A high diversity in fossil beaked whales (Mammalia, Odontoceti, Ziphiidae) recovered by trawling from the sea floor off South Africa

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ABSTRACT

Eight new genera and 10 new species of fossil beaked whales (Cetacea, Odontoceti, Ziphiidae) are described on the basis of cranial material recovered by trawling from the sea floor off South Africa. Although no exact stratigraphic information is known for these fossils, most are strongly phosphoritised (some even have phosphorite concretions attached), indicating that their fossilization could be related to one or more of the phosphogenic episodes that occurred in the South African coastal waters since the latest Oligocene. Considering the main phosphogenic epochs and the evolutionary level of the majority of the ziphiids here described, a middle-late Miocene age may be suggested for most, but not all, of these fossils. The new genera named here more than double the known diversity of the fossil beaked whales and represent more than one third of the total diversity of this family (fossil and extant). A parsimony analysis within the family including the Recent taxa reveals that some of the new fossil taxa belong to three extant subfamilies redefined here, while the others are outside these subfamilies; this indicates the presence in the past of some ziphiid lineages now extinct. In detail, *Microberardius africanus* n. gen., n. sp. is placed in the subfamily Berardiinae together with the Recent *Berardius*; *Izikoziphius rossi* n. gen., n. sp. and *I. angustus* n. gen., n. sp. are related to the Recent *Ziphius* inside the subfamily Ziphiinae and *Khoikhoicetus agulhasis* n. gen., n. sp., *Ihlengesi saldanhae* n. gen., n. sp., and *Africanacetus ceratopsis* n. gen., n. sp. belong to

the Hyperoodontinae together with the Recent *Hyperoodon*, *Mesoplodon*, and *Indopacetus*. However, *Nenga meganasalis* n. gen., n. sp., *Pterocetus benguelae* n. gen., n. sp., and *Xhosacetus hendeysi* n. gen., n. sp., together with the Recent *Tasmacetus*, do not fit in any of the three subfamilies mentioned above. Taking into account the high number of unnamed fragmentary specimens, the fossil taxa listed above, together with *Mesoplodon slangkopi* n. sp. and *Ziphius* sp., probably represent only a part of the South African fossil ziphiid fauna(s), revealing an unexpected high diversity for the previously poorly known southern hemisphere fossil beaked whales. Such a high ziphiid diversity might be locally related to the upwelling system and resulting high productivity linked to the northward running cool oceanic Benguela Current entering the shallower waters along the south-west coast of South Africa and Namibia since the middle Miocene.

RÉSUMÉ
Une grande diversité de baleines à bec fossiles (Odontoceti, Ziphiidae) remontées du fond de la mer au large de l'Afrique du Sud.
Huit nouveaux genres et 10 nouvelles espèces de baleines à bec fossiles (Cetacea, Odontoceti, Ziphiidae) sont décrits sur base de matériel crânien remonté du fond de la mer au large de l'Afrique du Sud. Même si aucune information stratigraphique exacte n'est connue pour l'ensemble de ces fossiles, la plupart sont fortement phosphoritisés (certains montrent même des concrétions de phosphorite attachées), ce qui indique que leur fossilisation/enfouissement pourrait être lié à l'un ou l'autre des épisodes de phosphogenèse se produisant dans les eaux côtières d'Afrique du Sud depuis l'Oligocène terminal. Considérant les principales époques de phosphogenèse et le degré d'évolution des ziphiidés décrits ici, un âge Miocène moyen à supérieur peut être proposé pour la plupart de ces fossiles. Les nouveaux genres décrits doublent la diversité connue des baleines à bec fossiles et représentent plus du tiers de la diversité totale de la famille. Une analyse de parcimonie au sein de la famille incluant les taxons actuels révèle qu'une partie des nouveaux taxons fossiles appartiennent aux trois sous-familles actuelles redéfinies ici alors que les autres taxons restent en dehors de ces sous-familles, ce qui indique la présence dans le passé de lignées de ziphiidés maintenant éteintes. En détail, *Microberardius africanus* n. gen., n. sp. se place dans la sous-famille Berardiinae avec le genre actuel *Berardius* ; *Izikoziphius rossi* n. gen., n. sp. et *I. angustus* n. gen., n. sp. sont regroupés avec le genre actuel *Ziphius* dans la sous-famille Ziphiinae et *Khoikhoicetus agulhasis* n. gen., n. sp., *Ihlengesi saldanhae* n. gen., n. sp., et *Africanacetus ceratopsis* n. gen., n. sp. appartiennent à la sous-famille Hyperoodontinae avec les genres actuels *Hyperoodon*, *Mesoplodon*, et *Indopacetus*. Cependant, *Nenga meganasalis* n. gen., n. sp., *Pterocetus benguelae* n. gen., n. sp., *Xhosacetus hendeysi* n. gen., n. sp. et le genre actuel *Tasmacetus* ne rentrent dans aucune des sous-familles mentionnées ci-dessus. En tenant compte du grand nombre de spécimens trop fragmentaires pour être nommés, la liste de taxons fossiles ci-dessus ne représente probablement avec *Mesoplodon slangkopi* n. sp. et *Ziphius* sp. qu'une partie de la ou des faune(s) de ziphiidés fossiles d'Afrique du Sud, ce qui révèle une diversité étonnamment élevée pour les baleines à bec de l'hémisphère sud, jusqu'ici très mal connues. Une telle diversité de ziphiidés pourrait se corréler localement avec le système d'upwelling et la haute productivité résultante liés à la remontée du courant océanique froid Benguela dans les eaux moins profondes de la côte sud-ouest d'Afrique du Sud et de Namibie depuis le Miocène moyen.
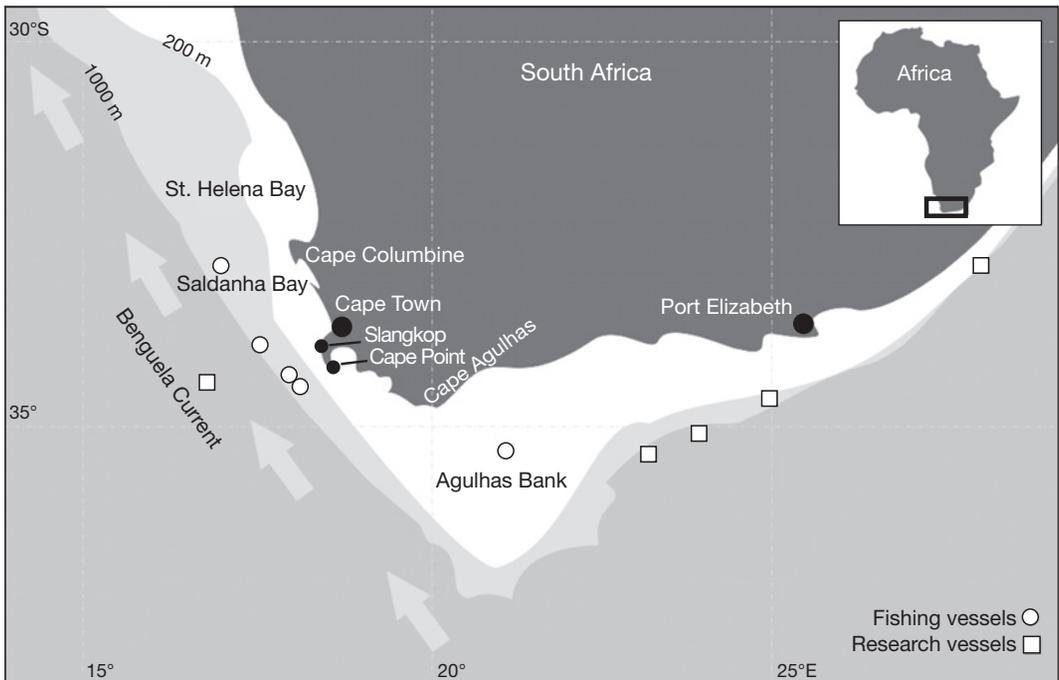
Fig. 1. — Map of South African coast showing mainland localities near which fossil ziphiid skulls have been recovered by trawling. Marine locations of precisely recorded (with geographic coordinates) sites where ziphiid skulls were recovered by fishing and research vessels are also indicated.

INTRODUCTION

The fossil history of the beaked whales (Ziphiidae) is poorly known. Although the sheer amount of described fossil species might seem impressive, the lack of fossils from large areas of the world (especially the entire southern hemisphere) and long geological periods (late Pliocene to early Holocene) prevents a comprehensive view.

From the northern hemisphere currently eight Miocene to Pliocene fossil genera are recognised on the basis of cranium material, with 12 species described. The North Sea area (mainly from Belgium) yielded most descriptions with members of the genera *Aporotus* du Bus, 1868, *Archaeoziphius* Lambert & Louwye, 2006, *Beneziphius* Lambert, 2005, *Caviziphius* Bianucci & Post, 2005, *Choneziphius* Duvernoy, 1851, and *Ziphirostrum* du Bus, 1868. From the Mediterranean (all from Italy) *Messapicetus longirostris* Bianucci, Landini & Varola, 1992 and *Tusciziphius crispus* Bianucci,

1997 were reported. *Choneziphius macrops* (Leidy, 1876) was first described from the east coast of the USA and *Messapicetus longirostris* and *Tusciziphius crispus* have been recognised there (Whitmore *et al.* 1986; Fuller & Godfrey 2007; Post pers. obs.). The Pacific coast of the USA yielded *Squaloziphius emlongi* Muizon, 1991 from the early Miocene of Washington State (in its original description this species was considered as the oldest known ziphiid, but scholars still debate whether or not this species should be considered a basal ziphiid or belonging to a separate family [Fordyce & Barnes 1994; Lambert 2005]). Lastly, a series of undetermined ziphiids including a possible fossil member of the genus *Berardius* (Takahashi *et al.* 1989) and an unnamed ziphiine (Horikawa *et al.* 1987) are mentioned from the Pacific coast of Japan.

Contrary to the multitude of fossil species from the northern hemisphere, only one fossil species has been described from the southern hemisphere: *Ninoziphius platyrostris* Muizon, 1983 from the

early Pliocene of Peru. A few more ziphiid fossils have been mentioned in the literature (e.g., Glaessner 1947; Mead 1975), but none of these fossils showed diagnostic characters enabling a more precise identification.

All the above-mentioned fossil members of the ziphiid family come from Miocene to early Pliocene strata and, to date, only a few fragmentary ziphiid remains have been recovered from younger strata (Oishi & Hasegawa 1994; Cozzuol 1996). Given the extant record of the family – at least 21 known species in six genera (Dalebout *et al.* 2002) – more fossils from Pliocene and Pleistocene strata are to be expected.

The purpose of this work is to describe several fossil ziphiid skulls recovered by trawling from the Neogene strata outcropping on the sea floor off the South African coasts (Fig. 1). Ten new species of ziphiids belonging to nine genera (of which eight are new to science) are reported. These taxa greatly increase our knowledge of the fossil ziphiids and reveal the high diversity of Mio-Pliocene ziphiids from the southern hemisphere. These preliminary results also yield new insights concerning the phylogeny of the family.

Most fossils examined here are strongly phosphatised and have phosphorite concretions attached. The worldwide phenomenon of phosphatised, glauconised, and/or cemented fossil ziphiid remains dredged from sea floor is often mentioned in the literature. Isolated fossil rostra occur remarkably abundantly within middle-late Miocene and/or early Pliocene marine transgression gravels, together with phosphorite nodules, bones from other marine mammals, and shark teeth. Such fossils are trawled from the sea floor near the Thornton Bank in the North Sea off the Netherlands and in the North Atlantic off the Canary Islands (Post pers. obs.); from the Miami Terrace in the Northern Strait of Florida, the Blake Plateau off the east coast of Florida, off San Clemente Island California, the Clarion-Clipperton Fracture zone in the Pacific, and off the Peruvian coast in the South Pacific (Whitmore *et al.* 1986); about 1200 km south of Tasmania in the South Pacific Ocean (Fordyce & Cullen 1979); and off Sado Island in the sea off Japan (Horikawa *et al.* 1987; Tazaki *et al.* 1987).

The striking abundance of these fossils in South African waters and many seas worldwide, combined with their petrologic appearance and the fact that these faunas are characterised by unusually high and dominant ziphiid diversity illustrates the need of further study of this interesting and worldwide phenomenon.

ABBREVIATIONS
IGF   Museo di Geologia e Paleontologia, Università di Firenze;
IRSNB   Institut royal des Sciences naturelles de Belgique, Brussels;
MNHN   Muséum national d'Histoire naturelle, Paris;
MSNTUP   Museo di Storia Naturale e del Territorio, Università di Pisa;
MZUF   Museo di Zoologia, Università di Firenze;
NMR   Natuurhistorisch Museum Rotterdam;
NNML   Nationaal Natuurhistorisch Museum Naturalis, Leiden;
PEM   Port Elizabeth Museum, Port Elizabeth, South Africa;
SAM   Iziko South African Museum, Cape Town;
USNM   United States National Museum, Smithsonian Institution, Washington D.C.;
ZMA   Zoölogisch Museum Amsterdam.

MATERIAL AND METHODS

SPECIMENS

Although some fragmentary rostra were already listed and referred to extant genera *Mesoplodon* and *Ziphius* by Haughton (1956), all fossil ziphiids examined in this article are described for the first time. The fossils are kept in SAM except the holotypes of *Izikoziphius rossi* n. gen., n. sp. and *Africanacetus ceratopsis* n. gen., n. sp. kept respectively in PEM and in NMR.

During this study and from previous works on fossil ziphiids (Bianucci 1997; Lambert 2005), we realized that the regularly found isolated rostra of fossil beaked whales are poorly diagnostic. For example, the *Mesoplodon*-like heavy rostra with a mesorostral groove filled by the vomer are generally referred to several fossil species of the Recent genus *Mesoplodon* (e.g., Owen 1870; Capellini 1885) but morphological characters or arguments have never been presented. These nominal species have sometimes been grouped into Cuvier's species *Mesoplo-*

don longirostris (Abel 1905; Bianucci 1997). Mead (1975) and Bianucci (1997) already predicted that similar rostral morphologies with strong mesorostral ossification, today mostly observed in the genus *Mesoplodon*, might be present in some unknown fossil genera of this family. The well preserved and diversified material from South Africa confirms this hypothesis. In fact, among these fossils there are clearly some well preserved skulls with a peculiar vertex unlike all other known beaked whales, but with a *Mesoplodon*-like rostrum. So in this study for the description of new taxa and for comparison we decided to use only those specimens including at least the more diagnostic dorsal surface of the cranium with the vertex.

The South Africa fossil ziphiids described here are compared with most significant described taxa of fossil beaked whales, all directly examined by us, and with the skulls of most Recent ziphiid species, mostly available in the SAM collection (see Appendix 1).

SYSTEMATICS

The systematic classification used in the following section anticipates the results of our phylogenetic analysis (see below), where the three subfamilies of the Ziphiidae (Berardiinae, Hyperoodontinae, and Ziphiinae) are redefined. Some new genera here described do not fit in these subfamilies and are considered as Ziphiidae *incertae sedis*.

SYSTEMATICS

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

Subfamily BERARDIINAE Moore, 1968

TYPE GENUS. — *Berardius* Duvernoy, 1851.

OTHER GENERA INCLUDED. — *Archaeoziphius* Lambert & Louwye, 2006 and *Microberardius* n. gen.

EMENDED DIAGNOSIS. — Berardiinae differ from all other Ziphiidae in the presence of a nodular protuberance formed by the interparietal or the frontals on the vertex *Berardius* spp. are further characterized by two pairs of apical and subapical enlarged teeth on the mandible; this character still needs to be confirmed in *Archaeoziphius* and *Microberardius* n. gen.

Other characters differentiating Berardiinae from more derived taxa are mostly symplesiomorphies: narrow and thin premaxillary crest on the low vertex; supraoccipital lower than the frontals on the vertex.

DISCUSSION

The content of the subfamily Berardiinae as defined here is more similar to the subtribe Berardiina of Moore (1968) (only including *Berardius*) than to the tribe Berardiini of Muizon (1991) (including *Berardius*, *Ninoziphius*, and *Tasmacetus*) or to the subfamily ?Berardiinae of Lambert (2005) (including *Berardius* and *Tasmacetus*). Additional specimens of *Ninoziphius* with a well preserved vertex could clarify the relationships of this genus in the proposed framework. A fragmentary cranium from the Neogene of Japan is referred to *Berardius* sp. (Takahashi *et al.* 1989); despite general shape similarities with *Berardius*, the vertex might be too incomplete to provide diagnostic characters.

The presence of an ossified mesethmoid filling a significant portion of the mesorostral groove, observed in *Berardius*, but not verifiable in *Microberardius* n. gen., is also noted in SAM PQ 69676 (see below, *Nenga* n. gen.).

Genus *Microberardius* n. gen.

TYPE SPECIES. — *Microberardius africanus* n. gen., n. sp., by present designation.

ETYMOLOGY. — From the Ancient Greek "mikros", small and *Berardius*, a Recent ziphiid genus. *Microberardius* n. gen. for the small size of the species and its cranial similarities with *Berardius* spp. Gender masculine.

DIAGNOSIS. — Same as for the species.

Microberardius africanus n. sp.

HOLOTYPE. — SAM PQ 3003, a partial skull including the anteriorly worn rostrum, most of the dorsal surface of the cranium and the nearly complete vertex.

ETYMOLOGY. — "africanus" for the African origin of the holotype.
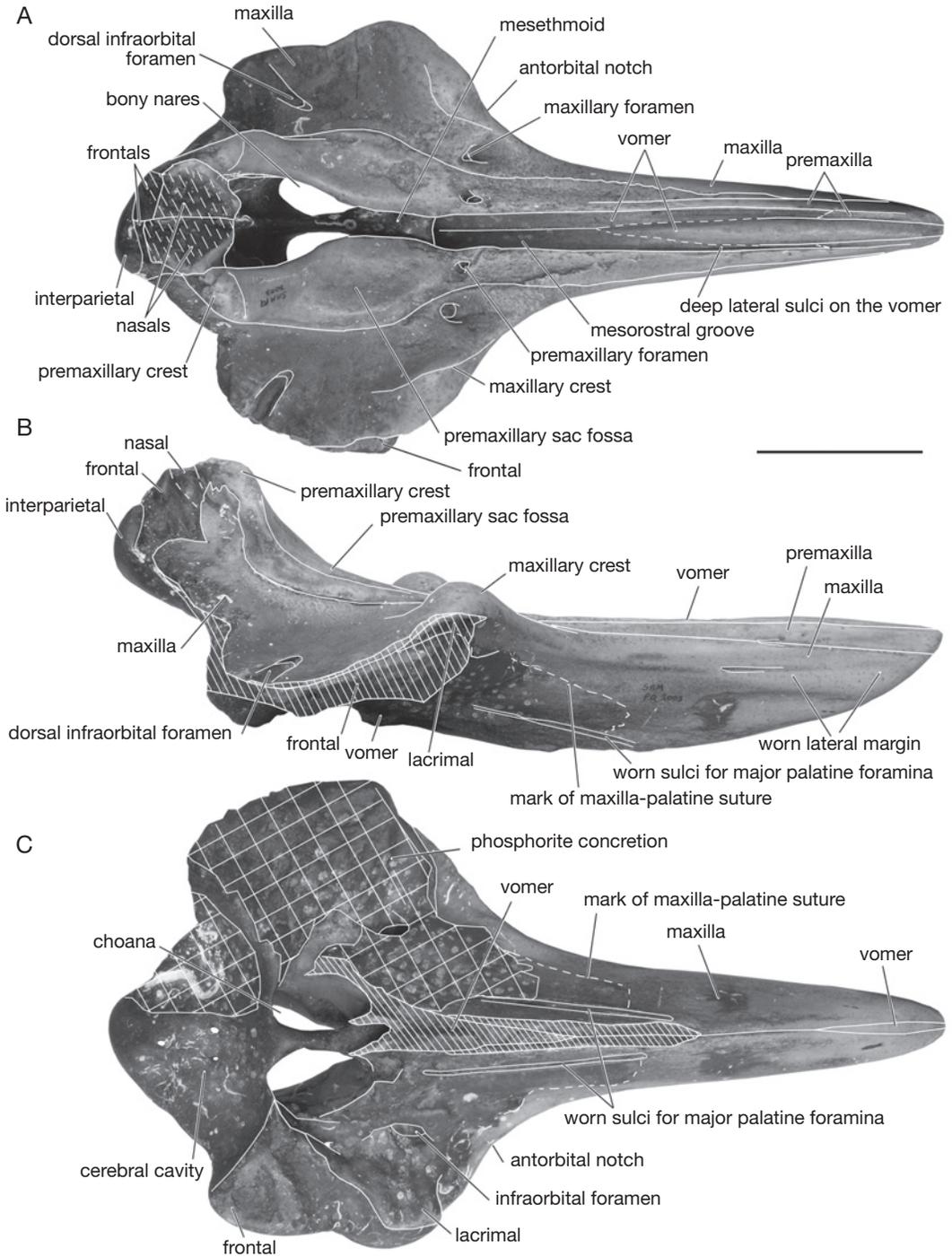
FIG. 2. — Skull of *Microberardius africanus* n. gen., n. sp. (SAM PQ 3003, holotype): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.
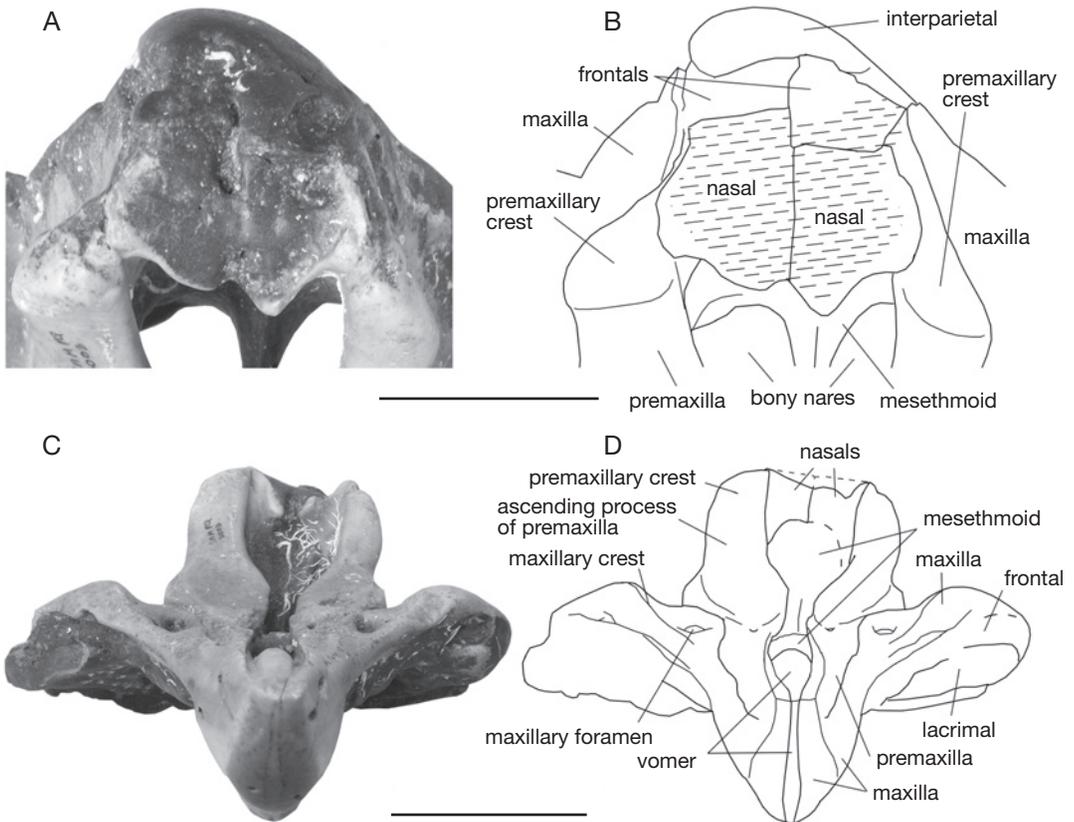
Fig. 3. — Skull of *Microberardius africanus* n. gen., n. sp. (SAM PQ 3003, holotype): **A**, detail of the vertex in dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: A, B, 5 cm; C, D, 10 cm.

