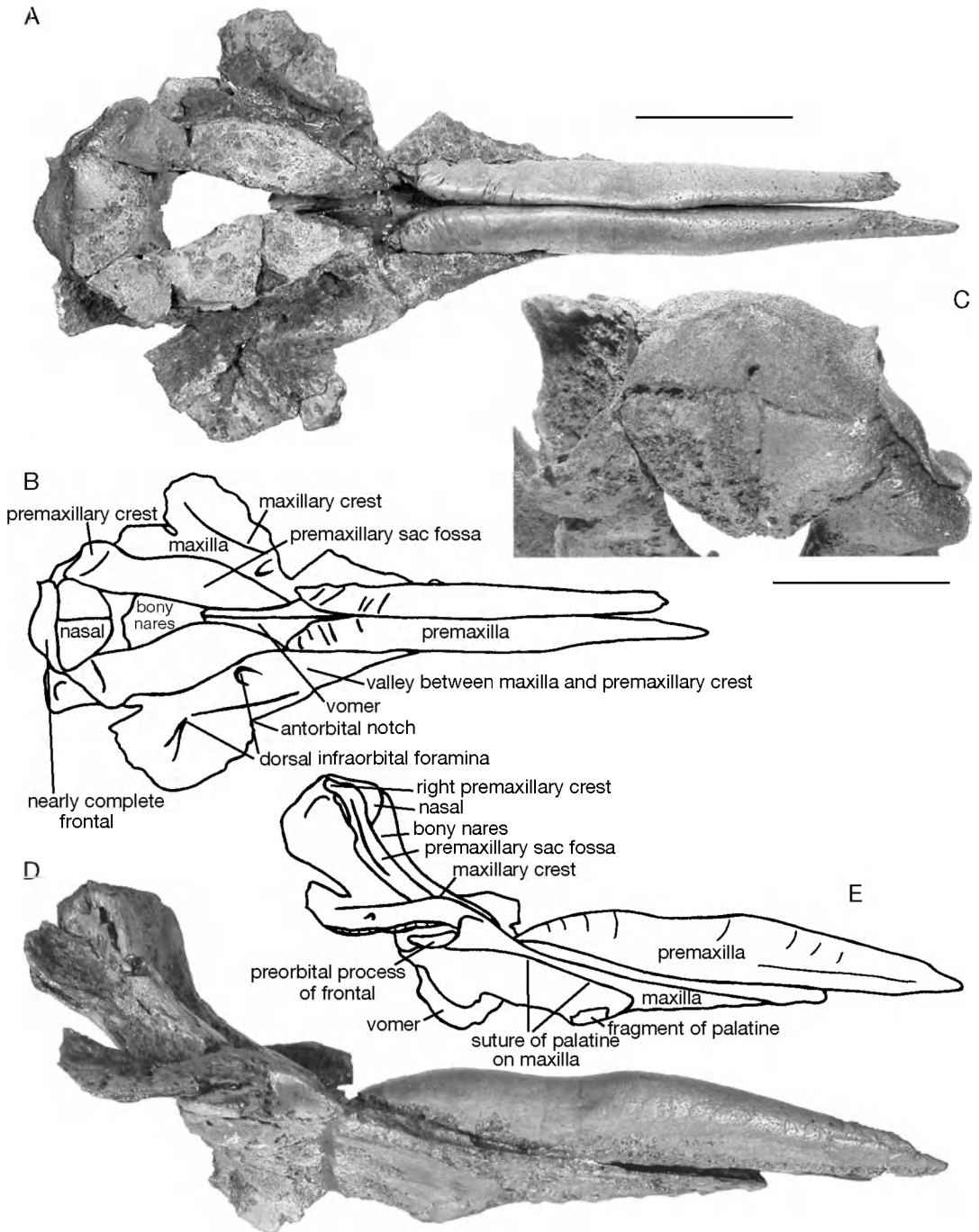
FIG. 31. — Skull of *Aporotus dicyrtus* du Bus, 1868 (IRSNB 3808-M.541, holotype); **A**, dorsal view; **B**, line drawing of the dorsal view; **C**, detail of the vertex in dorsal view; **D**, right lateral view; **E**, line drawing of the right lateral view. Scale bars: A, D, 100 mm; C, 50 mm.