TYPE LOCALITY. — No data. Trawled off the South African coast.

DIAGNOSIS. — *Microberardius africanus* n. gen., n. sp. differs from *Berardius* in: smaller size; thickening of the vomer in the anterior portion of the mesorostral groove; rostrum higher than wide along most of its length; narrower rostrum base and maxillary crest not extended on the rostrum base. It differs from *Archaeoziphius* in: slightly concave premaxillary sac fossa; higher maxillary crest; more anteriorly pointed nasals; larger distance between the maxillae across the vertex and the nodular bone in the posterior vertex being the interparietal instead of the frontals.

DESCRIPTION (FIGS 2; 3; TABLE 1)
Considering the height of the preserved apex of the rostrum, a significant part of the anterior portion is probably missing. Where preserved, the rostrum height is larger than the width at the same level, except along the base. The dense vomer fills the anterior part of the mesorostral groove, leaving a widely open space posteriorly for the presumed anterior extension of the ossified mesethmoid. Among Recent ziphiids, a lengthened ossified portion of the mesethmoid is only observed in *Berardius* spp. (e.g., *B. arnuxii*, SAM ZM 39296; *B. bairdii* in True 1910: pl. 26). A marked sulcus laterally separates the thickened vomer from the premaxilla.

The premaxillary sac fossa is slightly concave. The ascending process of the premaxilla lacks a constriction under the premaxillary crest in anterior view. The moderate elevation towards the vertex does not reach vertical. The premaxillary crest is transversely oriented without a distinct dorsal thickening or
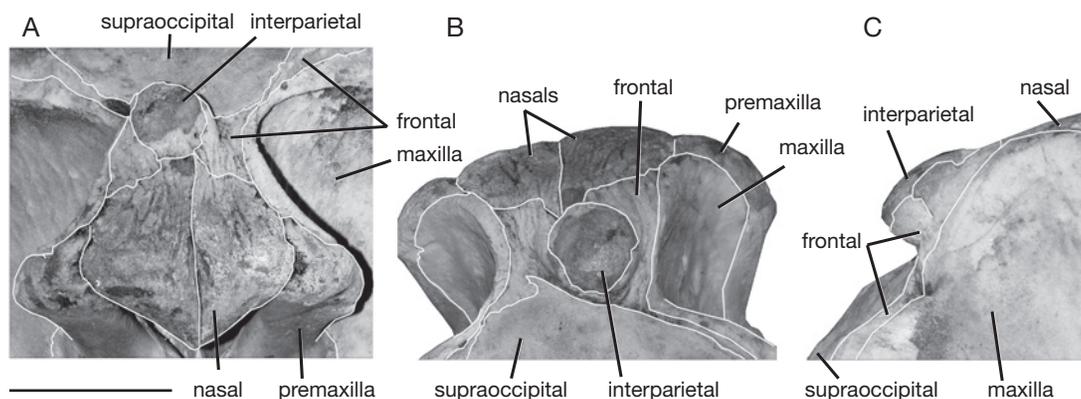
F<small>IG</small>. 4. — Vertex of skull of *Berardius arnuxii* (SAM ZM 39296): **A**, dorsal view; **B**, posterior view; **C**, lateral view. Note the nodular interparietal between the frontals and the supraoccipital that does not reach the vertex dorsally. Scale bar: 10 cm.

widening, similar to *Archaeoziphius* and *Berardius*. The right crest is somewhat wider than the left. The large maxillary foramen just posterior to the level of the antorbital notch is anteriorly followed by a wide and short groove. Both right premaxillary and maxillary foramina are located more posteriorly than their left side counterparts. A high maxillary crest culminating on the preorbital process adjoins the maxillary foramen laterally. Unlike in *Berardius*, the crest does not extent onto the rostrum base.

The dorsal surface of the nasals is damaged. Their outline is pentagon-shaped, their anterior point reaches the level of the premaxillary crest and the anterolateral corner does not thrust into the premaxillary crest. The anteromedian groove between the nasals seen in dorsal view is probably caused by erosion. The naso-frontal suture is irregular with a posteriorly longer right nasal. The frontals are more transversely compressed and lower than the nasals on the vertex. Posterior to the frontals, lower and slightly shifted to the right, is a nodular uneven bone interpreted as an interparietal. Its low position relative to the vertex in lateral view suggests that the supraoccipital did not reach the vertex dorsally. Such a bone is at least occasionally observed in a similar position in *Berardius arnuxii* (e.g., SAM ZM 39296, Fig. 4; Moore 1968: figs 19, 23). In other specimens of *Berardius* spp. and in *Archaeoziphius*, the frontals

themselves form a nodular eminence between the lower supraoccipital and the nasals.

Berardiinae indet.

R<small>EFERRED SPECIMEN</small>. — SAM PQ 2198, a partial skull including the rostrum base, the premaxillary sac fossae, and the vertex.

L<small>OCALITY</small>. — No data. Trawled off the South African coast.

D<small>ESCRIPTION AND DISCUSSION</small> (F<small>IG</small>. 5; T<small>ABLE</small> 1)
This specimen shows a severely worn rostrum and a damaged vertex with poorly preserved premaxillary crests. The rostrum base is similar to that of *Nenga* n. gen. (see below). However, differences within the cranium prevent an attribution to the latter genus: the premaxillary sac fossa is much longer (quantified as the distance between the anterior margin of the bony nares and the premaxillary foramen); the elevation of the premaxilla towards the lower vertex is more progressive and the nasals are longer and transversely narrower. Posterior to the nasals, the sutures between the transversely compressed frontals and a median rounded bone could be distinguished. As in *Berardius arnuxii* and *Microberardius* n. gen., this bone is interpreted as the interparietal. This character
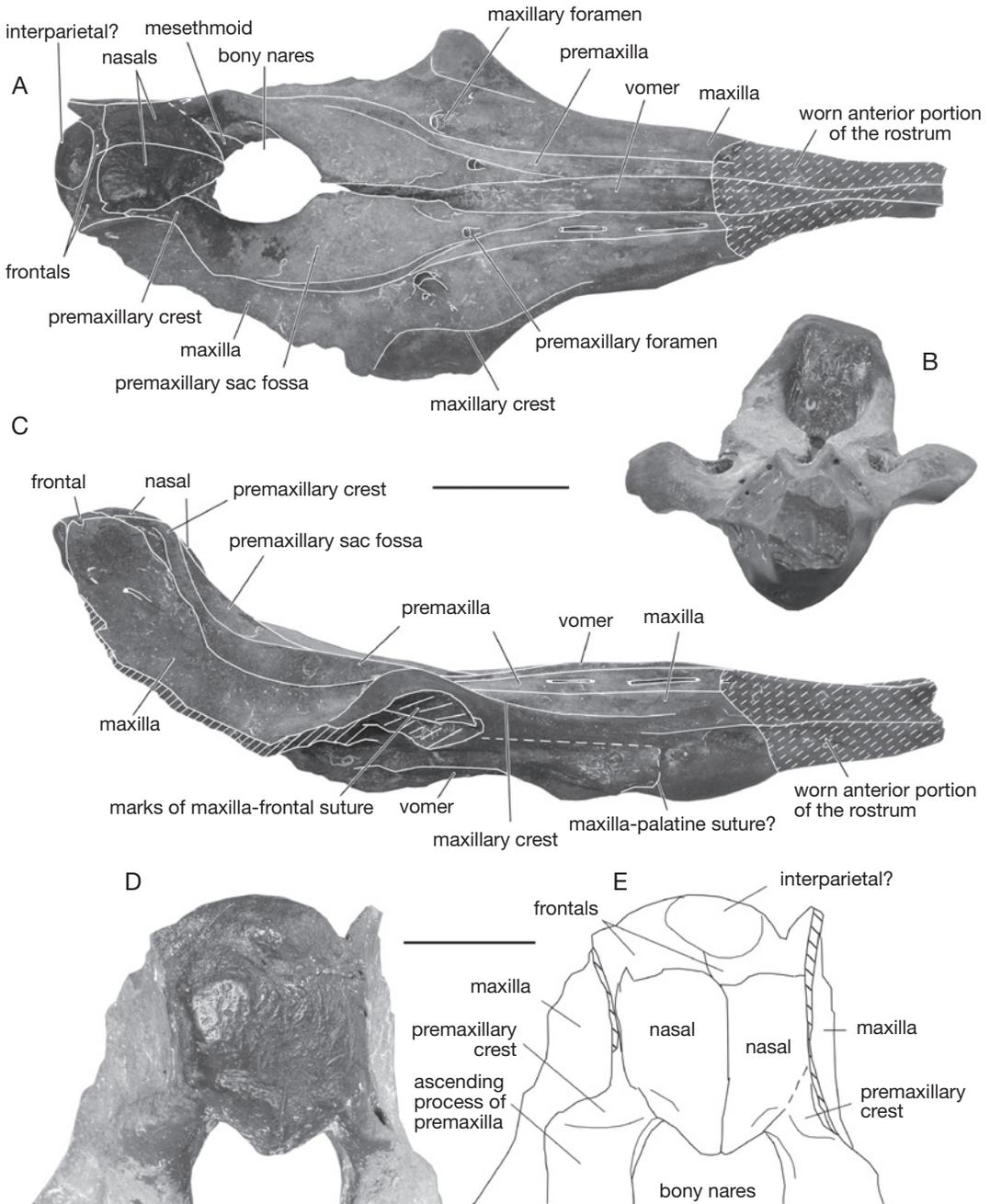
FIG. 5. — Skull of Berardiinae indet. (SAM PQ 2198): **A**, dorsal view; **B**, anterior view; **C**, lateral view; **D**, detail of the vertex in dorsal view; **E**, corresponding line drawing. Scale bars: A-C, 10 cm; D, E, 5 cm.

is our main reason to include SAM PQ 2198 in the subfamily Berardiinae.

Subfamily ZIPHIINAE Gray, 1850

TYPE GENUS. — *Ziphius* Cuvier, 1823.

OTHER GENERA INCLUDED. — *Aporotus, Beneziphius, Caviziphius, Choneziphius, Messapicetus, Tusciziphius, Ziphirostrum* and *Izikoziphius* n. gen.

EMENDED DIAGNOSIS. — The subfamily Ziphiinae differs from all other Ziphiidae in having the contact between nasal and premaxillary crest reduced and the transverse premaxillary crest directed anterolaterally. It further differs from the Berardiinae in the lack of a nodular interparietal on the vertex, from the Hyperoodontinae, *Khoikhoicetus* n. gen., *Pterocetus* n. gen., *Xhosacetus* n. gen. (three new genera described below), and *Tasmacetus* in the lack of an intrusion of the nasal into the narrow premaxillary crest.

Genus *Izikoziphius* n. gen.

TYPE SPECIES. — *Izikoziphius rossi* n. gen., n. sp., by present designation.

OTHER SPECIES INCLUDED. — *Izikoziphius angustus* n. gen., n. sp.

ETYMOLOGY. — Iziko is the network of South African museums, which includes the South African Museum where most of the specimens studied here are stored, *Ziphius* is a Recent ziphiid genus. Gender masculine.

DIAGNOSIS. — *Izikoziphius* n. gen. differs from all the other members of the Ziphiinae in the presence of a fossa on the anterior surface of the ascending process of the premaxilla distinct from the premaxillary sac fossa. It differs from *Ziphius* in: longer rostrum; lack of a prenarial basin; lesser asymmetry of the premaxillary sac fossae (< 0.40) and longer contact between nasal and premaxillary crest. It differs from *Tusciziphius* in: the barely concave premaxillary sac fossa and the anterior part of the nasal not contacting the premaxillary crest. It differs from *Choneziphius* in: longer rostrum; premaxillae medially separated on the rostrum by the thickened vomer and barely concave premaxillary sac fossa. It differs from *Caviziphius* in: premaxillae medially separated on the rostrum by the thickened vomer; lower rostrum base and less asymmetric and barely concave premaxillary sac fossa. It differs from *Aporotus, Beneziphius, Messapicetus*, and *Ziphirostrum* in: longitudinally elongated nasals; premaxillae medially separated

on the rostrum by the thickened vomer and lack of a constriction of the ascending process of the premaxilla (last character less clearly present in *Messapicetus*). Both species of *Izikoziphius* n. gen. have a somewhat smaller cranium size than *Ziphius cavirostris*.

Izikoziphius rossi n. sp.

HOLOTYPE. — PEM N 3265, a partial skull including the rostrum, the anterior part of the cranium, and the vertex.

REFERRED SPECIMEN. — SAM PQ 2086, a partial skull including the rostrum, the anterior part of the cranium, and the vertex, trawled off the South African coast

ETYMOLOGY. — Honouring Dr. Graham J. B. Ross, a cetologist formerly at the PEM who studied in detail extant cetaceans, including the ziphiids, of South African waters.

TYPE LOCALITY. — No data. Trawled off the South African coast.

DIAGNOSIS. — *Izikoziphius rossi* n. gen., n. sp. differs from *I. angustus* n. gen., n. sp. in: rostrum wider than high at mid-length; wide rostrum base; maxillary crest extending on the rostrum base; wide fossa on the anterior surface of the ascending process of the right premaxilla excavating the nasal; anteromedian depression of the dorsal surface of the nasals and a distinctly more elevated right side of the vertex.

DESCRIPTION (FIGS 6-9; TABLE 2)

The rostrum is wider than high at mid-length. The rostrum base is particularly wide (more prominent in the holotype); the lateral margin of the subhorizontal platform of the maxilla present from midway along the rostrum progressively diverges and rises to a crest towards the antorbital notch. The highest dome-like portion of the crest is located on the preorbital process. Medially to this dome, the large maxillary foramen opens anterolaterally with a circular section.

The premaxilla is longer anteriorly than the maxilla. The alveolar groove is either absent or much reduced.

The mesorostral groove is filled with the thickened vomer, but a wide median groove is retained posteriorly. The maximum elevation of the vomer is around two thirds of the length of the rostrum in SAM PQ 2086, less pronounced in PEM N 3265.
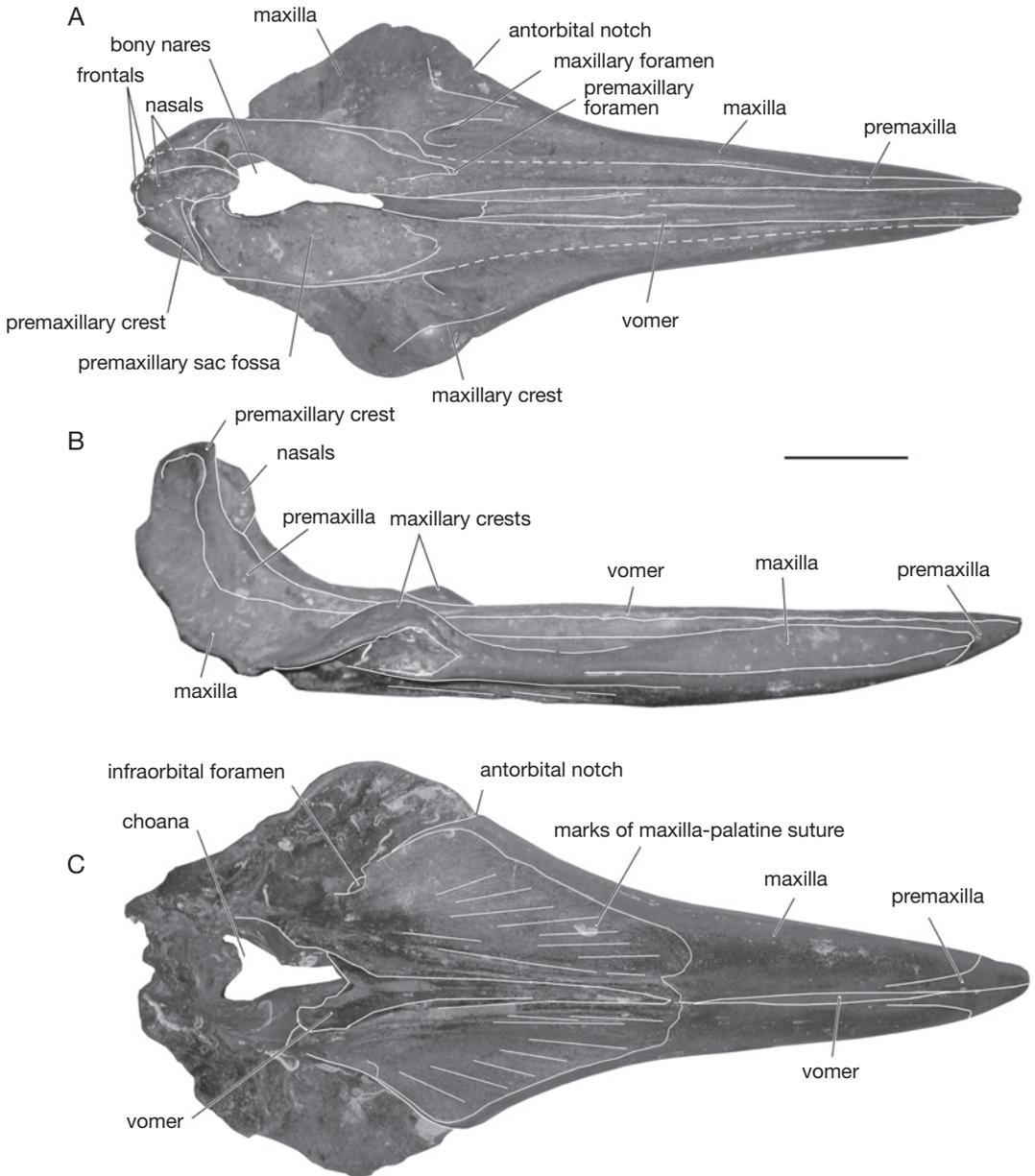
FIG. 6. — Skull of *Izikoziphius rossi* n. gen., n. sp. (PEM N 3265, holotype): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.

The narrow premaxillary foramen, posterior to the antorbital notch, is depressed compared to the slightly concave premaxillary sac fossa. The elevated lateral margin of the fossa overhangs the maxilla along its posterior half. The lateral margins of the ascending processes of the premaxillae are parallel until the elevated vertex. The vertical anterior surface of each ascending process is hollowed out by
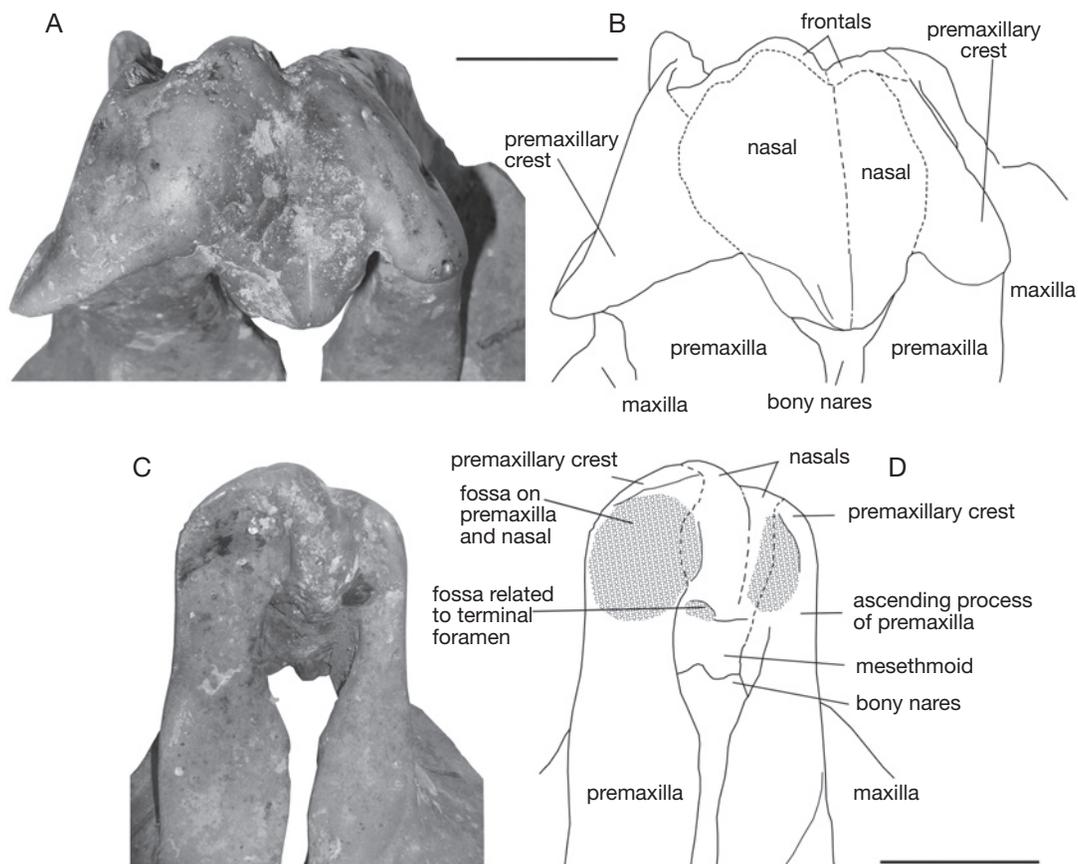
Fig. 7. — Vertex of skull of *Izikoziphius rossi* n. gen., n. sp. (PEM N 3265, holotype): **A**, dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: A, B, 5 cm; C, D, 10 cm.

a deep elliptical fossa, extending medially on the anterolateral surface of the nasal. The right fossa is wider than the left. In relation to the morphology of the air sacs connected to the nasal passages and the surrounding bony configuration in Recent ziphiids and other odontocetes (Heyning 1989; Cranford *et al.* 1996), this fossa corresponds to the location of the posterior nasal sac (*sensu* Heyning 1989, more generally the caudal sac in Cranford *et al.* 1996). We suggest that in *Izikoziphius* n. gen. a homologous air sac was located in this elliptical fossa. A pair of smaller fossae is present ventromedially at the naso-mesethmoid suture (best seen in SAM PQ 2086), probably related to the foramina of the

terminal nerve. The mesethmoid is weakly or not keeled under the nasals.