TABLE 6. — Measurements (in mm) on the skull of the holotype of *Aporotus dicyrtus* du Bus, 1868 (IRSNB 3808-M.541), from the Neogene of Antwerp. +, incomplete. The maximum height is taken parallel to the lateral surface of the crest, and the maximum width, perpendicular.

	IRSNB 3808-M.541
1. length rostrum	+390
3. maximal anterior height rostrum	75
4. maximal anterior width rostrum	59
7. width base rostrum	170
10. width premaxillary sac fossae	115
11. width right premaxillary sac fossa	56
12. width left premaxillary sac fossa	42
13. width bony nares	48
14. width nasals	74
15. width transverse premaxillary crests	129
16. minimal posterior distance between maxillae	64

DESCRIPTION OF THE HOLOTYPE (FIG. 31)

This eroded specimen includes a nearly complete straight rostrum, the premaxillary sac fossae, the vertex, and parts of the supraorbital processes. The skull has a size close to *Choneziphius planirostris*, slightly smaller than *Ziphirostrum marginatum* (see Table 6), with a relatively shorter rostrum.

The aspect of the premaxilla on the rostrum is completely different from the rest of the skull, even from the underlying maxillae: the surfaces are smooth and non-eroded, indicating osteosclerotic bone (Fig. 31A, D). This portion of the premaxilla is dorsally and laterally thickened, with a maximum width and height at mid-length of the rostrum, where the bone overhangs the maxilla. The two premaxillae are roughly medially apposed, but without obvious sutural contact; the internal surface of those bones is hollowed by numerous small vascular sulci, as in *Aporotus recurvirostris*. This dense part of the premaxilla nearly reaches the premaxillary sac fossa, with a short posterior separation between the premaxillae, opening the mesorostral groove for 40 mm before the premaxillary sac fossae. The dorsal surface of the premaxillary sac fossa is flat, smooth, and higher than the adjacent lateral maxilla. The right premaxilla is wider than the left at that level (with a maximum width of respectively 56 and 42 mm). The ascend-

ing process of the premaxilla does not become vertical. The poorly thickened transverse premaxillary crest is anterolaterally directed, with a terminal lateral curvature (Fig. 31C).

The triangular nasals are well developed between the premaxillary crests; the rounded anteromedian tip overhangs the bony nares. The median suture of the nasals is slightly anteriorly deflected on the left side. The nasals do not go farther posteriorly than the premaxillary crests and their suture with the frontals is roughly rectilinear.

The width of the strip of frontals on the vertex is more than two times its length and the median suture is not distinct.

At the base of the rostrum, the maxilla occupies a large and poorly elevated portion of the dorsal surface, progressively anteriorly narrowing, disappearing under the premaxilla before half the length of the rostrum. The main feature in the dorsal view of the supraorbital process is the longitudinal crest starting 40 mm anteromedially to the antorbital notch and ending before the large dorsal infraorbital foramen on the supraorbital process. The inner slope of the crest is more pronounced than the outer, and a large foramen is present between the crest and the premaxillary sac fossa, at the level of the antorbital notch.

There is no trace of alveoli for maxillary teeth on the poorly preserved lateral face of the rostrum. The ventral face is not better preserved; only small fragments of the palatine indicate an anterior limit of that bone 130 mm anteriorly to the antorbital notches.