The relatively thin premaxillary crests are anterolaterally directed. The right crest is twice longer than the left (best preserved in PEM N 3265).

The large nasals, widest at mid-length and slightly longer than wide, are anteriorly longer than the premaxillary crests. Their dorsal surface is slightly anteromedially depressed. The naso-frontal suture is posteriorly irregularly convex with the right nasal longer than the left. The frontals were originally probably short.

In anterior view, the right side of the vertex is considerably higher than the left side.
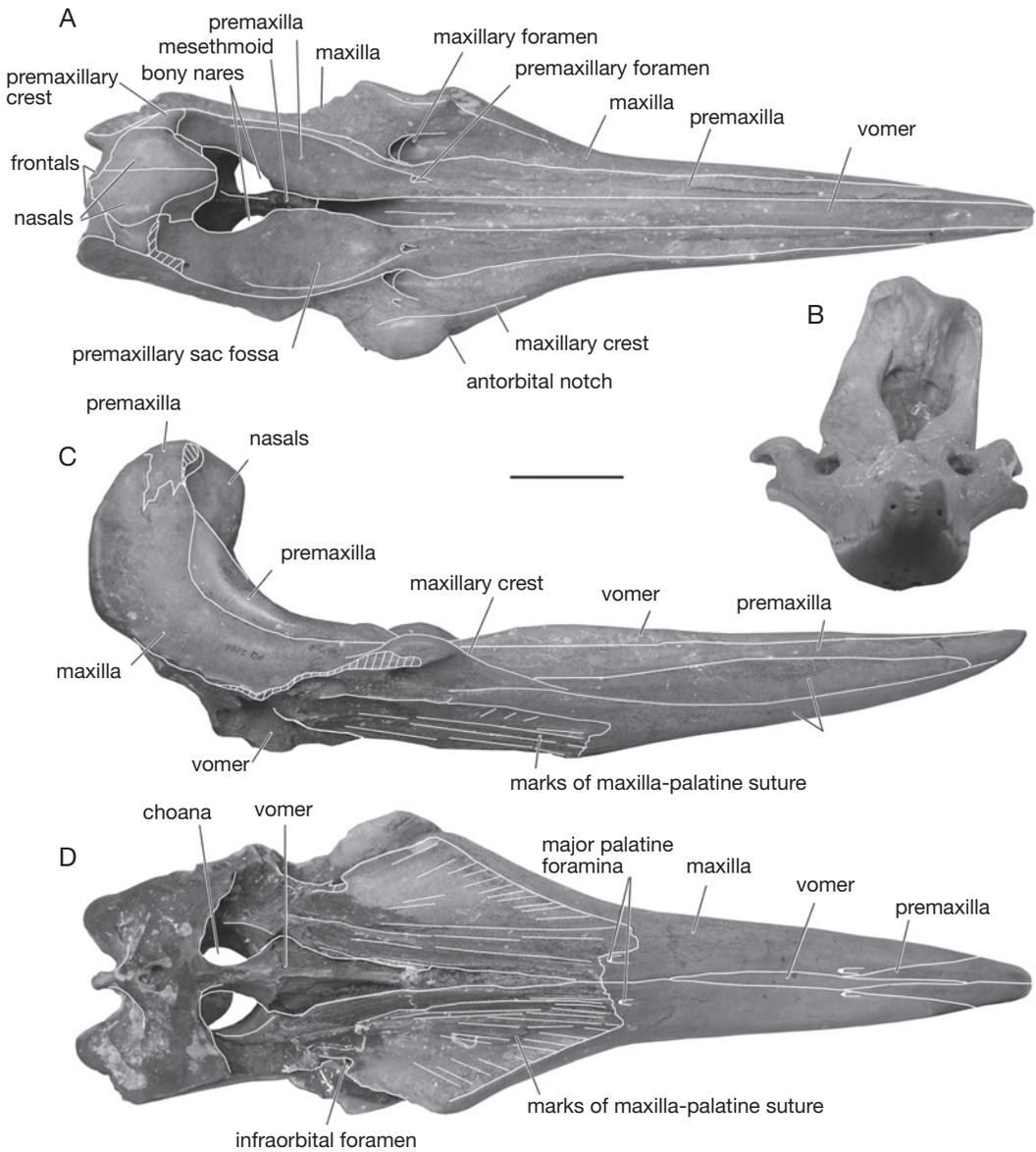
FIG. 8. — Skull of *Izikoziphius rossi* n. gen., n. sp. (SAM PQ 2086): **A**, dorsal view; **B**, anterior view; **C**, lateral view; **D**, ventral view. Scale bar: 10 cm.

Izikoziphius angustus n. sp.

HOLOTYPE. — SAM PQ 3004, a partial skull including the rostrum and most of the dorsal surface of the cranium with the vertex.

ETYMOLOGY. — From Latin "angustus", narrow, for the transversely compressed rostrum, narrower than in the type species *I. rossi* n. gen., n. sp.

TYPE LOCALITY. — Trawled at 34°39'82"S, 18°03'31"E, south-west of Cape Town, Atlantic Ocean, depth of 450 m.

DIAGNOSIS. — *Izikoziphius angustus* n. gen., n. sp. differs from *I. rossi* n. gen., n. sp. in: longer rostrum higher than wide; narrower rostrum base; more elevated maxillary
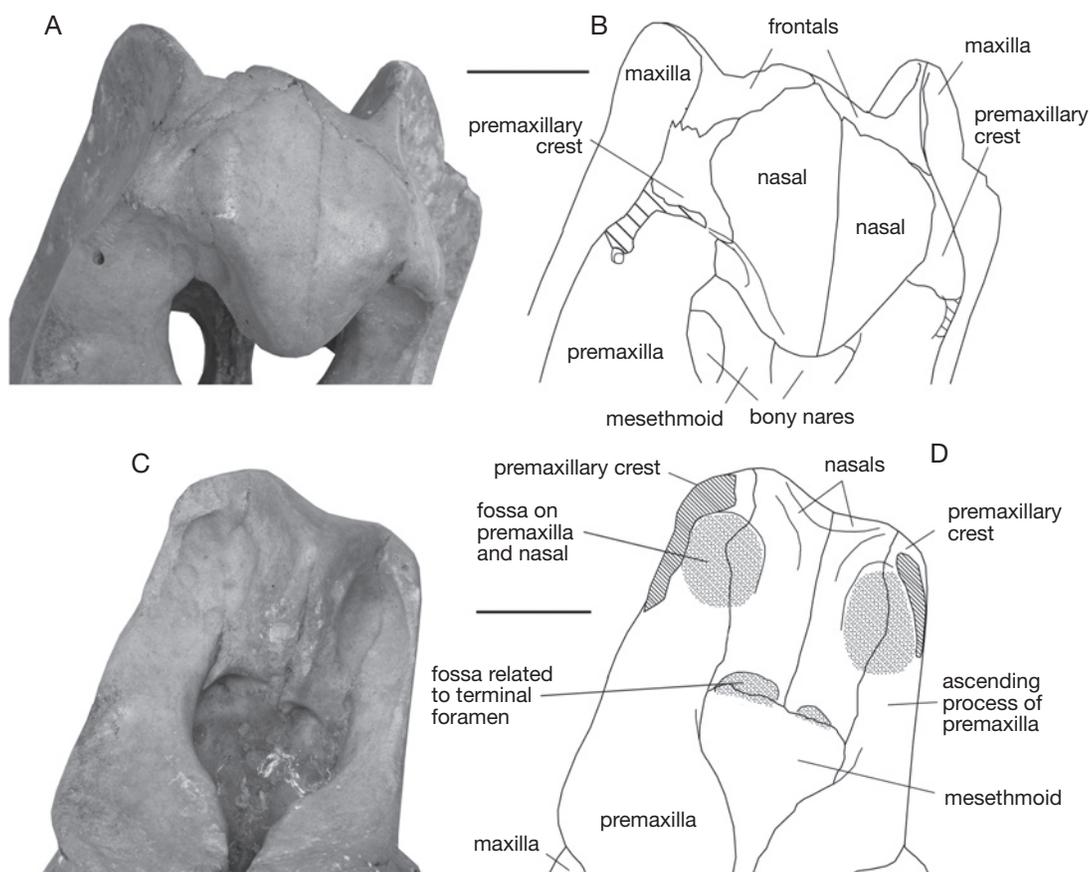
Fig. 9. — Vertex of skull of *Izikoziphius rossi* n. gen., n. sp. (SAM PQ 2086): **A**, dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: 5 cm.

crest, not extending on to the rostrum; mesethmoid distinctly keeled under the nasals; nasals much longer than wide and right side of vertex less elevated.

DESCRIPTION (FIGS 10; 11; TABLE 2)

The only known specimen is a well preserved skull including the complete rostrum, most of the dorsal surface of the cranium, and the vertex.

The moderately elongated rostrum is higher than wide at mid-length and the dorsal surface of the maxilla is narrow. The rostrum base is narrower than in *Izikoziphius rossi* n. gen., n. sp.; the widening toward the antorbital notch is abrupt. The thickened vomer completely fills the mesorostral groove and is slightly higher than the

premaxilla for its entire length. Only the apical premaxillary portion of the rostrum shows a concave dorsal surface. No alveolar groove could be detected.

The premaxillary foramen is posterior to the antorbital notch, roughly in line with the large, but transversely compressed, maxillary foramen. The slightly concave premaxillary sac fossa, as in *Izikoziphius rossi* n. gen., n. sp., overhangs the maxilla along its posterior part. The vertical anterior surface of the ascending process of the right premaxilla is excavated by a fossa less developed medially than in *Izikoziphius rossi* n. gen., n. sp., only contacting the nasal for a short distance. The left premaxilla is too damaged to determine
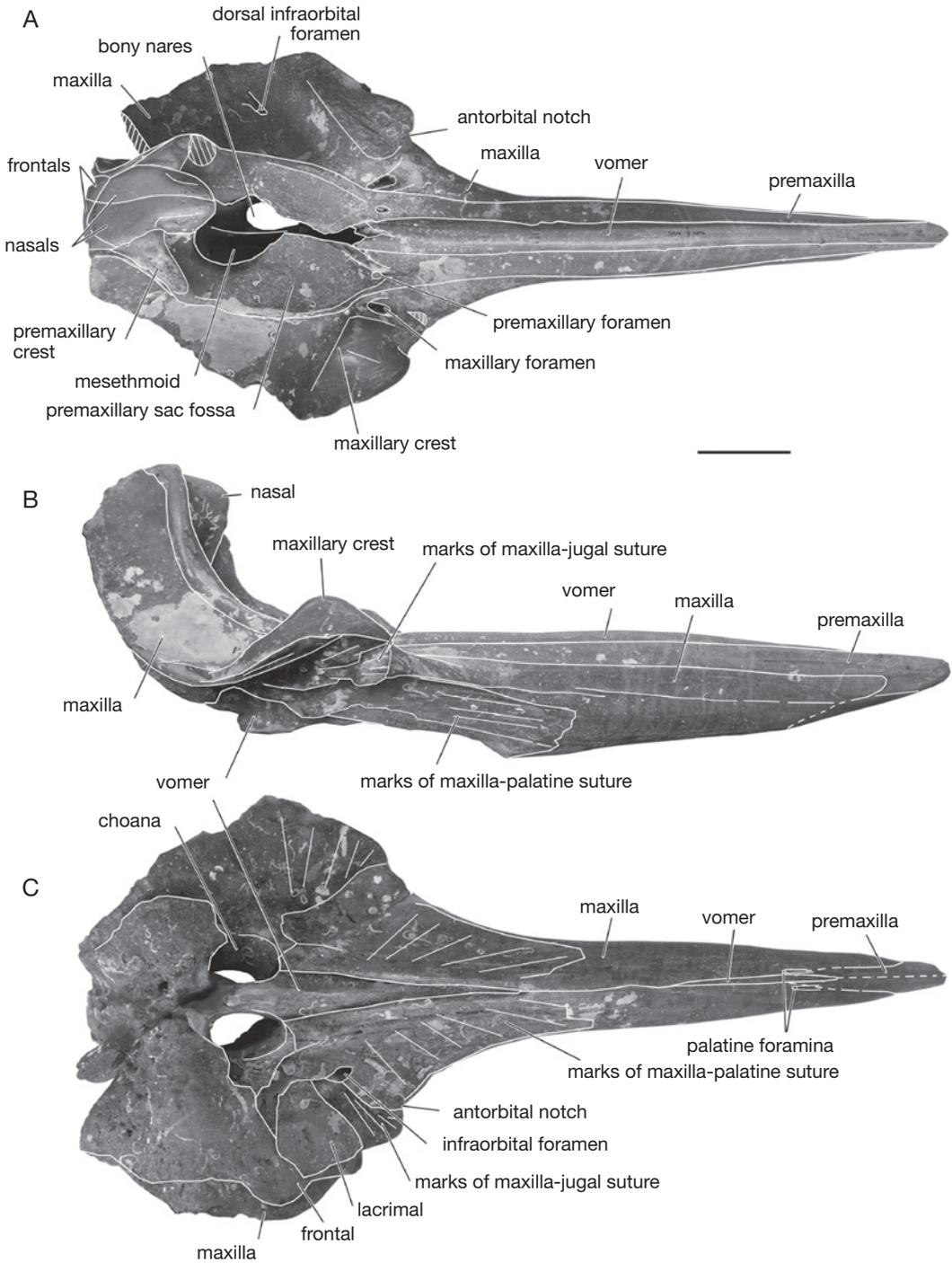
FIG. 10. — Skull of *Izikoziphius angustus* n. gen., n. sp. (SAM PQ 3004, holotype): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.
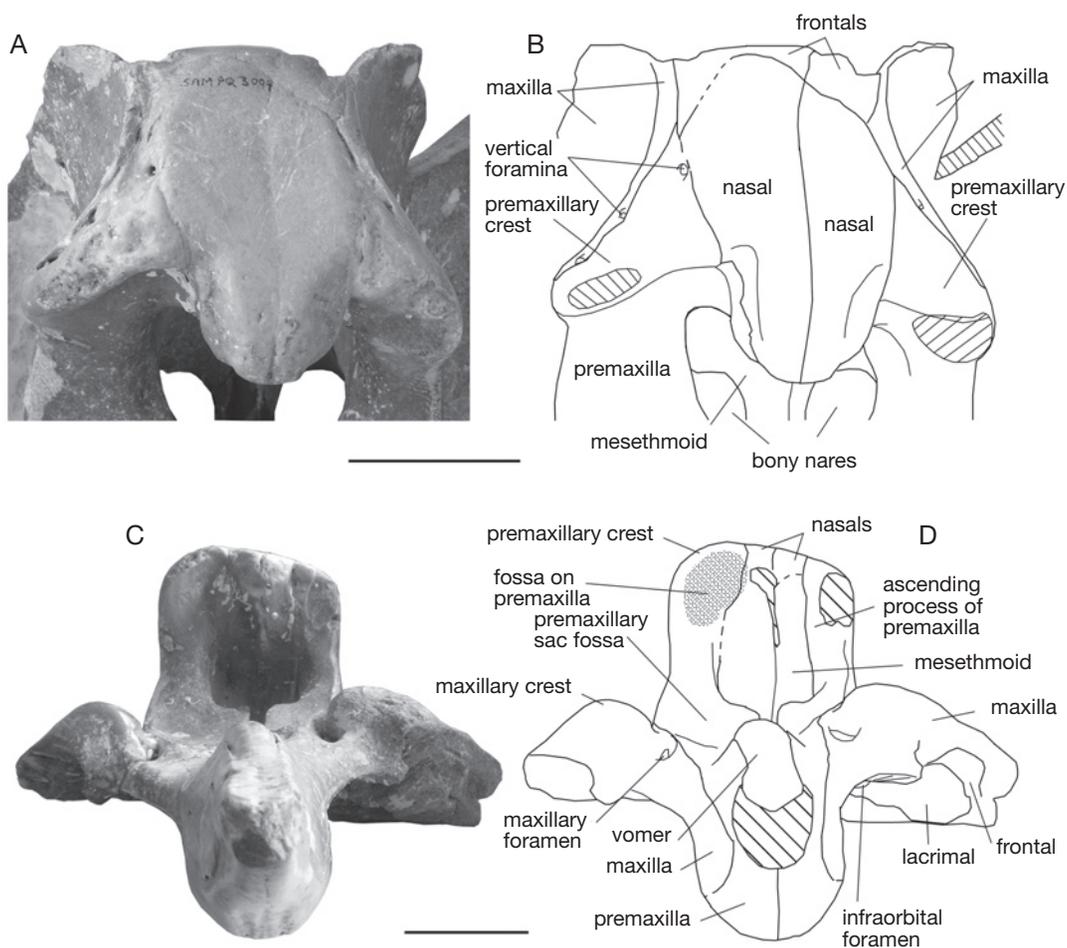
FIG. 11. — Skull of *Izikoziphius angustus* n. gen., n. sp. (SAM PQ 3004, holotype): **A**, detail of the vertex in dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: A, B, 5 cm; C, D, 10 cm.

the presence of a fossa. The keeled mesethmoid nearly completely covers the anterior surface of the nasals.

At the level of the preorbital process, the dome-like maxillary crest is more elevated than in *Iziko-ziphius rossi* n. gen., n. sp. and does not extend into the rostrum base.

On the elevated vertex the premaxillary crests are anterolaterally directed, similar to *Izikoziphius rossi* n. gen., n. sp. The nasals are longer compared to their width than in the latter species and their dorsal surface is flat.

Genus *Ziphius* Cuvier, 1823

TYPE AND ONLY SPECIES. — *Ziphius cavirostris* Cuvier, 1823, by monotypy.

Ziphius sp.

REFERRED SPECIMEN. — SAM PQ 2826, a fragment of cranium including most of the vertex, the right and part of the left premaxillary sac fossae.

LOCALITY. — Trawled at 35°11'S, 23°26'E, south coast of South Africa, Indian Ocean, depth of 1000 m.
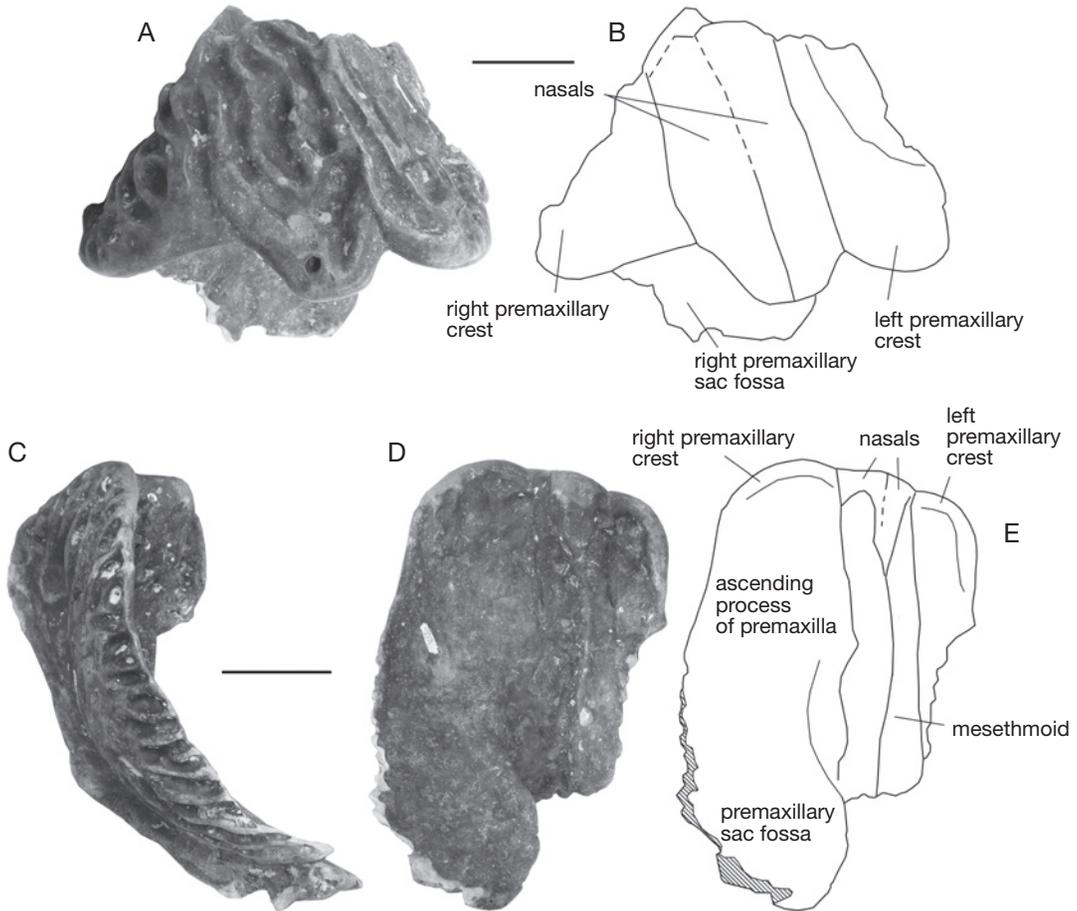
FIG. 12. — Skull fragment of *Ziphius* sp. (SAM PQ 2826): **A**, dorsal view; **B**, corresponding line drawing; **C**, lateral view; **D**, anterior view; **E**, corresponding line drawing. Scale bars: A, B, 5 cm; C-E, 10 cm.

DESCRIPTION AND DISCUSSION
(FIG. 12; TABLE 3)

The anterior surface of the ascending process of the premaxilla is distinctly concave up to its dorsal portion, overhanging the premaxillary sac fossa. The highly asymmetric premaxillary crests (the right crest two times wider than the left) are anterolaterally directed. The nasals are greatly elongated anteriorly, being almost twice longer than wide. Their median suture is anteriorly shifted to the left.

SAM PQ 2826 only differs from the Recent *Ziphius cavirostris* in: its larger size (see comparison of measurements with the largest skull of *Z. cavirostris* from the SAM collection, Table 3), the longer contact between nasal and premaxillary crest (a condition intermediary between *Z. cavirostris* and the Pliocene *Tusciziphius crispus*), and the relatively smaller nasals.

Considering the strong similarities with *Z. cavirostris* at the level of the vertex, this specimen should be referred to the same genus. Because of its clearly larger size it may represent a new species of *Ziphius*, but in view of its fragmentary preservation diagnosis at specific level is not currently possible.

Subfamily HYPEROODONTINAE Gray, 1866

TYPE GENUS. — *Hyperoodon* Lacépède, 1804.

OTHER GENERA INCLUDED. — *Indopacetus* Moore, 1968, *Mesoplodon* Gervais, 1850, *Ihlengesi* n. gen., *Africanacetus* n. gen., and *Khoikhoicetus* n. gen.

EMENDED DIAGNOSIS. — Hyperoodontinae differ from all the other Ziphiidae in the deep anteromedian excavation of the nasals.

DISCUSSION
Hyperoodontinae as defined here follows the content of the subfamily suggested by Muizon (1991); they correspond neither to the tribe Hyperoodontini *sensu* Moore 1968, including *Hyperoodon*, *Indopacetus*, *Mesoplodon*, and *Tasmacetus* nor to the subtribe Hyperoodontina *sensu* Moore 1968, only including *Hyperoodon* and *Mesoplodon*.

Genus *Khoikhoicetus* n. gen.

TYPE SPECIES. — *Khoikhoicetus agulhasis* n. gen., n. sp., by present designation.

ETYMOLOGY. — Khoikhoi is one of the ethnic groups occupying south-western Africa, closely related to the Bushmen, "cetus" from Latin, whale. Gender masculine.

DIAGNOSIS. — Same as for the species.

Khoikhoicetus agulhasis n. sp.

HOLOTYPE. — SAM PQ 2678, partial skull including most of the rostrum, the anterior part of the cranium, and the vertex.

ETYMOLOGY. — The holotype was found offshore from Cape Agulhas, a locality on the south coast of South Africa. The oceanic current running along the south-east coast of South Africa is also named Agulhas Current.

TYPE LOCALITY. — No exact locality. Trawled west of Cape Agulhas, south coast of South Africa, Indian Ocean.

DIAGNOSIS. — *Khoikhoicetus agulhasis* n. gen., n. sp. differs from all the other Hyperoodontinae in lacking the posterolaterally directed premaxillary crest. It differs from *Indopacetus* in: smaller size; narrow rostrum base; narrower premaxillary crests and nasals longer than the frontals on the vertex. It differs from *Africanacetus* n. gen., *Hyperoodon*, *Ihlengesi* n. gen., and *Mesoplodon* in:

shorter intrusion of the nasal in the premaxillary crest; premaxillary crest not overhanging the premaxillary sac fossa. The space between the premaxillary crests is wider than in *Hyperoodon* and *Mesoplodon*.

DESCRIPTION (FIGS 13; 14; TABLE 4)
On the only known skull, the rostrum was probably relatively short, not much longer than the preserved length. It is somewhat wider than high along its anterior half and as wide as high posteriorly. The mesorostral groove is filled by the vomer, with a median suture on the posterior half. The ventral margin of the alveolar groove, lacking marks of alveoli, extends to the antorbital notch; contrary to *Mesoplodon grayi*, *M. hectori*, *M. layardii*, and *M. slangkopi* n. sp. (see below) this feature is not visible in dorsal view.

The rostrum base lacks a prominental notch; the antorbital notch is wide and probably shallow, at the level of the premaxillary foramen and slightly anterior to the small maxillary foramen lying along the premaxilla-maxilla suture. Posterior to the antorbital notch, a low maxillary crest thickens the preorbital process, with a lateral slope similar to *Africanacetus* n. gen.

The weakly asymmetric premaxillary sac fossae are anteromedially tilted. The ascending process is moderately constricted in anterior view. The foramina for the terminal nerve in the mesethmoid are strongly asymmetric; the left foramen is much smaller than the right.

The premaxillary crest is thin and laterally elongated, with a vertical anterior surface. The posterior projection of the premaxilla along the nasal reaches the frontal. The anterolateral corner of the roughly pentagon-shaped nasals forms only a small part of the premaxillary crest; the dorsal surface is anteromedially depressed. The naso-frontal suture is anteriorly pointed; the left nasal extends longer posteriorly than the right nasal.

Genus *Ihlengesi* n. gen.

TYPE SPECIES. — *Ihlengesi saldanhae* n. gen., n. sp., by present designation.

ETYMOLOGY. — "Ihlengesi" means dolphin (smaller animal from the sea) in the native South African Xhosa language. Gender masculine.

DIAGNOSIS. — Same as for the species.
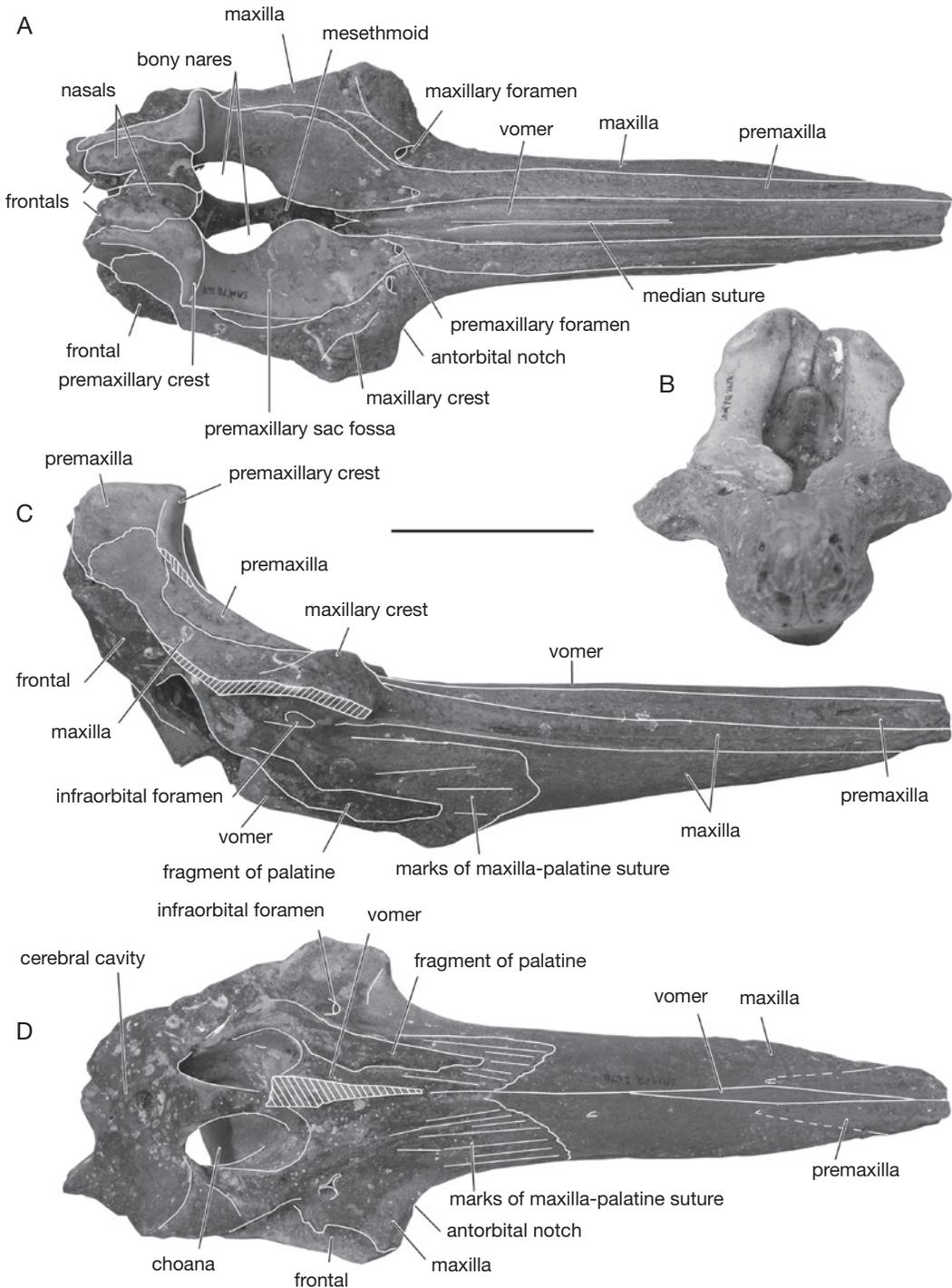
FIG. 13. — Skull of *Khoikhoicetus agulhasis* n. gen., n. sp. (SAM PQ 2678, holotype): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.
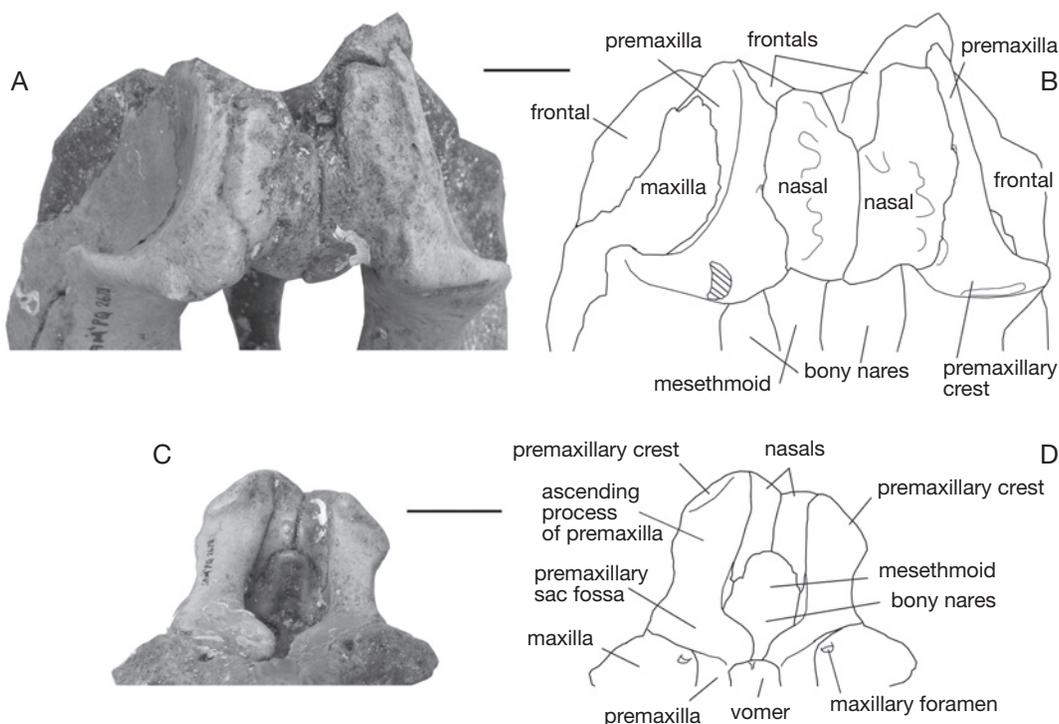
FIG. 14. — Vertex of skull of *Khoikhoicetus agulhasis* n. gen., n. sp. (SAM PQ 2678, holotype): **A**, dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: A, B, 2 cm; C, D, 5 cm.

Ihlengesi saldanhae n. sp.

HOLOTYPE. — SAM PQ 2792, partial skull including the rostrum base, anterior part of the cranium, and the vertex.

PARATYPE. — SAM PQ 69673, rostrum with anterior part of the cranium trawled off Cape Columbine, west coast of South Africa, Atlantic Ocean. This specimen was previously referred to "cf. *Mesoplodon densirostris*, *M. grayi*, *M. australis*" by Haughton (1956) on the basis of the location of the premaxillary foramina. This well preserved rostrum provides additional information for the species description.

ETYMOLOGY. — The holotype was found offshore from Saldanha Bay, a locality on the west coast of South Africa.

TYPE LOCALITY. — No exact locality. Trawled off Saldanha Bay, west coast of South Africa, Atlantic Ocean.

DIAGNOSIS. — *Ihlengesi saldanhae* n. gen., n. sp. differs from all other Hyperoodontinae in the shortened premaxillary sac fossa (ratio between measurements 15 and 16 lower than 0.30). It shares with *Africanacetus* n. gen., *Hyperoodon*, and *Mesoplodon:* the inclusion of the nasal into the premaxillary crest over at least half the length of the median margin of the crest and a deep anteromedian excavation of the nasals. Both characters are absent in *Khoikhoicetus* n. gen. and *Indopacetus*. It further differs from *Africanacetus* n. gen. in: smaller size; maxillary foramen close to the prominental notch at the rostrum base; roughly flat dorsal surface of the preorbital process and premaxillary sac fossa not laterally sloping. The space between the premaxillary crests is wider than in *Hyperoodon* and *Mesoplodon*.

DESCRIPTION (FIGS 15; 16; TABLE 4)

A large part of the elongated and transversely compressed rostrum, higher than wide, is preserved in SAM PQ 69673. The maxilla is roughly hidden from the dorsal view for the anterior half of the rostrum. A slight constriction is seen in dorsal view at *c.* 120 mm from the preserved apex. The vomer fills the mesorostral groove over its whole length.
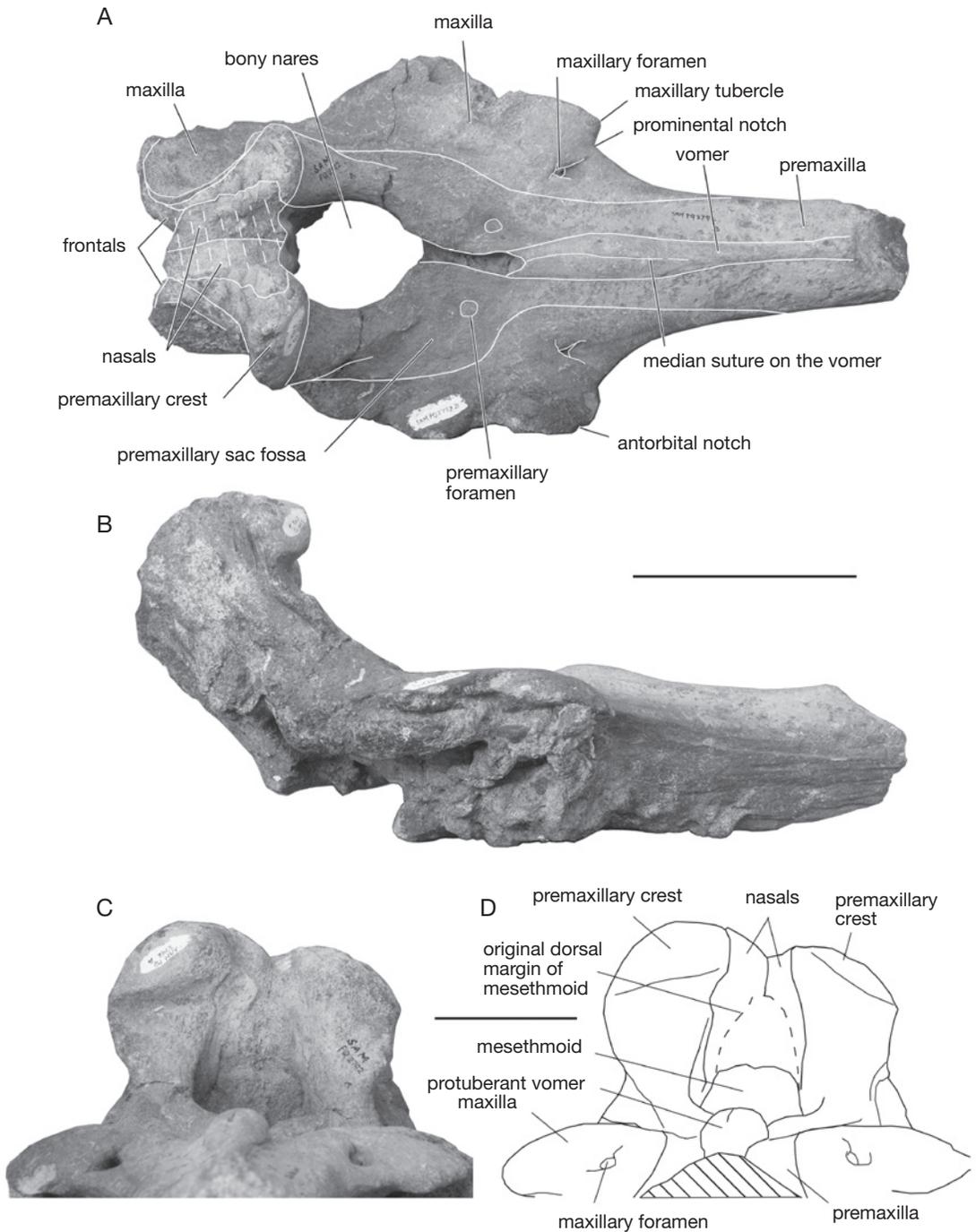
Fig. 15. — Skull of *Ihlengesi saldanhae* n. gen., n. sp. (SAM PQ 2792, holotype): **A**, dorsal view; **B**, lateral view; **C**, detail of the anterior view; **D**, corresponding line drawing. Scale bar: 10 cm.
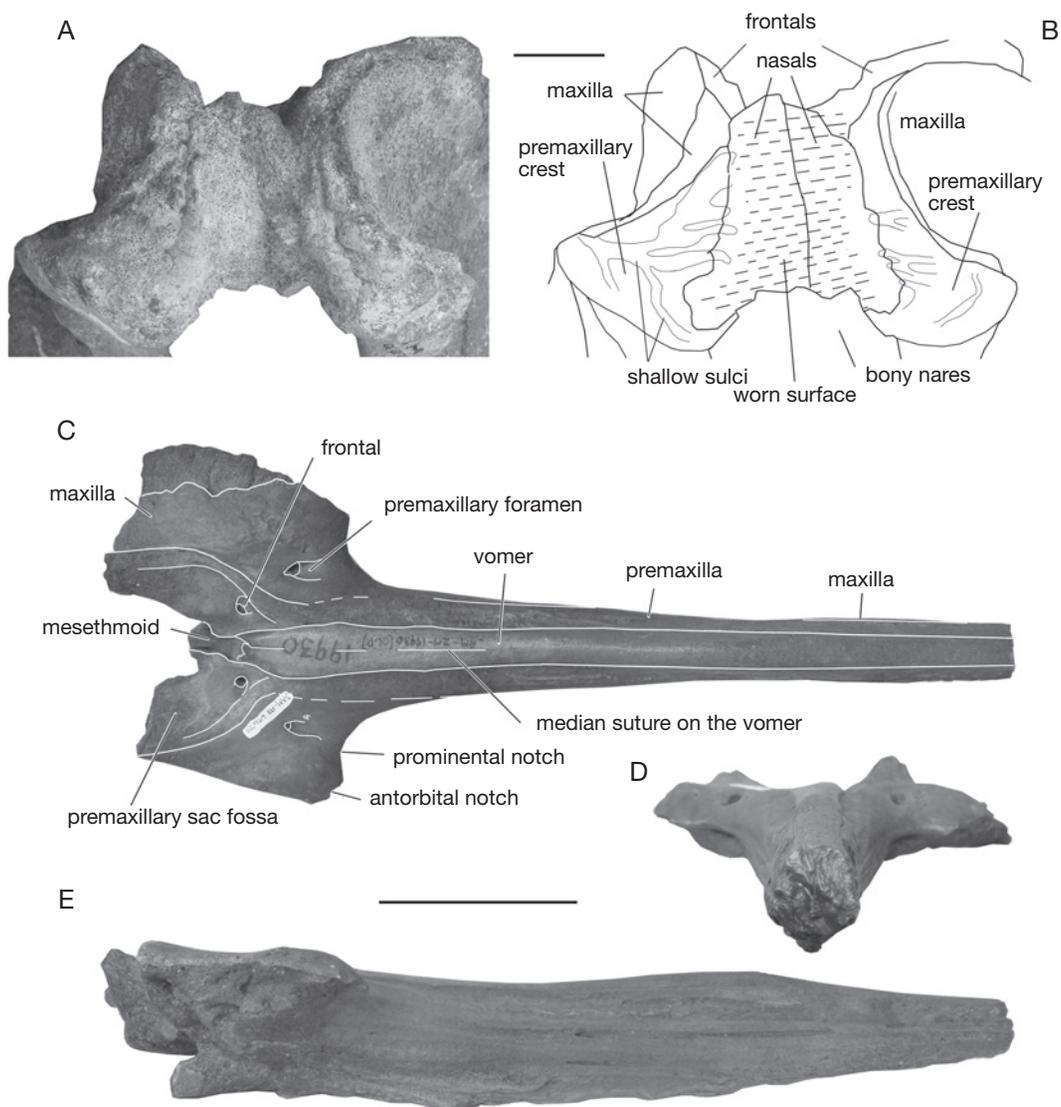
FIG. 16. — *Ihlengesi saldanhae* n. gen., n. sp.: **A**, **B**, vertex of skull (SAM PQ 2792, holotype); **A**, dorsal view; **B**, corresponding line drawing; **C-E**, incomplete skull (SAM PQ 69673, paratype); **C**, dorsal view; **D**, anterior view; **E**, lateral view. Scale bars: A, B, 2 cm; C-E, 10 cm.