SYSTEMATIC DISCUSSION

This partial skull IRSNB 3808-M.541, holotype and only specimen of the species *Aporotus dicyrtus*, possesses a set of characters that makes it difficult to clearly identify the genus. The attribution by du Bus (1868) to the same genus as *A. recurvirostris* is justified by the non-fusion of the premaxillae above the mesorostral groove, a character that might be considered as primitive, even if it is also present in the extant *Ziphius* – for which it was considered as a reversion by Bianucci *et al.* (1994). Owen (1870) criticized the separation of *Aporotus* from
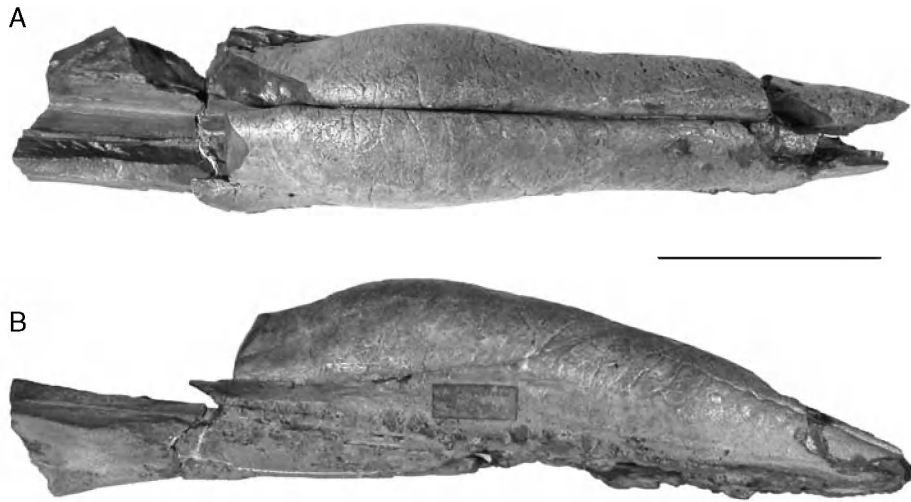
A

B

FIG. 32. — Rostrum referred to Ziphiidae aff. *A. dicyrtus* (*Ziphirostrum tumidum* sensu du Bus, 1868) (IRSNB 3807-M.1889); **A**, dorsal view; **B**, right lateral view. Scale bar: 100 mm.

Ziphirostrum, thinking that the unfused premaxillae constitute a feature not admissible as a generic character. In my opinion, this character might be valid because of functional consequences at the level of the vascularization: the strong vascularization described on the median surface of the premaxillae in the two species of *Aporotus* is a feature impossible to retain if the two premaxillae are fused, as in *Ziphirostrum* or *Choneziphius*. This surface of vascularization might help to develop larger prominences of the premaxillae. The lack of fusion of the premaxillae might therefore be related to the higher premaxillary prominences of *Aporotus*, which are likely derived.

IRSNB 3808-M.541 also shares with *A. recurvirostris* a longitudinal maxillary crest on the preorbital process and the valley between this crest and the elevated dense premaxilla on the rostrum. However, that morphology, separating the two species of *Aporotus* from *Ziphirostrum*, is also observed in *Ziphius*; rostro-facial structure might group *Ziphius* and *Aporotus* in a monophyletic taxon, with *Ziphius* more derived because of the more dorsoanteriorly elongated nasals and the more asymmetrical premaxillary sac fossae.

REVISION OF *ZIPHIROSTRUM TUMIDUM* DU BUS, 1868
The species *Ziphirostrum tumidum* was established by du Bus (1868) for the single rostrum IRSNB 3807-M.1889, stressing the spectacular dorsolateral development of the premaxillae. The partial fusion of the premaxillae above the mesorostral groove probably lead du Bus (1868) to include the species in *Ziphirostrum*. This specimen was later included in the species *Mioziphius belgicus* by Abel (1905).

Description of the rostral fragment (Fig. 32)
This rostrum, 410 mm long, lacks the base and fragments of the apex. The premaxillae are extremely developed to form a massive elongated dome, hiding the maxillae from the dorsal view. The maximum height of the rostrum, roughly at mid-length, is 92 mm, with a maximum width of 82 mm at the same level. The premaxillae are only partly fused along their dorsomedian contact above the reduced mesorostral groove; a clear break surface is only present on the ventral part of the contact surface. The surface of the premaxillae is smooth, hollowed by numerous small vascularization sulci, in a way similar to *Aporotus dicyrtus*. A main longitudinal sulcus on the lateral surface, progressively dividing from the

apex of the rostrum, is reminiscent of *Ziphirotrum turniense*. The maxillae have a more eroded surface, only partially preserved.