In the holotype, the maximum height and width of the vomer is reached at the rostrum base; a second hump at one third of the length of the rostrum is observed in SAM PQ 69673 (not preserved in the holotype). A median suture marks the dorsal surface of the vomer at the rostrum base. In the holotype, the two premaxillae nearly contact each other above the mesorostral groove 70 mm anterior to the antorbital notches, a condition sometimes observed in Recent *Mesoplodon densirostris*. The ventrolateral surface of the rostrum of both specimens is worn.

The prominental notch is wide and roughly as deep as in *Mesoplodon layardii*. A reduced maxillary

foramen opens anterolaterally as a triangular fissure towards the prominental notch. At the level of the well developed maxillary tubercle, the preorbital process is barely convex, lacking a distinct maxillary crest.

The distinctly asymmetric premaxillary sac fossae are short; the distance between the anterior margin of the bony nares and the premaxillary foramen is small. The premaxillary foramen is located in a shallow depression behind the level of the antorbital notch. The ascending process of the premaxilla is strongly constricted in anterior view.

The vertex is moderately elevated. The premaxillary crest is thick and wide, posterolaterally directed. An oblique transverse groove limits ventrally the anterior surface of each premaxillary crest. The thicker right crest overhangs the ascending process. The lateral margins of the longitudinally elongated nasals are anteriorly diverging; the anterolateral corner is distinctly thrust into the medial part of the premaxillary crest. The anteromedial surface of the nasals is strongly excavated; it forms a deep vertical groove between the premaxillary crests. The naso-frontal suture is convex posteriorly.

Genus *Africanacetus* n. gen.

TYPE SPECIES. — *Africanacetus ceratopsis* n. gen., n. sp., by present designation.

ETYMOLOGY. — From "Africana", the Marine Coastal Management fishery research vessel, which trawled three specimens of this genus at the same locality off the south coast of South Africa, "cetus" from Latin, whale. Gender masculine.

DIAGNOSIS. — Same as for the species.

Africanacetus ceratopsis n. sp.

HOLOTYPE. — NMR 9991-00001993, a partial skull including the rostrum and the dorsal part of the cranium with the vertex.

REFERRED SPECIMENS. — SAM PQ 2162, trawled off Cape coast; SAM PQ 2235, trawled off Cape coast, Atlantic Ocean; SAM PQ 2708, trawled at 35°01'S, 24°06'E, south coast of South Africa, Indian Ocean, depth of 914 m; SAM PQ 2709, trawled at 35°01'S, 24°06'E, south coast of South Africa, Indian Ocean,

depth of 914 m; SAM PQ 2713, trawled at 35°01'S, 24°06'E, south coast of South Africa, Indian Ocean, depth of 914 m; SAM PQ 3002, trawled at 34°50'S 18°14'E, south of Cape Town, depth of 604 m; SAM PQ 3062, trawled off Cape coast; SAM PQ 69683, trawled off Cape Peninsula, between Cape Point and Slangkop lighthouse, depth of 160-170 m. Most of the referred specimens are rostra, usually preserved with the anterior of the cranium, but lacking the vertex. SAM PQ 69683 is an isolated vertex.

ETYMOLOGY. — From the combination of the following two Ancient Greek words: "keras" (genitive "keratos"), horn, and "opsis", aspect, appearance. For the protuberant paired maxillary crests.

TYPE LOCALITY. — No exact locality. Trawled south west off the South African coast, Atlantic Ocean, depth less than 600 m.

DIAGNOSIS. — *Africanacetus ceratopsis* n. gen., n. sp. differs from all other Hyperoodontinae in: presence of a dome-like elevated maxillary crest on the supraorbital process and laterally sloping premaxillary sac fossa. It shares with *Ihlengesi* n. gen., *Hyperoodon*, and *Mesoplodon*: the dorsal part of the ascending process of the premaxilla partly overhanging the bony nares, and the larger portion of the nasal thrust into the premaxillary crest, differing in these characters from *Khoikhoicetus* n. gen. and *Indopacetus*. It further differs from *Hyperoodon* and *Mesoplodon* in the wide median separation of the premaxillary crests.

DESCRIPTION (FIGS 17; 18; TABLE 4)
The robust rostrum is long (rostrum of SAM PQ 2235 originally longer than 671 mm) and elevated, higher than wide over its entire length. The vomer fills the mesorostral groove, showing a median suture, between its two thickened lateral walls, on its posterior part; the vomer is more elevated than the premaxilla over its complete length. The width of the vomer in the groove varies within the species, sometimes occupying most of the dorsal surface of the rostrum (e.g., SAM PQ 3002). It widens at mid-length on several specimens. At the contact with the premaxilla, the vomer usually shows a slight constriction and therefore the dorsal prominent part of the vomer slightly overhangs the premaxilla. The alveolar groove is barely visible.

The lateral margins of the rostrum diverge abruptly towards the prominental notches, creating a wide concave dorsal surface of the maxilla at the rostrum base, with an acute lateral margin. The antorbital
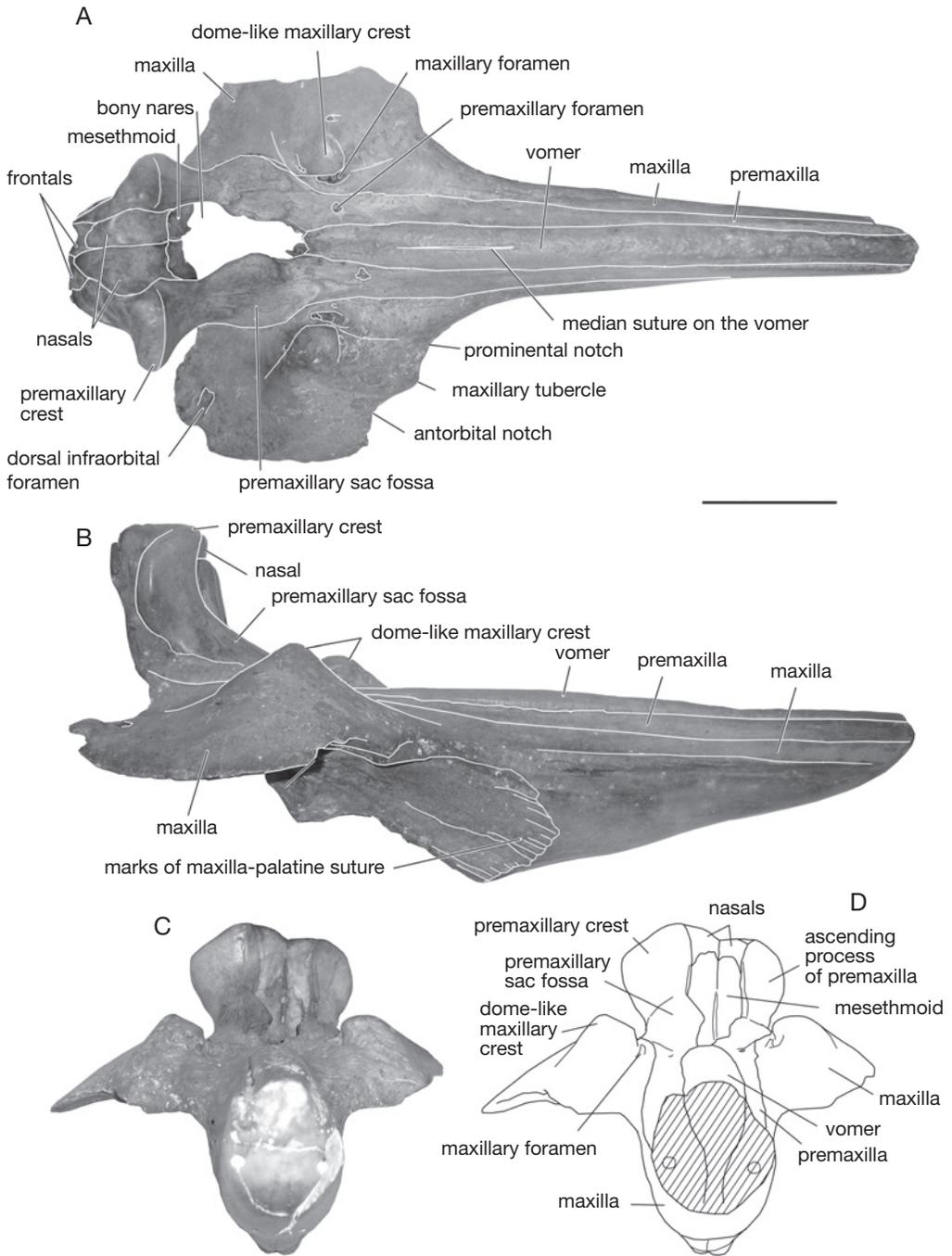
FIG. 17 – Skull of *Africanacetus ceratopsis* n. gen., n. sp. (NMR 9991-00001993, holotype); **A**, dorsal view; **B**, lateral view; **C**, anterior view; **D**, corresponding line drawing. Scale bar: 10 cm.
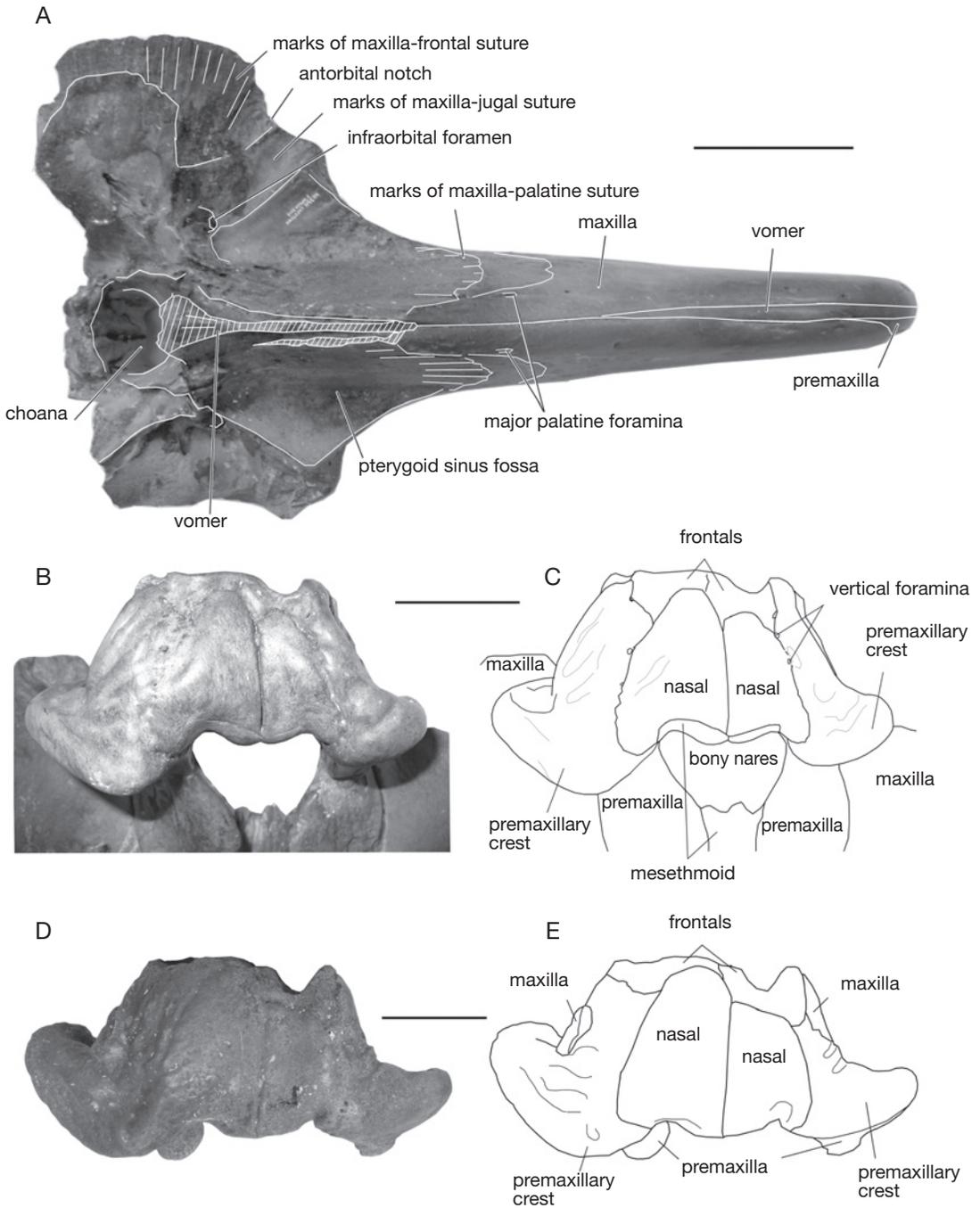
FIG. 18. — *Africanacetus ceratopsis* n. gen., n. sp.: **A-C**, skull (NMR 9991-00001993, holotype); **A**, ventral view; **B**, detail of vertex in dorsal view; **C**, corresponding line drawing. **D, E**, skull fragment (vertex) of *Africanacetus ceratopsis* n. gen., n. sp. (SAM PQ 69683); **D**, dorsal view; **E**, corresponding line drawing. Scale bars: A, 10 cm; B-E, 5 cm.

notch, separated from the prominental notch by a distinct maxillary tubercle, is positioned roughly at the longitudinal level of the premaxillary foramen. Posteromedial to the maxillary tubercle rises a characteristic elevated dome-like maxillary crest, not extending onto the rostrum base. The median slope of the dome is nearly vertical. In several specimens a large maxillary foramen is transversely compressed between this crest and the premaxilla, somewhat more posterior than the premaxillary foramen.

The premaxillary sac fossa is thicker medially, laterally lowering as in *Mesoplodon layardii*. The ascending process is short and constricted in anterior view; the upper part of its anterior surface is vertical. The lateral margins of the bony nares continue parallel dorsally. On the moderately elevated vertex, the premaxillary crest is thick, wide, and posterolaterally directed. The robust posterior projection of the premaxilla along the nasal contacts the frontal.

The nasals are distinctly wider anteriorly, with the anterolateral corner included in the posterior half of the premaxillary crest. The anteromedian surface of the nasals is excavated, leaving a large space between the premaxillary crests. The nasofrontal suture is W-shaped; the right nasal is longer than the left. The frontal is much shorter than the nasal on the vertex.

Genus *Mesoplodon* Gervais, 1850

Type species. — *Physeter bidens* Sowerby, 1804, by original designation.

Other Recent species included. — *Mesoplodon bowdoini* Andrews, 1908, *M. carlhubbsi* Moore, 1963, *M. densirostris* (Blainville, 1817), *M. europaeus* (Gervais, 1855), *M. ginkgodens* Nishiwaki & Kamiya, 1958, *M. grayi* Haast, 1876, *M. hectori* (Gray, 1871), *M. layardii* (Gray, 1865), *M. mirus* True, 1913, *M. perrini* Dalebout, Mead, Baker, Baker & van Helden, 2002, *M. peruvianus* Reyes, Mead & van Waerebeek, 1991, *M. stejnegeri* True, 1885, and *M. traversii* (Gray, 1874).

Fossil species included. — Until now, the only fossil species for which the vertex is described is *M. slangkopi* n. sp.

Mesoplodon slangkopi n. sp.

Holotype. — SAM PQ 2069, partial skull including the rostrum base and the dorsal surface of the cranium with the vertex.

Referred specimen. — SAM ZM 35107, partial skull including the deeply worn rostrum base, the premaxillary sac fossae, and the vertex, trawled off the South African coast.

Etymology. — The holotype was found offshore from Slangkop (meaning snake head in old Dutch), a locality on the south coast of South Africa.

Type locality. — No exact locality. Trawled off Slangkop, Cape Province.

Diagnosis. — *Mesoplodon slangkopi* n. sp. is a small member of the genus, with cranial dimensions close to *M. perrini* and *M. peruvianus*. It shares with *M. carlhubbsi*, *M. densirostris*, *M. grayi*, and *M. layardii* the extension of the ventral margin of the alveolar groove until the prominental notch. The rostrum base is narrower than in *M. bidens*, *M. bowdoini*, *M. europaeus*, *M. ginkgodens*, *M. hectori*, *M. mirus*, *M. peruvianus*, *M. stejnegeri*, and *M. traversii*; the prominental notch is more excavated than in *M. bidens*, *M. hectori*, *M. mirus*, *M. perrini*, *M. peruvianus*, and *M. stejnegeri*; the maxillary crest is distinctly lower than in *M. bowdoini*, *M. carlhubbsi*, *M. europaeus*, *M. ginkgodens*, *M. mirus*, and *M. traversii*; the maxillary ridge along the lateral margin of the supraorbital process is much lower than in *M. carlhubbsi* and *M. layardii*; the premaxillary foramen is more anterior, closer to the level of the antorbital notch, than in *M. bowdoini*, *M. carlhubbsi*, *M. densirostris*, and *M. stejnegeri*; the premaxillary sac fossae and premaxillary crests are less asymmetric than in *M. layardii* and *M. traversii*; the distance between the premaxillary crests is shorter than in *M. carlhubbsi*, *M. layardii*, and *M. mirus*; the premaxillary crest (especially the right crest) is laterally shorter than in *M. bowdoini*, *M. carlhubbsi*, *M. densirostris*, *M. layardii*, *M. mirus*, and *M. traversii*; the premaxillary crest overhangs the bony nares more than in *M. grayi*, less than in *M. bowdoini* and *M. traversii*, the nasal is shorter along the median margin of the premaxillary crest than in *M. bowdoini*, *M. ginkgodens*, and *M. traversii*; the nasal is longer posteriorly, compared to the frontal, than in *M. bidens*, *M. xcarlhubbsi*, *M. densirostris*, *M. hectori*, *M. layardii*, *M. peruvianus*, and *M. stejnegeri* and the vertex is wider posterior to the premaxillary crests than in *M. grayi*, *M. peruvianus*, and *M. traversii*.

DESCRIPTION (Figs 19; 20; Table 4)
From its base, the rostrum quickly narrows forwards. The anterior part is unknown but the rostrum is
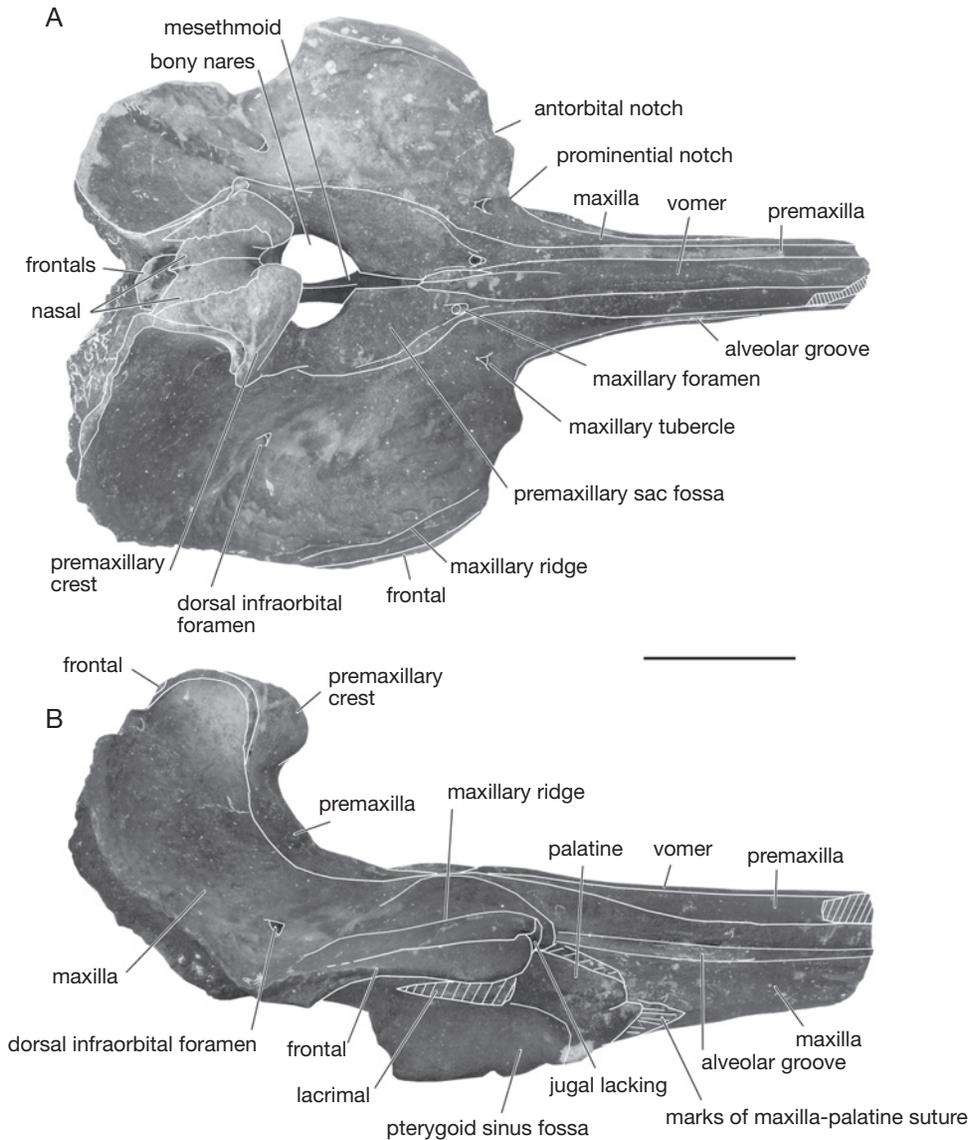
FIG. 19. — Skull of *Mesoplodon slangkopi* n. sp. (SAM PQ 2069, holotype): **A**, dorsal view; **B**, lateral view. Scale bar: 10 cm.