Discussion

The general morphology of the premaxillae is similar to *A. dicyrtus*; even the position of the top of the dome is roughly at the same level relatively to the anterior margin of the palatine (only 20 mm more anterior in IRSNB 3807-M.1889). The two main differences are the much more important development of the dome and the partial fusion of the premaxillae above the mesorostral groove on IRSNB 3807-M.1889. This fragmentary specimen probably belongs in or is close to *A. dicyrtus*; if the former, then individual variation is marked, and it might correspond to an important sexual dimorphism and/or ontogenetic development. If it was the case, the definition of the genus *Aporotus*, including *A. recurvirostris* and *A. dicyrtus*, would be weakened, as IRSNB 3807-M.1889 does not share with those two species the character "absence of fusion of the premaxillae above the mesorostral groove". IRSNB 3807-M.1889 is provisionally referred to Ziphiidae aff. *A. dicyrtus*.

SUMMARY OF THE SYSTEMATIC REVISION – NUMBER OF SPECIMENS FROM ANTWERP IN EACH REVISED TAXON

Ziphirostrum marginatum du Bus, 1868: 16 specimens;
Z. turniense du Bus, 1868: two specimens;
Z. recurvus (du Bus, 1868) n. comb.: one specimen;
Choneziphius planirostris (Cuvier, 1823): 20 specimens;
C. macrops (Leidy, 1876): one specimen;
Beneziphius brevirostris n. gen., n. sp.: two specimens;
Aporotus recurvirostris du Bus, 1868: 10 specimens ;
A. dicyrtus du Bus, 1868: one specimen;
Ziphiidae aff. *A. dicyrtus*: one specimen;
Ziphiidae aff. *Eboroziphius*: two specimens;
Ziphiidae *incertae sedis*: four specimens.

GENERAL PHYLOGENETIC CONSIDERATIONS

INTRODUCTION

To investigate the phylogenetic relationships of the fossil and extant ziphiids, a cladistic analysis was carried out with the parsimony program PAUP, version 4.0 beta 10 (Swofford 1998). All the extant genera were used here. For the fossil ziphiids, only the taxa represented by the anterior of the cranium and the vertex were selected. For that reason, *Ninoziphius* was not included in the analysis. The definition of the genus *Aporotus* is too weak to allow its inclusion in the analysis and the information about the cranium of the type species *A. recurvirostris* is too fragmentary. Bianucci *et al.* (1992, 1994) noticed similarities between *Messapicetus* and *Ziphirostrum*. Nevertheless, the differences between the two taxa highlighted by these authors for the cranium might be slightly overweighted. For example, the rostrum of *Messapicetus* is longer but the more elongated braincase could reflect *post-mortem* lateral crushing. The nasals of *Ziphirostrum marginatum* reconstructed by Bianucci *et al.* (1994: fig. 7) are too long: *Z. marginatum* has actually triangular nasals similar to *Messapicetus*. Furthermore, the latter drawing does not show the clear angle of the lateral portion of the premaxillary crest (see Fig. 5D), in a way similar to *Messapicetus* (a misinterpretation probably due to the too anterior orientation of the figure of Abel [1905: fig. 17], hiding the angle). The absence of a prenarial basin suggested by Bianucci *et al.* (1994) in *Messapicetus* is difficult to check because of the incomplete preparation of the holotype of *M. longirostris*, but the medial side of the premaxillae is clearly partly resorbed. *Messapicetus* and *Ziphirostrum* should at least be considered as sister-groups. For this reason, *M. longirostris* is not taken as a separate taxon in the phylogenetic study here, because it has the same polarity than *Ziphirostrum* for all the characters.

The taxa included in the analysis are: the extant ziphiids *Berardius*, *Hyperoodon*, *Indopacetus*, *Mesoplodon*, *Tasmacetus*, and *Ziphius*; the fossil

ziphiids *Beneziphius* n. gen., *Choneziphius*, *Tusciziphius*, and *Ziphirostrum*; the primitive odontocete *Squaloziphius* Muizon, 1991 and the eurhinodelphinid *Ziphiodelphis* Dal Piaz, 1908. *Squalodon* is chosen *a priori* as outgroup. The information about *Indopacetus*, *Squaloziphius*, and *Tusciziphius* is taken from the literature (Longman 1926; Muizon 1991; Bianucci 1997; photographs of *Indopacetus* kindly sent by G. Bianucci). For all the other genera, personal observations were made in the collections of the IRSNB, MGPD, MNHN, MP, USNM, and ZMA. A matrix of 21 characters, all informative and treated as unordered and unweighted, was built for these 13 taxa (see Appendices 1 and 2 for the data-matrix and the description of the characters).

RESULTS

The heuristic analysis used is a general heuristic search with parsimony as optimality criterion, the branch-swapping algorithm is a tree-bisection-reconnection (TBR).

The heuristic search resulted in four shortest trees with: tree length 32 steps; CI 0.94; RI 0.95. The consensus tree and one of the shortest trees are shown in Figure 33. The consensus tree shows a sister-group relationship between *Ziphirostrum* + *Beneziphius* n. gen. and *Choneziphius* + (*Tusciziphius* + *Ziphius*). The position of *Indopacetus* is not fully resolved, only sister-group of *Mesoplodon* + *Hyperoodon* in two of the four shortest trees. *Tasmacetus* and *Berardius* are both more basal than the other ziphiids of the analysis; they form a monophyletic group in two trees, and *Tasmacetus* is more basal in the two others.

DISCUSSION

In spite of the low resolution for the position of *Berardius*, *Tasmacetus*, and *Indopacetus*, the consensus tree differs from several morphological analyses (Moore 1968: phenetic; Muizon 1991; Bianucci *et al.* 1994; Geisler & Sanders 2003) in the more basal position of *Berardius* and *Tasmacetus* relatively to the other extant ziphiids. Close relationships between *Ziphius*, *Mesoplodon*, and *Hyperoodon* were revealed by the study of the

DNA satellite (Grétarsdottir & Arnason 1993) and by morphological studies (Messenger & McGuire 1998), isolating the more primitive *Berardius* and *Tasmacetus*, and therefore not contradicting the consensus tree presented here.

The subfamily Hyperoodontinae *sensu* Muizon, 1991, including *Indopacetus* + (*Hyperoodon* + *Mesoplodon*) is only found in half the shortest trees (Fig. 33B), even if the similarities of *Indopacetus* with the two other genera (especially *Mesoplodon*) are obvious (review in Dalebout *et al.* 2003).

For the fossil ziphiids of Antwerp, the consensus tree proposes that *Choneziphius* and *Ziphius* are more closely related to each other than any of them is to *Ziphirostrum*, as suggested by Bianucci *et al.* (1994), but differing from Muizon (1991) who obtained a sister-group relationship between *Ziphirostrum* and *Choneziphius*. The interpretation is also different from the hypothesis of Bianucci (1997), who grouped *Hyperoodon*, *Mesoplodon*, *Tusciziphius*, and *Ziphius* by "the ascending portions of premaxillae anteriorly curved near the vertex"; the condition of the premaxillary crests in *Hyperoodon* and *Mesoplodon* is estimated non-homologous to the overhanging seen in *Choneziphius*, *Tusciziphius*, and *Ziphius*, in which it is correlated to the concavity/excavation of the premaxillary sac fossae, with a premaxillary crest anterolaterally directed. The vomerian mesorostral ossification seems also non-homologous in *Ziphius* and *Mesoplodon*: it is much denser and has a smoother surface in *Mesoplodon*, and the similarity is considered here as a convergency, contrary to the assertion of Bianucci (1997).