much higher than wide along its preserved part; it is particularly narrow compared to the width of the cranium at the antorbital notch, a condition somewhat similar to *Mesoplodon grayi*. The vomer fills the mesorostral groove, forming a hump at the rostrum base; a median suture is seen on its dorsal surface, shifted to the left. The alveolar groove is distinct until the rostrum base; the ventral margin of the groove extends to the prominental notch and is visible in dorsal view, strengthening the lateral margin of the rostrum base, as in *M. grayi*, and *M. layardii*. Shallow depressions in the groove
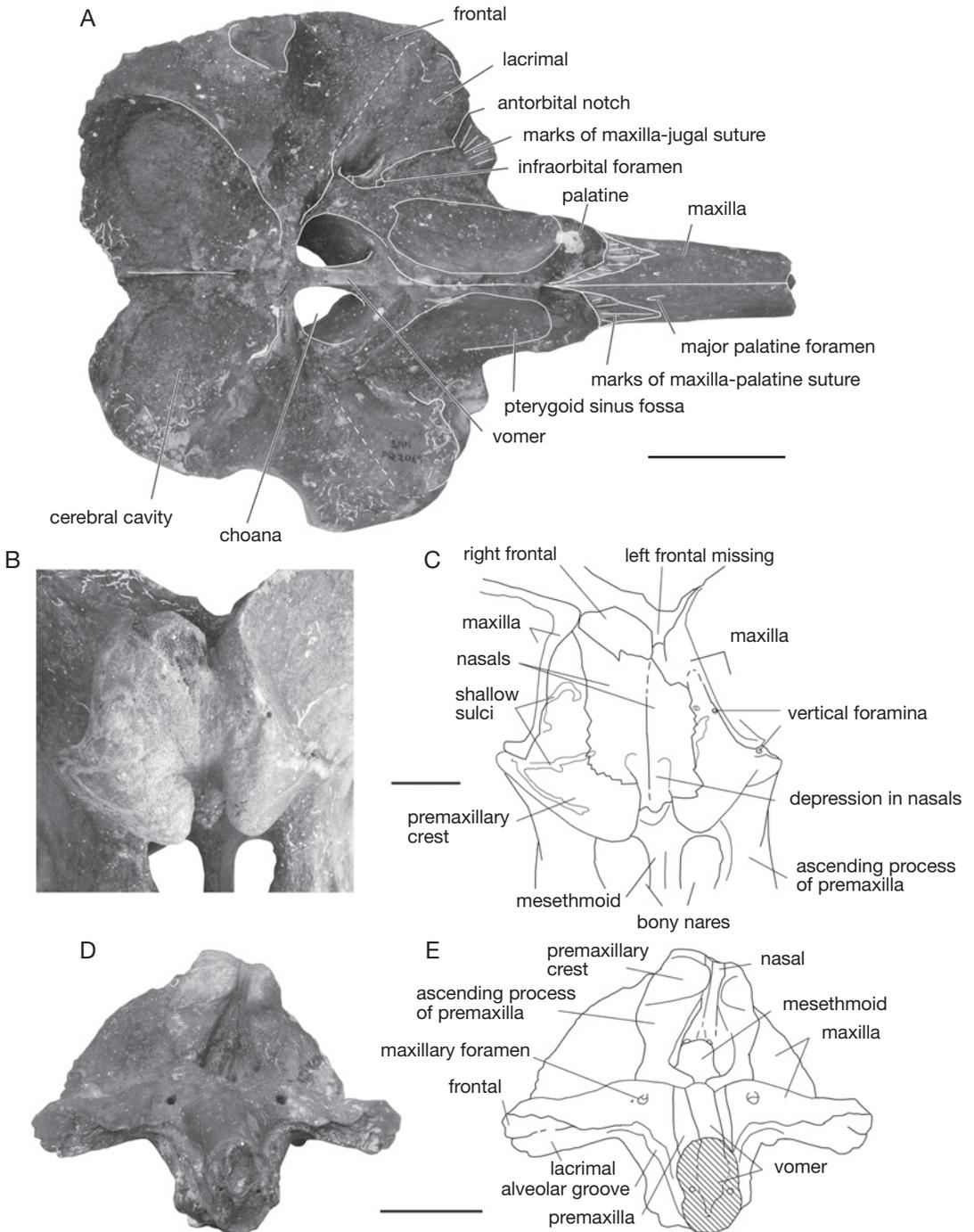
FIG. 20. — Skull of *Mesoplodon slangkopi* n. sp. (SAM PQ 2069, holotype): **A**, ventral view; **B**, detail of the vertex in dorsal view; **C**, corresponding line drawing; **D**, anterior view; **E**, corresponding line drawing. Scale bars: A, D, E, 10 cm; B, C, 2 cm.

indicate remnants of alveoli. The maxilla-palatine suture is pointed and located 87 mm anterior to the antorbital notch. The preserved anterior part of the pterygoid is robust and anterolaterally limits an elliptical pterygoid sinus fossa distinctly anterior to the prominental notch.

A small foramen pierces the maxilla close to the wide prominental notch. Only a low crest follows the prominent maxillary tubercle posteriorly. A low maxillary ridge extends parallel to and near the lateral margin of the supraorbital process.

The premaxillary foramen is located at the level of the antorbital notch. The ascending process of the premaxilla is strongly constricted in anterior view; the lateral margins of the bony nares are strongly converging dorsally.

The vertex is moderately elevated and transversely compressed in its posterior part. The thick and wide, distinctly posterolaterally directed and asymmetric premaxillary crests overhang the ascending process and the bony nares. The distance between the two crests is small and an oblique transverse groove limits ventrally the anterior surface of each crest, with a general configuration close to *M. densirostris*. The posterior projection of the premaxilla along the nasal is approximately as long as the nasal and much widened, especially on the right side, similar to *M. hectori*. The lateral margins of the elongated nasals are parallel; the anterolateral corner of each nasal is included in the corresponding premaxillary crest for approximately half the median length of the crest. The anteromedian excavation of the nasals is deep and narrow. The frontals were probably much shorter than the nasals.

Ziphiidae *incertae sedis*

Genus *Nenga* n. gen.

TYPE SPECIES. — *Nenga meganasalis* n. gen., n. sp., by present designation.

ETYMOLOGY. — "Nenga" means whale (larger animal from the sea) in the native South African Xhosa language. Gender masculine.

DIAGNOSIS. — Same as for the species.

Nenga meganasalis n. sp.

HOLOTYPE. — SAM PQ 69675, a partial skull including the rostrum, the premaxillary sac fossae, and the vertex.

REFERRED SPECIMENS. — SAM PQ 2117, a partial rostrum, trawled off the South African coast; SAM PQ 2339, a partial skull including the rostrum base, the premaxillary sac fossae, and the vertex, trawled off Cape coast; SAM PQ 69676, a partial rostrum and anterior of the cranium, trawled west of Cape Point, Atlantic Ocean (depth 347 m).

ETYMOLOGY. — From the Ancient Greek "megas", large; "meganasalis" for the large nasals of this species.

TYPE LOCALITY. — No exact locality. Trawled west of Cape Town, Atlantic Ocean.

DIAGNOSIS. — *Nenga meganasalis* n. gen., n. sp. differs from all the other Ziphiidae in the nearly rectangular wide nasals occupying most of the vertex dorsally. It differs from the Ziphiinae in the mesorostral ossification of the mesethmoid and it lacks the main synapomorphy of the subfamily, the anterolaterally directed premaxillary crest. It differs from the Hyperoodontinae, *Pterocetus* n. gen., *Tasmacetus*, and *Xhosacetus* n. gen., in the mesorostral ossification of the mesethmoid and lacks the constriction of the ascending process of the premaxilla and the intrusion of the nasal in the narrow premaxillary crest. It differs from *Ninoziphius* in the rostrum elevated at its base and the reduction of the maxillary alveoli.

DESCRIPTION (FIGS 21-23; TABLE 5)
The almost complete rostrum of the holotype is robust and long. The maxilla ends more than 45 mm from the apex. At mid-length, the rostrum is wider than high. The morphology of the rostrum base varies within the species: it is wider in SAM PQ 2339 and SAM PQ 69676 with a wide concave sub-horizontal surface of the maxilla following anteriorly the large maxillary foramen. In the holotype and SAM PQ 2117, the dorsal surface of the maxilla narrows more rapidly anteriorly, while the lateral slope is more pronounced. The lateral margin of the maxilla at the rostrum base is acute. The vomer is weakly thickened or not at all in the widely open mesorostral groove. In specimen SAM PQ 69676, the mesorostral groove is posteriorly filled by the ossified mesethmoid for a length of more than 100 mm (specimen incomplete anteriorly); in this species the ossified mesethmoid might have occupied
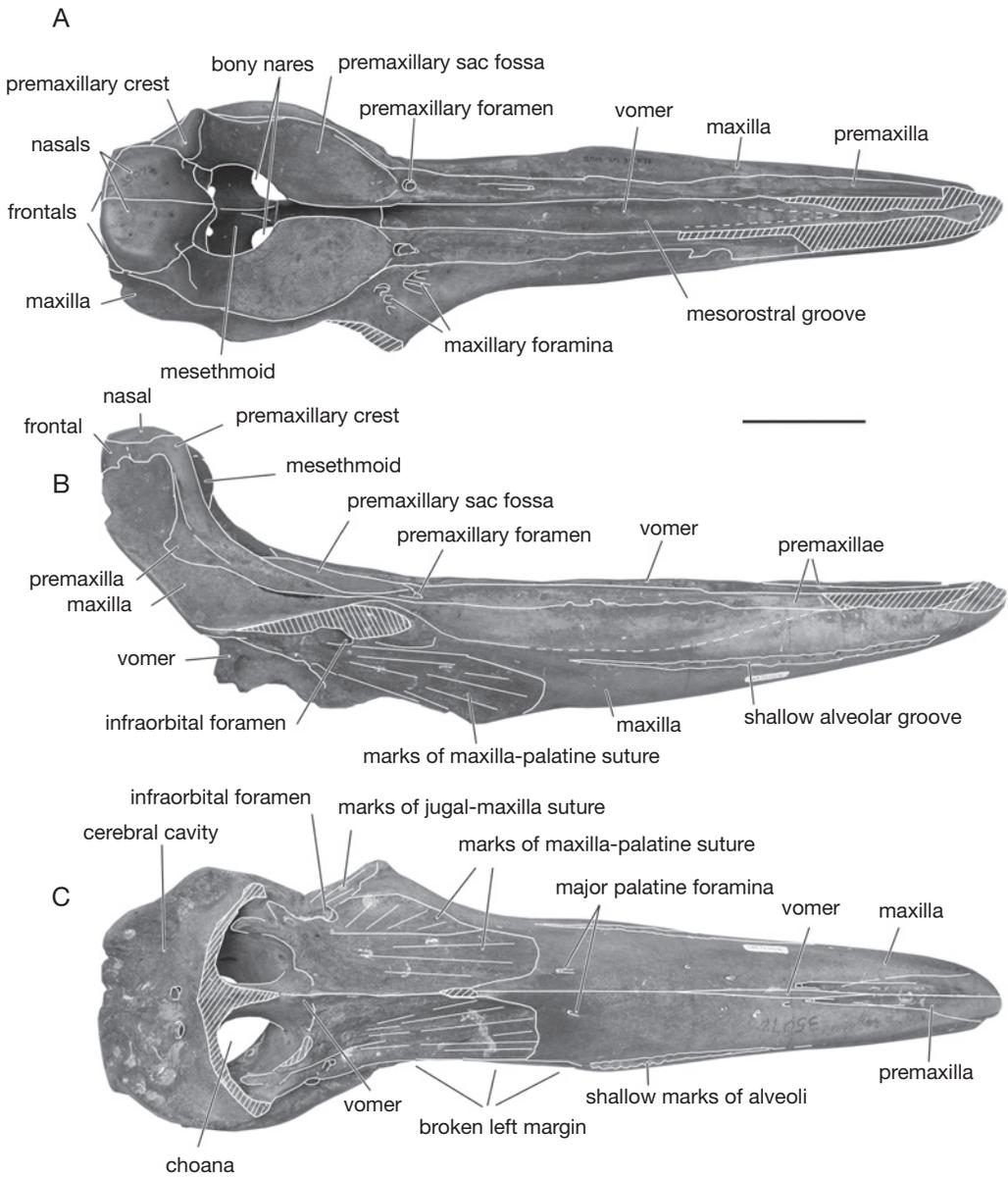
Fig. 21. — Skull of *Nenga meganasalis* n. gen., n. sp. (SAM PQ 69675, holotype): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.

most of the length of the mesorostral groove. Shallow alveoli marks are still visible on the maxillary alveolar groove of the holotype.

The premaxillary sac fossa is large and slightly concave; it rises slowly posteriorly until the ascending

process. The ascent to the vertex from this point is more abrupt, but barely reaching vertical. In anterior view, the lateral margins of the premaxillae are roughly parallel until the transversely directed, weakly laterally developed, premaxillary crests.
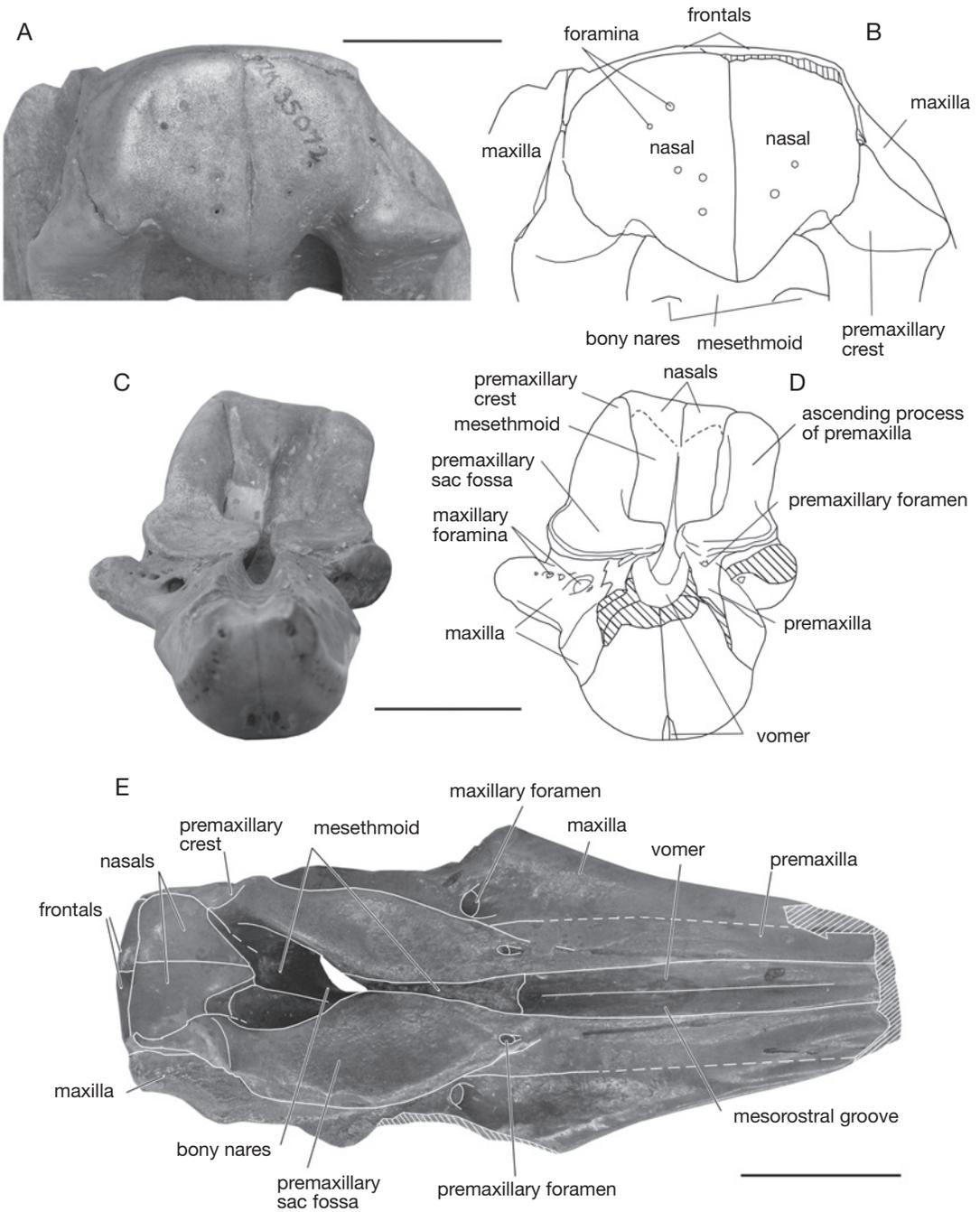
FIG. 22. — *Nenga meganasalis* n. gen., n. sp.: **A-D**, skull (SAM PQ 69675, holotype); **A**, detail of the vertex in dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing; **E**, incomplete skull (SAM PQ 2339), dorsal view. Scale bars: A, B, 5 cm; C-E, 10 cm.

mesorostral groove
filled by the mesethmoid

concave dorsal surface
of the vomer originally filled
by the mesethmoid

broken surface of the mesethmoid
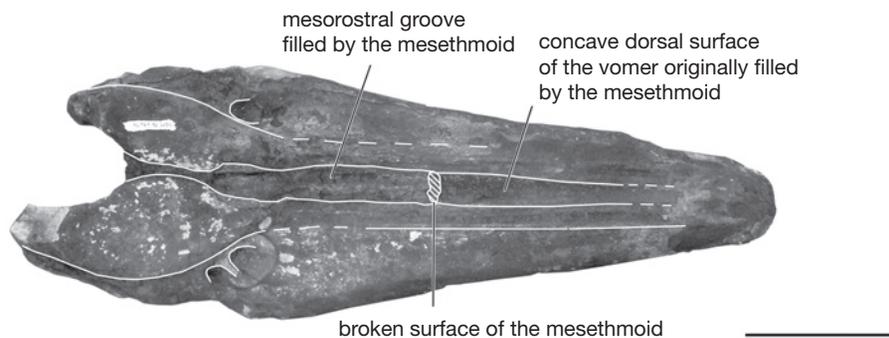
FIG. 23. — Rostrum of *Nenga meganasalis* n. gen., n. sp. (SAM PQ 69676), in dorsal view showing the mesorostral groove partially filled by the mesethmoid. Scale bar: 10 cm.

The posterior projection of the premaxilla along the nasal contacts the frontal. The outline of the bony nares varies within the species being more V-shaped and longer in SAM PQ 2339.

In the holotype, several smaller foramina pierce the maxilla just behind the large maxillary foramen at the rostrum base. The relative position of maxillary and premaxillary foramina varies within the species, around the level of the antorbital notch.

The nasals occupy a large nearly rectangular surface on the wide and low vertex, much longer than the short strip of frontals (complete on SAM PQ2339), and wider than long. The lateral margin of the nasal is moderately convex and its anterolateral corner forms only a small part of the premaxillary crest. A vertical groove excavates the anterior margin of each nasal and the rounded anterior point of the nasals is only slightly more anterior than the premaxillary crests. The naso-frontal suture is roughly rectilinear. The morphology of the posterior portion of the vertex is not as well preserved as in *Microberardius* n. gen. and in the Berardiinae indet. described above. We therefore are unable to detect the presence or absence of the interparietal, preventing firm attribution to the subfamily Berardiinae (see phylogeny below).

Genus *Xhosacetus* n. gen.

TYPE SPECIES. — *Xhosacetus hendeysi* n. gen., n. sp., by present designation.

ETYMOLOGY. — From Xhosa, one of the official languages of South Africa, characterized by prominent clicks (the word Xhosa itself starts with a click), somewhat reminiscent of the echolocative clicks produced by odontocetes, and from Latin "cetus", whale. Gender masculine.

DIAGNOSIS. — Same as for the species.

Xhosacetus hendeysi n. sp.

HOLOTYPE. — SAM PQ 2082, a partial skull including most of the rostrum, anterior part of the cranium, and the vertex.

ETYMOLOGY. — Honouring Dr. Q. Brett Hendey, geologist and palaeontologist formerly at the SAM who dedicated his career to Tertiary terrestrial and marine mammals from South Africa, particularly from the famous site of Langebaanweg.

TYPE LOCALITY. — No data. Trawled off the South African coast.