The content of the subfamily Ziphiinae is modified compared to Muizon (1991) and Bianucci *et al.* (1994), only including the last common ancestor of *Ziphius* and *Ziphirostrum* and all its descendants (= tribe Ziphiini in Bianucci *et al.* 1994). It is therefore possible to define a subfamily Berardiinae (= tribe Berardiini in Bianucci *et al.* 1994) including *Berardius* and *Tasmacetus*. However, the support is weak; it is only found in two trees, with one synapomorphy: "nasals distinctly wider than the frontals on
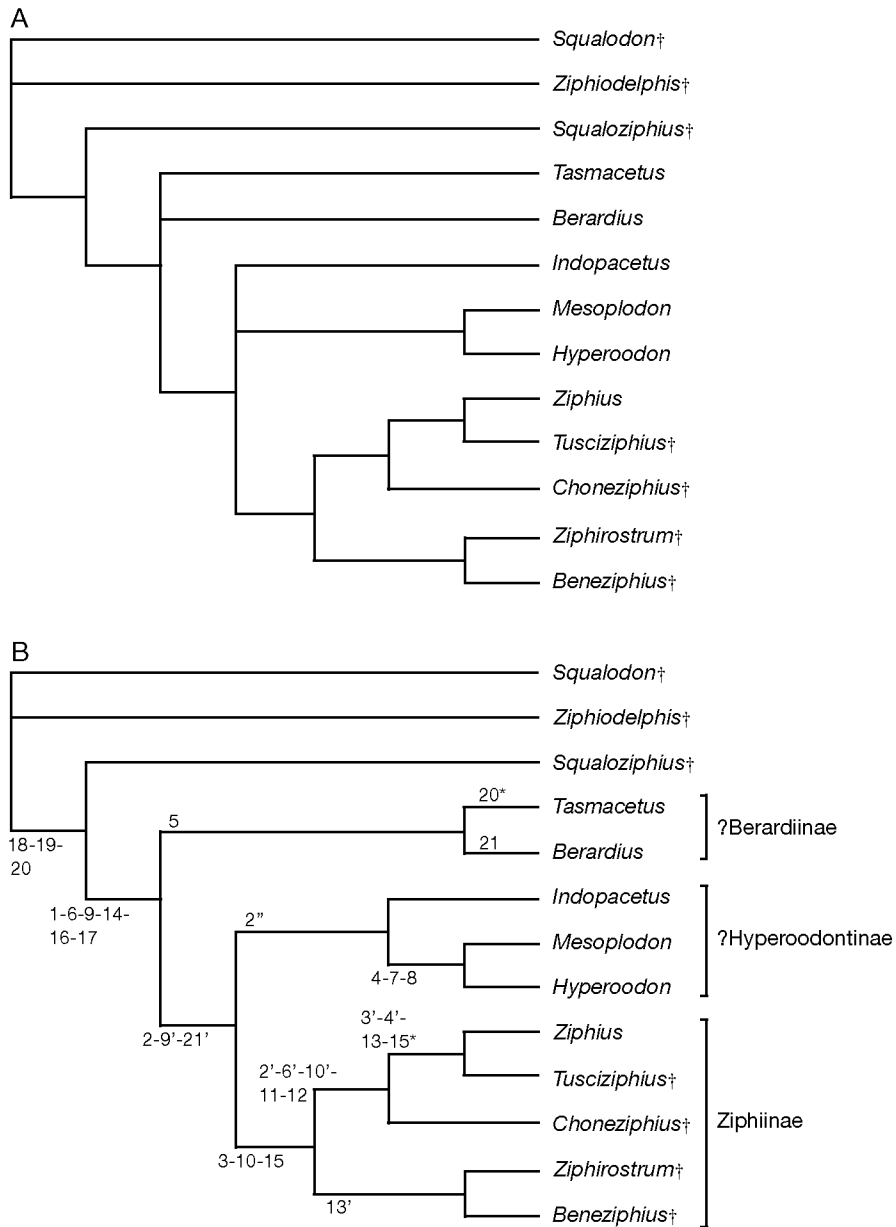
FIG. 33. — **A**, consensus tree showing the relationships of the fossil ziphiids from the Neogene of Antwerp with other fossil and extant genera; **B**, one of the four shortest trees. Tree length: 32; RI: 0.94; CI: 0.93. Character-state optimization: acctran. Numbers at each node refer to characters listed in the Appendix 2. Change from state 0 or 1 to state 2 ('); change from state 0, 1 or 2 to state 3 (''); reversal from state 1 to state 0 (*); †, strictly fossil genus.

the vertex". The molecular studies of Dalebout *et al.* (1998, 2002) and Van Helden *et al.* (2002), undertaken to identify extant *Mesoplodon* species by mitochondrial DNA, provided bootstrap values lower than 50 for the ziphiid nodes, with the exception of the basal position of *Berardius* relatively to *Hyperoodon*, *Mesoplodon*, *Tasmacetus*, and *Ziphius*, which is well supported.

Aporotus might be close to the clade *Choneziphius* + (*Ziphius* + *Tusciziphius*), with a developed maxillary crest on the preorbital process. Furthermore, *Aporotus recurvirostris* has a deep and wide prenarial basin, and more anteriorly directed premaxillary crests on the elevated vertex than *Beneziphius* n. gen. and *Ziphirostrum*. However, the asymmetry of the premaxillary sac fossae could not be estimated on the holotype of *A. recurvirostris*, and the second species, *A. dicyrtus*, has a shallower prenarial basin and more laterally directed premaxillary crests. Actually, this genus would necessitate additional material for a better definition and a more precise phylogenetic placement.

The early Miocene odontocete *Squaloziphius emlongi* was included in the family Ziphiidae by Muizon (1991) because of: the presence of an elevated vertex with transverse premaxillary crests and with the medial edge of the maxilla and the lateral edge of the premaxilla overhanging the maxilla laterally; a strong development of the hamular lobe of the pterygoid sinus and a consequent enlargement of the hamular process of the pterygoid. That hypothesis was discussed by Fordyce & Barnes (1994), who affirmed that this skull lacks convincing ziphiid features and appears more reminiscent of Eurhinodelphinidae. In a detailed morphological analysis of the cetaceans, Geisler & Sanders (2003) obtain a consensus tree where *Squaloziphius* is sister-group of crown-Odontoceti. The consensus tree presented here shows a sister-group relationship between *Squaloziphius* and all the known ziphiids; this relationship is supported by: 1) the widening of the pterygoid sinus fossa anterior to the ear bones by posterolateral development of the dorsal lamina of the pterygoid, reaching or going beyond the lateral level of the falciform process of the squamosal; and 2) the widening of the basioccipital basin. These two characters are absent in the eurhinodelphinid *Ziphiodelphis*, which is more stemward; this result confirms the opinion of Muizon (1991) that *Squaloziphius* is more closely related to the ziphiids than to the eurhinodelphinids. Nevertheless, *Squaloziphius* lacks several key-characters of the ziphiids: its vertex is not more elevated than in several eurhinodelphinids, with transverse premaxillary crests not wider; its hamular process is barely more developed than in *Ziphiodelphis abeli* (Pilleri 1985: pl. 39, fig. b), and it is not excavated until its ventral margin, contrary to the ziphiids; the nasals are small, not anteriorly developed; the postglenoid process is very long ventrally. It is therefore probably better to keep *Squaloziphius* outside the family Ziphiidae.

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APPENDIX 1

Data-matrix of 21 characters for one outgroup, *Squalodon*, and 12 analysed taxa. All characters with multiple states are treated as unordered; **0**, primitive state; **1**, **2**, **3**, derived states; **a**, variable between 0 and 1; **?**, missing character; -, irrelevant character. See Appendix 2 for explanation of the characters.

	5	1 0	1 5	2 1
Squalodon	00000	00000	00000	000000
Ziphiodelphis	00000	00000	00000	000000
Squaloziphius	00000	00000	00000	0011??
Tasmacetus	10001	10010	00010	111100
Berardius	10001	10010	00010	111111
Indopacetus	13000	10020	00010	111112
Mesoplodon	130a0	11120	00010	111112
Hyperoodon	13010	-112-	00010	111112
Ziphius	12220	20022	11110	111112
Ziphirostrum	11100	10021	00211	??1???
Beneziphius n. gen.	11100	100?1	00211	??????
Choneziphius	12100	200?2	11011	??????
Tusciziphius	12220	20022	1????	1?11??

APPENDIX 2

List of characters used in the cladistic analysis.

1 - Elevated vertex with transverse premaxillary crests and the medial plate of the maxillae overhanging the lateral part of the bone
(0) No.
(1) Yes.
The vertex and the premaxillary crests of *Squaloziphius* are not as developed as in the known ziphiids, and that area is not distinct enough from some eurhinodelphinids to allow the elaboration of a clear diagnostic character.
2 - Transverse premaxillary crests (orientation best seen on the posterolateral edge of the premaxillary crest)
(0) Absent or narrow and transversely oriented.
(1) Median portion anterolaterally directed separated from the more laterally directed lateral portion by a distinct angle.
(2) More anteriorly directed, without angle.
(3) Much thickened, laterally elongated and slightly to more deeply lateroposteriorly bent.
3 - Contact between nasal and transverse premaxillary crest (or sketch of crest)
(0) Wide, on the whole length of the premaxilla on the vertex.
(1) Much reduced, only on the posterolateral corner of the nasal.
(2) Secondary filling of the space between premaxilla and nasal by cartilage (*Ziphius*) or bone (*Tusciziphius*).
4 - Overhanging of the more ventral part of the premaxillae and the bony nares by the transverse premaxillary crests
(0) No, premaxillae not reaching (*Berardius*, *Squaloziphius*) or just reaching the vertical.
(1) Yes, by anterodorsal curvature of the median portion of the premaxillary crest.