DIAGNOSIS. — *Xhosacetus hendeysi* n. gen., n. sp. differs from all other ziphiids except *Nenga* n. gen. in possessing relatively large nasals, as wide as long, with roughly parallel lateral margins. It further differs from members of the Berardiinae and Ziphiinae in: the short intrusion of the nasal in the premaxillary crest; the filling of the mesorostral groove by the vomer at least partly by thickening of the lateral walls and from the Berardiinae in a moderate constriction of the ascending process of the premaxilla. It differs from the Hyperoodontinae and Ziphiinae in the transversely oriented premaxillary crest. It further differs from the Hyperoodontinae, *Pterocetus* n. gen., and *Tasmacetus* in the lack of an anteromedian depression of the nasals and from the same group, except *Khoikhoicetus* n. gen.,
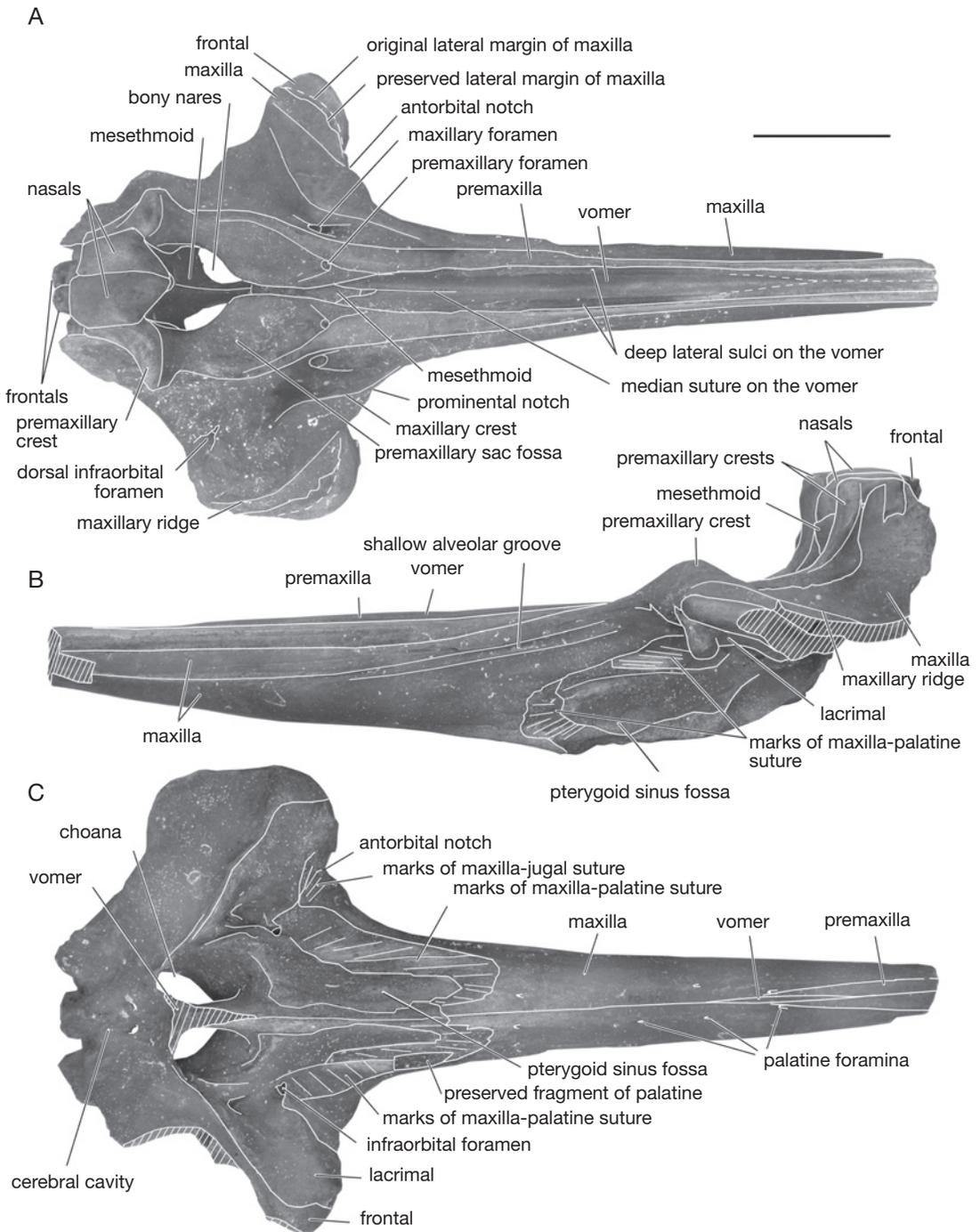
FIG. 24. — Skull of *Xhosacetus hendeysi* n. gen., n. sp. (SAM PQ 2082, holotype): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.
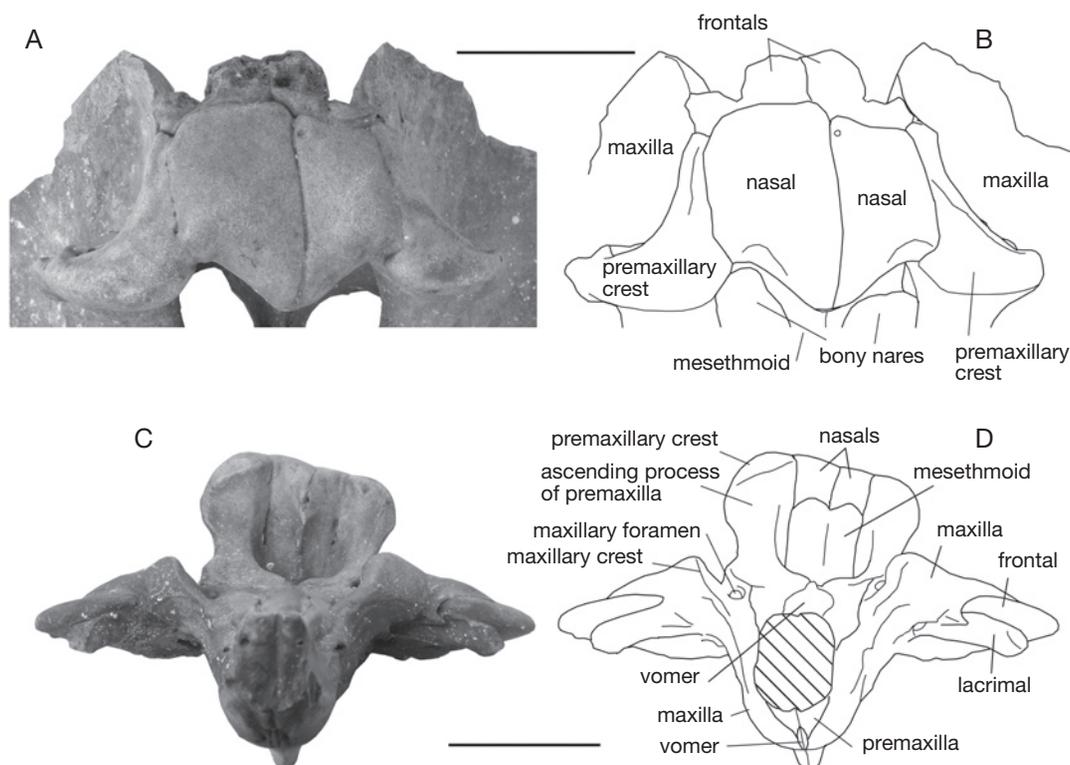
FIG. 25. — Skull of *Xhosacetus hendeysi* n. gen., n. sp. (SAM PQ 2082, holotype): **A**, detail of the vertex in dorsal view; **B**, corresponding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: A, B, 5 cm; C, D, 10 cm.

in a weaker constriction of the ascending process of the premaxilla. It differs from *Tasmacetus* in: smaller size, mesorostral groove filled with ossified vomer and shallower alveolar groove. It differs from *Ninoziphius* in: elevated and narrow rostrum, mesorostral groove filled with ossified vomer and reduction of the maxillary alveoli.

DESCRIPTION (FIGS 24; 25; TABLE 5)
The anterior part of the rostrum is not complete; it might have originally measured 500 mm; its preserved part is higher than wide. The surface of the premaxilla is nearly vertical anteriorly. The widening of the rostrum posteriorly is progressive up to the faint prominental notch, followed by an abrupt divergence towards the antorbital notch. The shallow alveolar groove has slightly depressed areas interpreted as remains of alveoli.

The vomer completely fills the mesorostral groove and its height in the groove decreases anteriorly.

A deep sulcus separates the thickened vomer from the premaxilla laterally for its whole length. At the rostrum base, a median suture between the two walls of the vomer joins the anterior point of the ossified mesethmoid, at the level of the prominental notch.

The premaxillary foramen is located just posterior to the shallow antorbital notch. The concave premaxillary sac fossae are weakly asymmetric. In anterior view a distinct constriction marks the lateral margin of the ascending process of the premaxilla.

A sharp maxillary crest separates the large maxillary foramen from the antorbital notch. The lateral slope of the crest, leading to the laterally developed preorbital process, is weaker than the median slope. The left crest is more robust. The lacrimal bears a prominent knob-like anterolateral projection.

The vertex is moderately elevated and the dorsal part of the ascending process of the premaxilla is vertical. The premaxillary crest is moderately thickened and transversely oriented, slightly overhanging the premaxillary sac fossa on the right side. The posterior projection of the premaxilla along the nasal contacts the frontal on both sides. The nasals are large, as wide as long, with roughly parallel lateral margins. The right nasal is somewhat wider and longer than the left nasal. The dorsal surface of the nasals is slightly sloping without an anteromedian depression; the anterior margin is excavated by a vertical groove and the anterolateral corner forms only a small part of the premaxillary crest. The frontal was originally probably much shorter than the nasal.

Genus *Pterocetus* n. gen.

TYPE SPECIES. — *Pterocetus benguelae* n. gen., n. sp., by present designation.

ETYMOLOGY. — From Ancient Greek "pteryx", wing, for the large wing-like preorbital processes and from Latin "cetus", whale. Gender masculine.

DIAGNOSIS. — Same as for the species.

Pterocetus benguelae n. sp.

HOLOTYPE. — SAM PQ 2803, partial skull including most of the rostrum, the anterior part of the cranium, and the vertex.

REFERRED SPECIMENS. — SAM PQ 69684, partial skull including a part of the rostrum and anterior part of the cranium, trawled west of Cape Town, Atlantic Ocean; SAM PQ 2163, partial skull including rostrum base and anterior part of the cranium, trawled off the South African coast.

ETYMOLOGY. — From Benguela Current, the oceanic current running along south-east Africa, probably since the Miocene epoch. The holotype of this species was found off the west coast of South Africa.

TYPE LOCALITY. — No exact locality. Trawled south of Saldanha Bay, west coast of South Africa, Atlantic Ocean, depth of 700 m.

DIAGNOSIS. — *Pterocetus benguelae* n. gen., n. sp. differs from all other Ziphiidae in wider and deeper antorbital notch with much anterolaterally developed preorbital process and from all other Ziphiidae, except *Indopacetus* and *Ziphirostrum*, in the premaxillary foramen positioned distinctly anterior to the level of the antorbital notch. It shares with the Hyperoodontinae, and *Tasmacetus* an anteromedian depression of the dorsal surface of the nasals and a strong constriction of the ascending process of the premaxilla. It differs from Hyperoodontinae in lesser dorsomedial reabsorbing of the nasals. It differs from *Tasmacetus* in: smaller size; less pointed rostrum with narrower rostrum base; mesorostral groove filled with vomer and a shallower alveolar groove. It further differs from *Xhosacetus* n. gen. in the lower maxillary crest. It differs from *Ninoziphius* in: elevated and narrow rostrum; mesorostral groove filled with ossified vomer and reduction of the maxillary alveoli.

DESCRIPTION (FIGS 26; 27; 29A, B; TABLE 5)

None of the three known specimens includes the apex of the rostrum; several centimetres are probably missing in the holotype and SAM PQ 69684.

The rostrum is moderately elongated, slightly higher than wide with lateral margins parallel for most of its length. The mesorostral groove is completely filled by the vomer. A distinct median suture is visible on the vomer for the first centimetres of the rostrum base, indicating a posterior development of the bone by thickening of the lateral walls until their median contact. A shallow alveolar groove is still present without alveoli marks. The acute ventral margin of the alveolar groove extends until the antorbital notch where it ventrally limits a small basin.

The premaxillary foramen is located distinctly anterior to the antorbital notch, which indicates an elongated premaxillary sac fossa, a character also present in *Indopacetus*. An even more anterior position of the premaxillary foramen is seen for example in *Ziphius cavirostris* and *Ziphirostrum marginatum*, but associated with a deep prenarial basin. A large circular maxillary foramen opens anterodorsally just medial to the antorbital notch. The notch is widely open and deep, because of the strong development of the preorbital process, which forms a peculiar anterolateral extension of the cranium. In anterior view, the frontal is visible in the preorbital process between maxilla and lacrimal.

In anterior view, the ascending process of the premaxilla is strongly constricted ventral to the vertical, thick and wide, transversely directed premaxillary crest.
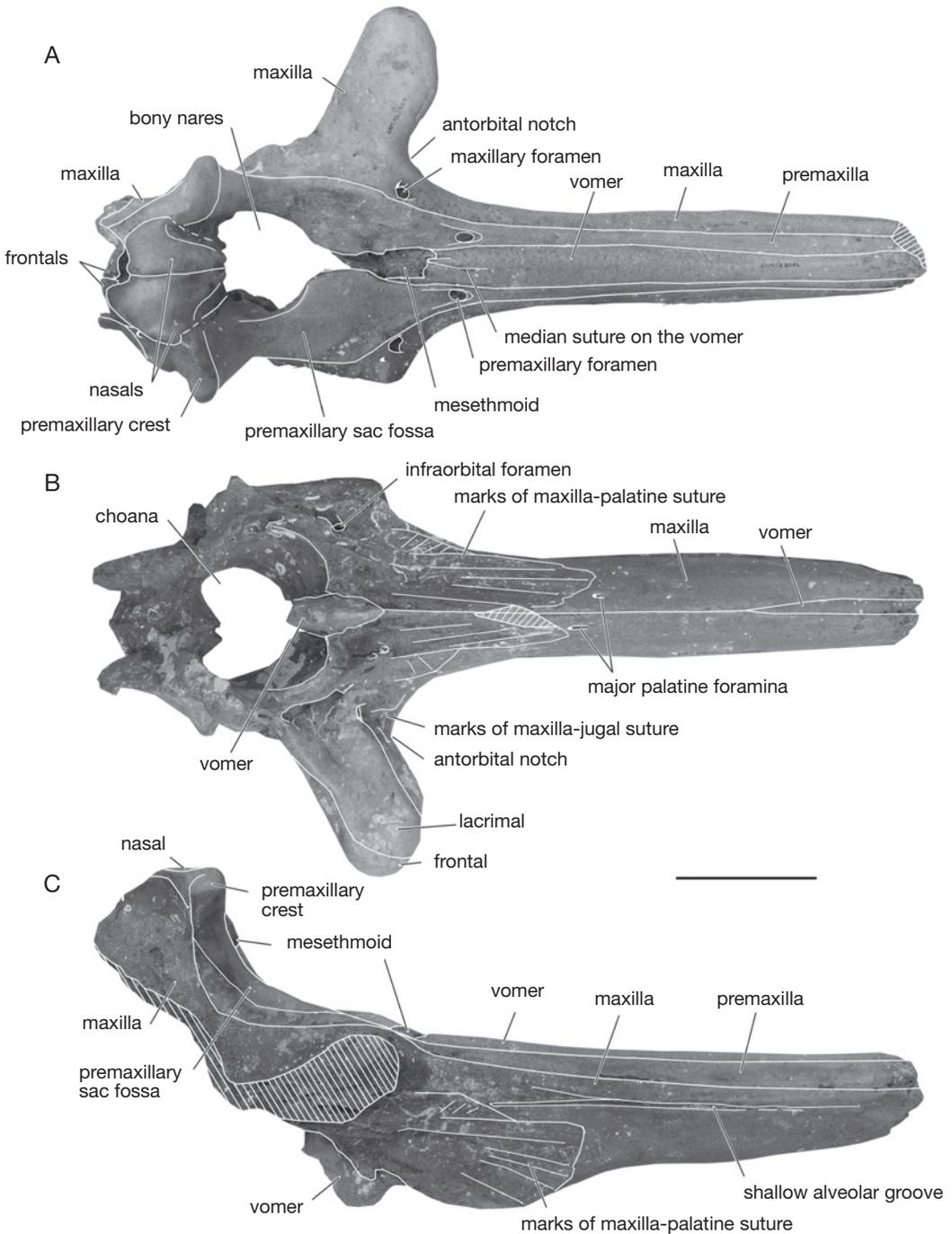
FIG. 26. — Skull of *Pterocetus benguelae* n. gen., n. sp. (SAM PQ 2803, holotype): **A**, dorsal view; **B**, ventral view; **C**, lateral view. Scale bar: 10 cm.
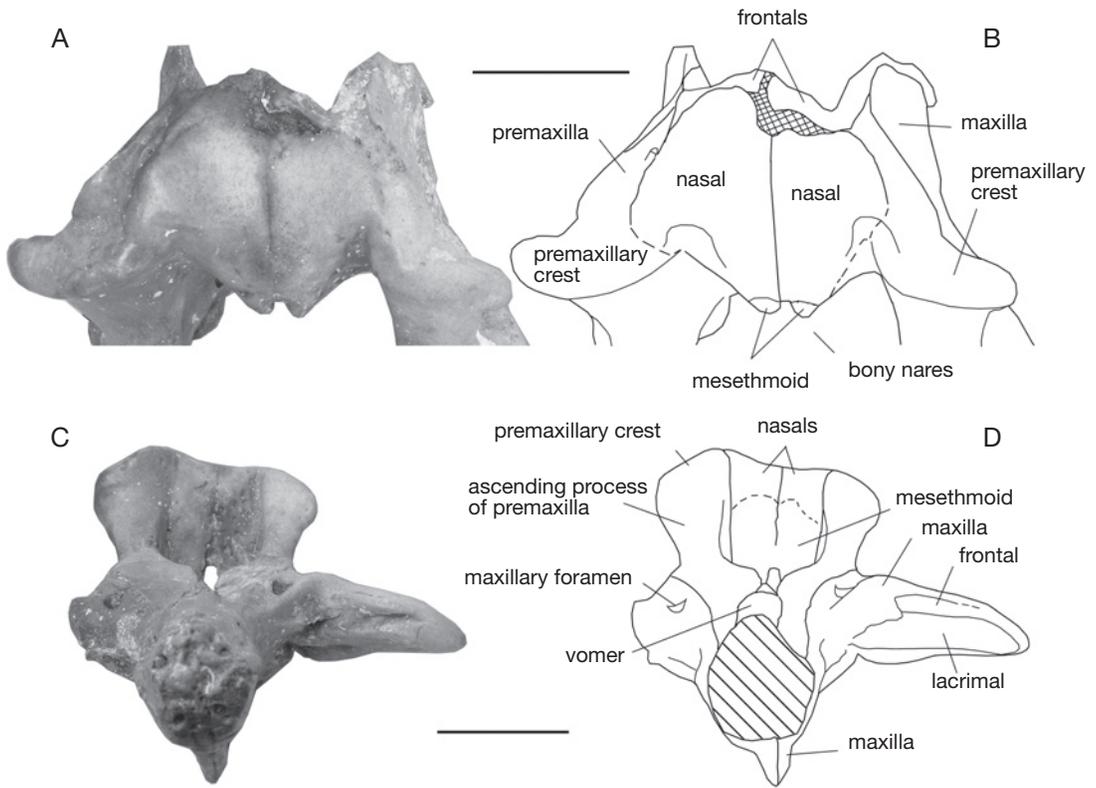
FIG. 27. — Skull of *Pterocetus benguelae* n. gen., n. sp. (SAM PQ 2803, holotype): **A**, detail of the vertex in dorsal view; **B**, correspon-ding line drawing; **C**, anterior view; **D**, corresponding line drawing. Scale bars: A, B, 5 cm; C, D, 10 cm.

On the moderately elevated vertex, the nasals are wide and pentagon-shaped. Their anterolateral corner extends only a short distance into the pre-maxillary crest. A vertical groove excavates the anterior margin of each nasal. The right nasal is longer posteriorly than the left. The dorsal surface of the nasals is slightly depressed anteromedially, similar to *Tasmacetus*. Posteriorly, the frontals are narrower than the nasals with a minimum length of 21 mm. On the vertex, the frontal is contacted by the long posterior projection of the premaxilla.

Pterocetus aff. benguelae

REFERRED SPECIMENS. — SAM PQ 1770, partial skull including the rostrum and most of the dorsal surface of the cranium with vertex, trawled 6.4 km west of Slang-kop, Atlantic Ocean, depth of 274 m; SAM PQ 2751, rostrum, trawled off the South African coast.

DESCRIPTION AND DISCUSSION
(FIGS 28; 29C, D; TABLE 5)

The general shape and the anterior position of the premaxillary foramen cause us to refer the two specimens to *Pterocetus* n. gen. Moreover, SAM PQ 1770 shows the deep and wide antor-bital notch characteristic for *Pterocetus* n. gen. Nevertheless, both specimens differ from those referred above to *Pterocetus benguelae* n. gen., n. sp. in their lower rostrum with an anteriorly flatter ventral surface. This difference in robust-ness might correspond to an intraspecific sexual dimorphism, as observed in the extant *Mesoplodon densirostris*, whose rostrum is considerably more robust in the males than in the females (Fig. 30).
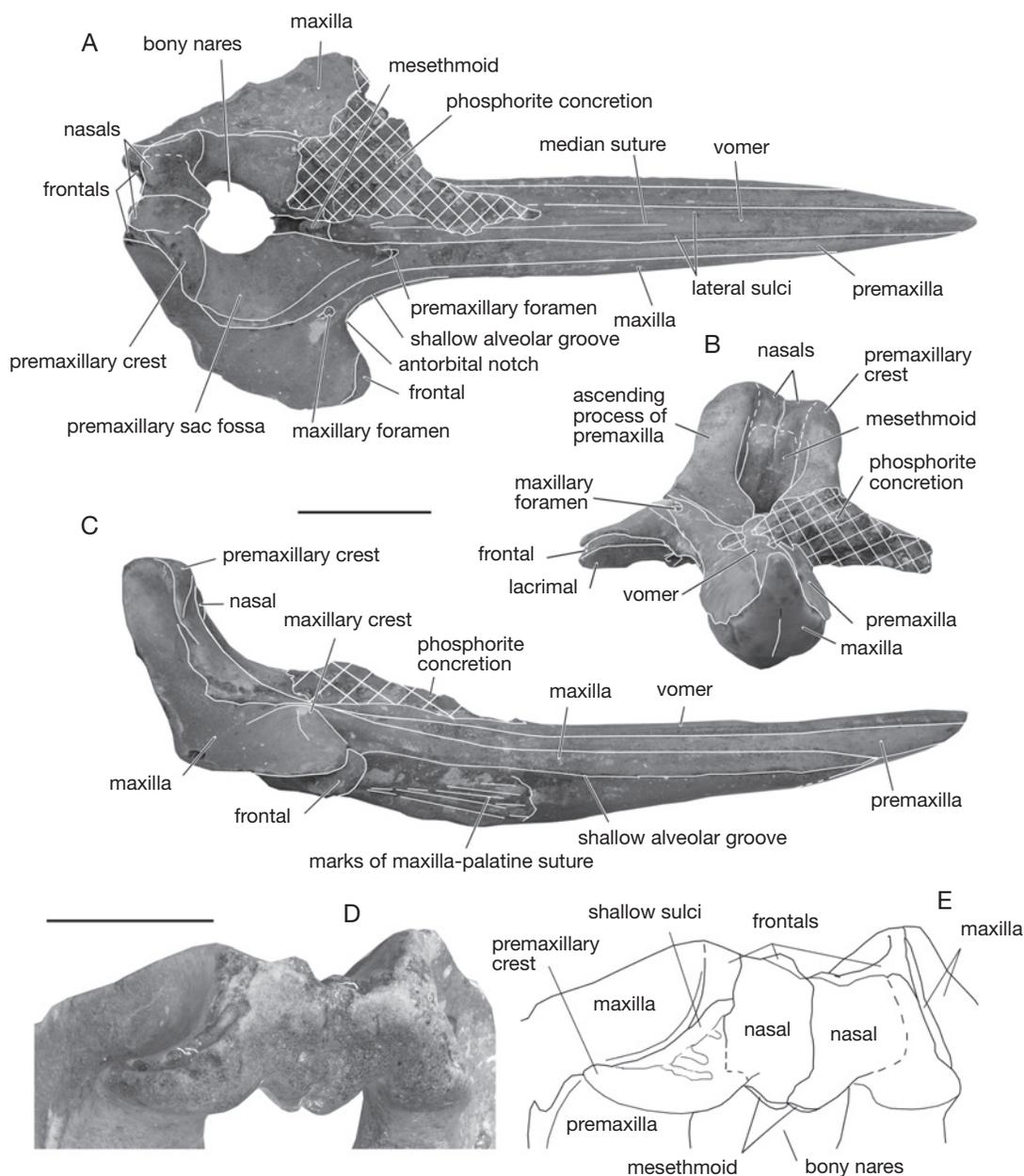
Fig. 28. — Skull of *Pterocetus* aff. *benguelae* (SAM PQ 1770): **A**, dorsal view; **B**, anterior view; **C**, lateral view; **D**, detail of the vertex in dorsal view; **E**, corresponding line drawing. Scale bars: A-C, 10 cm; D, E, 5 cm.