(2) Yes, mostly by anterodorsal development of the lateral portion of the crest.
5 - Nasals distinctly wider than the frontals on the vertex
(0) No.
(1) Yes.
6 - Anterior development of the nasals with a relatively pointed apex anterior to the premaxillary crests
(0) No.
(1) Yes.
(2) Further anterior development of the nasals, with the maximum width of the bones at the anterior margin.
The more pronounced median excavation of the nasals in *Hyperoodon* and several specimens of *Mesoplodon* precludes the estimation of the character state. Even if most of the nasals is lost in *Choneziphius*, the condition is suggested to be homologous to *Tusciziphius* and *Ziphius*.
7 - Excavation of a median valley on the anterodorsal surface of the nasals
(0) No.
(1) Yes.
8 - Nasals thrusted into the median portion of the premaxillary crests
(0) No.
(1) Yes.
9 - Anteromedian projection of the supraoccipital between the posterior margins of the maxillae
(0) Absent.
(1) Present, but lower than the vertex.
(2) Roughly reaching the level of the vertex.
Contrary to *Ziphirostrum*, the frontals of *Choneziphius* and *Beneziphius* n. gen. are not sufficiently preserved on the vertex to estimate this character.

10 - Asymmetry of the premaxillae at the level of the premaxillary sac fossae: ratio between maximum widths of left and right premaxillae
(0) Higher than 0.79.
(1) From 0.69 to 0.79.
(2) Lower than 0.69, with a much narrowed dorsal part of the left premaxilla.
The condition in *Hyperoodon* spp. could not be estimated due to the high development of the maxillary crests, modifying the proportions of the premaxillae medially.

11 - Excavation of the premaxillary sac fossae
(0) No.
(1) Yes.

12 - Premaxillary sac fossa laterally overhanging a longitudinal valley on the maxilla
(0) No.
(1) Yes.

13 - Prenarial basin
(0) Absent.
(1) Laterally margined by the premaxillae.
(2) Laterally margined by a thick strip of maxilla.

14 - Divergence of the lateral margins of the rostrum in direction of the antorbital notches
(0) Weak, margins stay nearly parallel.
(1) Stronger, lateral margins distinctly concave in dorsal view.
The morphology of the base of the rostrum is strongly modified in *Hyperoodon* by the development of the maxillary crests.

15 - Dorsal roofing of the mesorostral groove by dorsomedian development of the thickened premaxillae on the rostrum
(0) No.
(1) Yes.

16 - Ventral extension of the postglenoid process of the squamosal
(0) As long as or longer than the paroccipital process of the exoccipital.
(1) Shorter.

17 - Hamular process of the pterygoid much ventrally developed, at least until the ventral margin of the basicranium, and excavated by the large lobe of the pterygoid sinus roughly until its ventral edge
(0) No.
(1) Yes.
The hamular process of *Squaloziphius* is well ventrally developed, but it is not excavated on its whole height, in a way similar to eurhinodelphinids as *Ziphiodelphis*. The anterior pterygoid sinus fossa of *Squaloziphius* is also shorter than in ziphiids, not reaching the level of the antorbital notch.

18 - Widening of the pterygoid sinus fossa anterior to the ear bones by posterolateral development of the dorsal lamina of the pterygoid, reaching or going beyond the lateral level of the falciform process of the squamosal
(0) No.
(1) Yes.

19 - Width of the basioccipital basin: ratio between the width of the basin across the alaris processes and the bizygomatic width of the skull
(0) Lower than 0.52.
(1) Higher or equal to 0.52.

20 - Length of the mandibular symphysis
(0) More than one third of the total length of the mandible.
(1) Less than one third.

21 - Number of alveoli on the mandible bearing erupted teeth when adult
(0) More than two pairs, with alveoli for maxillary teeth.
(1) Two pairs.
(2) One pair, dimorphic at least in *Mesoplodon*, *Hyperoodon* and *Ziphius*.