However, in this case the difference in robustness of the rostrum is reinforced by the strong mesorostral ossification of the vomer, mostly present in the adult male, while both the robust and slender fossil rostra described above exhibit a complete mesorostral ossification. Other small
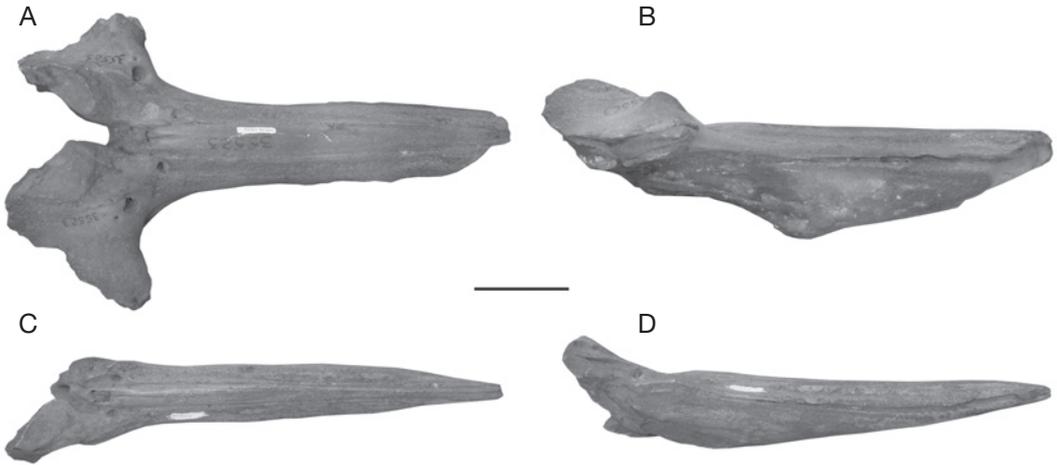
FIG. 29. — **A**, **B**, incomplete skull of *Pterocetus benguelae* n. gen., n. sp. (SAM PQ 69684); **A**, dorsal view; **B**, lateral view; **C**, **D**, rostrum of *P.* aff. *benguelae* (SAM PQ 2751); **C**, dorsal view; **D**, lateral view. Scale bar: 10 cm.
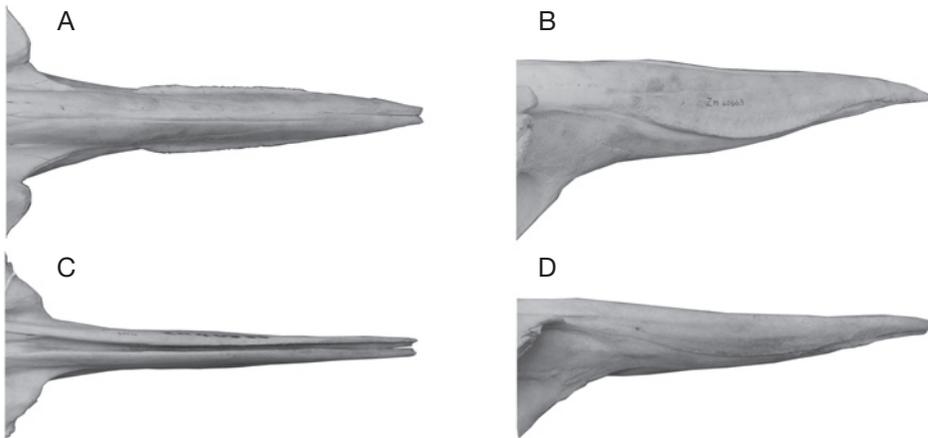
FIG. 30. — **A**, **B**, rostrum of male of *Mesoplodon densirostris* (SAM ZM 40663); **A**, dorsal view; **B**, lateral view; **C**, **D**, rostrum of female of *M. densirostris* (SAM ZM 40836); **C**, dorsal view; **D**, lateral view. Reduced to the same lenght.

differences are observed between SAM PQ 1770 and the holotype of *Pterocetus benguelae* n. gen., n. sp. at the level of the vertex: the nasals are narrower, the bony nares are smaller, the premaxillary crest seems laterally less developed, and the constriction of the ascending process is almost absent. Considering these differences, referral of SAM PQ 1770 and SAM PQ 2751 to *Pterocetus* aff. *benguelae* seems justified.

Odontoceti indet.

REFERRED SPECIMENS. — SAM PQ 2717, isolated rostrum, trawled off Saldanha Bay, west coast of South Africa, Atlantic Ocean, depth of 366 m; SAM PQ 2719, isolated rostrum, trawled off the South African coast.

DESCRIPTION AND DISCUSSION (FIGS 31; 32)
The isolated rostra SAM PQ 2717 and SAM PQ 2719, preserved for a length of respectively 519
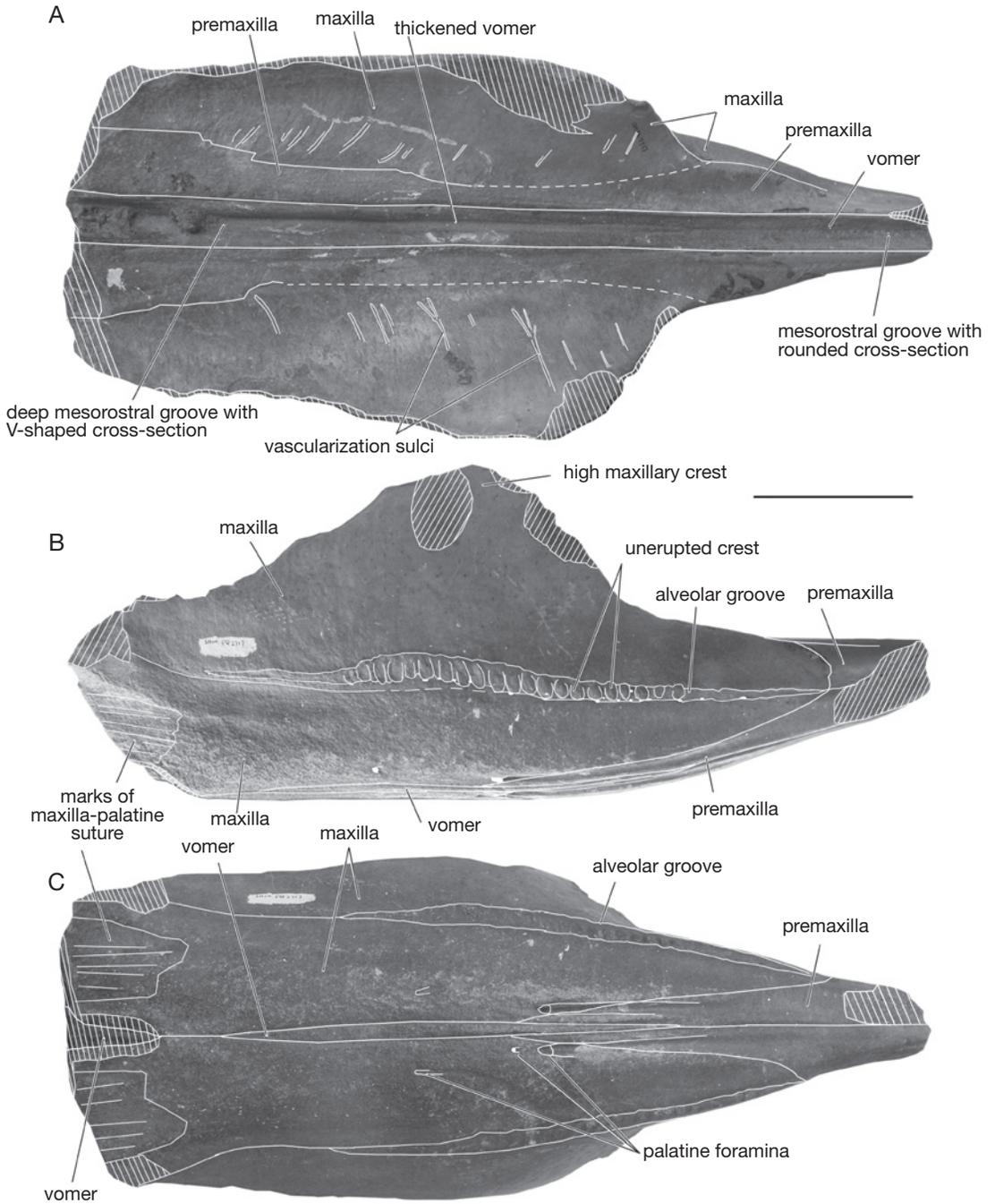
FIG. 31. — Rostrum of Odontoceti indet. (SAM PQ 2717): **A**, dorsal view; **B**, lateral view; **C**, ventral view. Scale bar: 10 cm.

and 547 mm, are characterized by a very unusual structure.

The premaxilla is weakly modified compared to the general odontocete plan. It occupies the margins of the mesorostral groove in dorsal view and the upturned apex of the rostrum, ventrally appearing on the first third of the rostrum. At the apex of the maxilla, the rostrum has a width of respectively 60 and 45 mm for SAM PQ 2717 and SAM PQ 2719 and a height of respectively 56 and 44 mm. The mesorostral groove is partially filled by the thickened lateral walls of the vomer, leaving an open median V-shaped groove. The development of the vomer in the mesorostral groove combined with high-density bone tissue is mostly observed in ziphiids (see above). Ventrally, the exposure of the vomer is respectively 290 and 240 mm.

The maxilla is highly modified; the lateral margin is considerably elevated laterodorsally along the posterior two thirds of the rostrum. This lateral maxillary crest is robust at its base, progressively thinning dorsally. The maximum height of the crest is mid-way along the rostrum. The two crests anteriorly delimit a wide and deep basin, ending at some distance before the apex of the maxilla. The inner wall of the crest is striated with vascularization sulci, best seen in SAM PQ 2717. On this specimen, the outer wall of the crest, continuous with the wide ventral surface of the rostrum, bears a shallow alveolar groove punctuated by a series of rounded protuberances interpreted as unerupted teeth. No alveolar groove is observed in SAM PQ 2719. The basin is considerably larger in SAM PQ 2717 (maximum width and height of the rostrum respectively 230 and 201 mm), a difference that might correspond to sexual dimorphism, as seen in *Physeter macrocephalus* for the supracranial basin, in *Ziphius cavirostris* for the prenarial basin, and in *Hyperoodon* spp. for the maxillary crests.

Similarities with *Hyperoodon* spp. at the level of the maxillary crests are functionally rejected: the high maxillary crests of the latter do not form a basin. If the prenarial basin of *Z. cavirostris* is differently built, the supracranial basin of the physeterids bearing the spermaceti organ is relatively similar, especially in *P. macrocephalus*. Significant thickening of the vomer has not been described in physeterids until now and we therefore may not refer with certainty these relatively small specimens to the Physeteridae. On the other hand, their maxilla differs significantly from the known ziphiids. Future information about the bony nares and additional cranial characters would be crucial to solve the familial affinities of this strange whale.

PHYLOGENY

INTRODUCTION

In order to investigate the phylogenetic relationships between the taxa described here and the main ziphiid lineages, a cladistic analysis was undertaken, using the software PAUP, version 4.0 b10 (Swofford 1998) to obtain a cladogram of minimum length. We used the heuristic search option, optimized by ACCTRAN, considering all characters as ordered and unweighted. Then we undertook the exhaustive search option, which guarantees to find the most parsimonious tree(s), with the following options: initial "MaxTrees" setting = 100, branches collapsed (creating polytomies) if maximum branch length = 0, "MulTrees" option in effect, topological constraints not enforced.

Because of the limited amount of cranial characters available and the increasing number of fossil taxa revised or newly described, we only added the Recent ziphiid genera to our set of South African species (Figs 33; 34). Due to the lack of a clear morphological diagnosis of the genus *Mesoplodon* and the considerable intrageneric variation in its cranial morphology, we decided to include isolated species of that genus in the analysis. The high number of Recent species currently known for this genus (14 now formally recognized; Dalebout *et al.* 2002) led us to select five species for the analysis: the type species *M. bidens* and four species for which several specimens were available in SAM (*M. densirostris*, *M. grayi*, *M. layardii*, and *M. mirus*).

The 18 characters used in this analysis (Appendices 1; 2) are either new or modified from previous studies on ziphiid phylogeny (mainly Moore 1968; Muizon 1991; Bianucci *et al.* 1994; Bianucci 1997; Lambert 2005; Lambert & Louwye 2006).
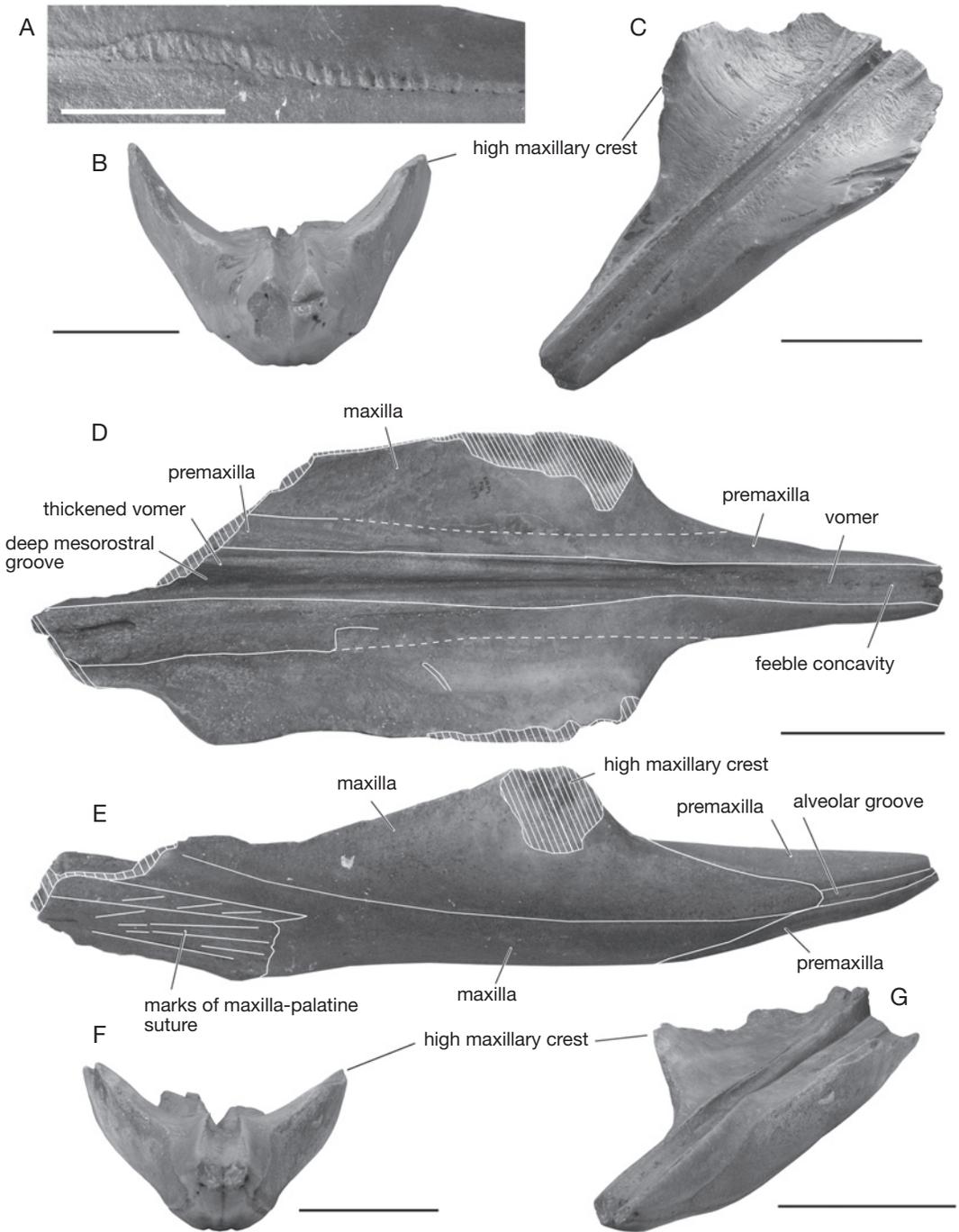
Fig. 32. — **A-C**, rostrum of Odontoceti indet. (SAM PQ 2717); **A**, detail of the alveolar groove; **B**, anterior view; **C**, anterolateral view; **D-G**, rostrum of Odontoceti indet. (SAM PQ 2719); **D**, dorsal view; **E**, lateral view; **F**, anterior view; **G**, anterolateral view. Scale bars: 10 cm.
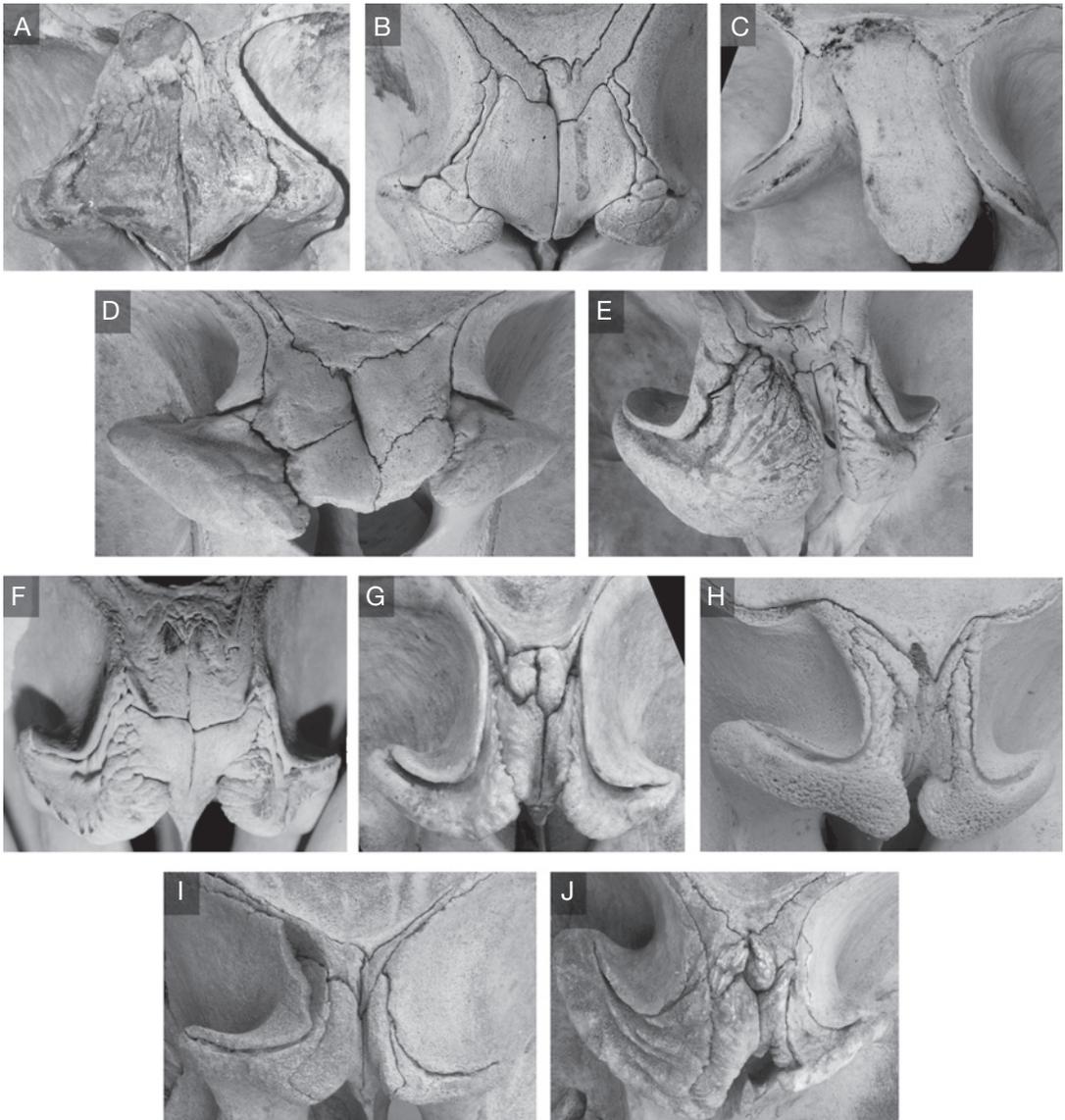
Fɪɢ. 33. — Comparison of vertex of extant ziphiids considered in the phylogenetic analysis: **A**, *Berardius arnuxi* (SAM ZM 39296); **B**, *Tasmacetus shepherdi* (SAM ZM 41113); **C**, *Ziphius cavirostris* (SAM ZM 38237); **D**, *Indopacetus pacificus* (MZUF M4854); **E**, *Hyperoodon planifrons* (SAM ZM 41123); **F**, *Mesoplodon bidens* (MNHN 1975-112); **G**, *M. densirostris* (SAM ZM 40713); **H**, *M. mirus* (SAM ZM 39932); **I**, *M. grayi* (SAM ZM 40478); **J**, *M. layardii* (SAM ZM 39566). Photographs not at the same scale.

RESULTS

The PAUP analysis resulted in four equally parsimonious cladograms of 53 steps, consistency index (CI) = 0.623 (reduced to 0.528 after excluding uninformative characters), and retention index (RI) = 0.847. The consensus tree of these cladograms is presented in Figure 35 and discussed below.

Several new taxa described here are positioned in lineages including Recent genera. *Microberardius* n. gen. is closely related to *Berardius* in the Berardiinae,
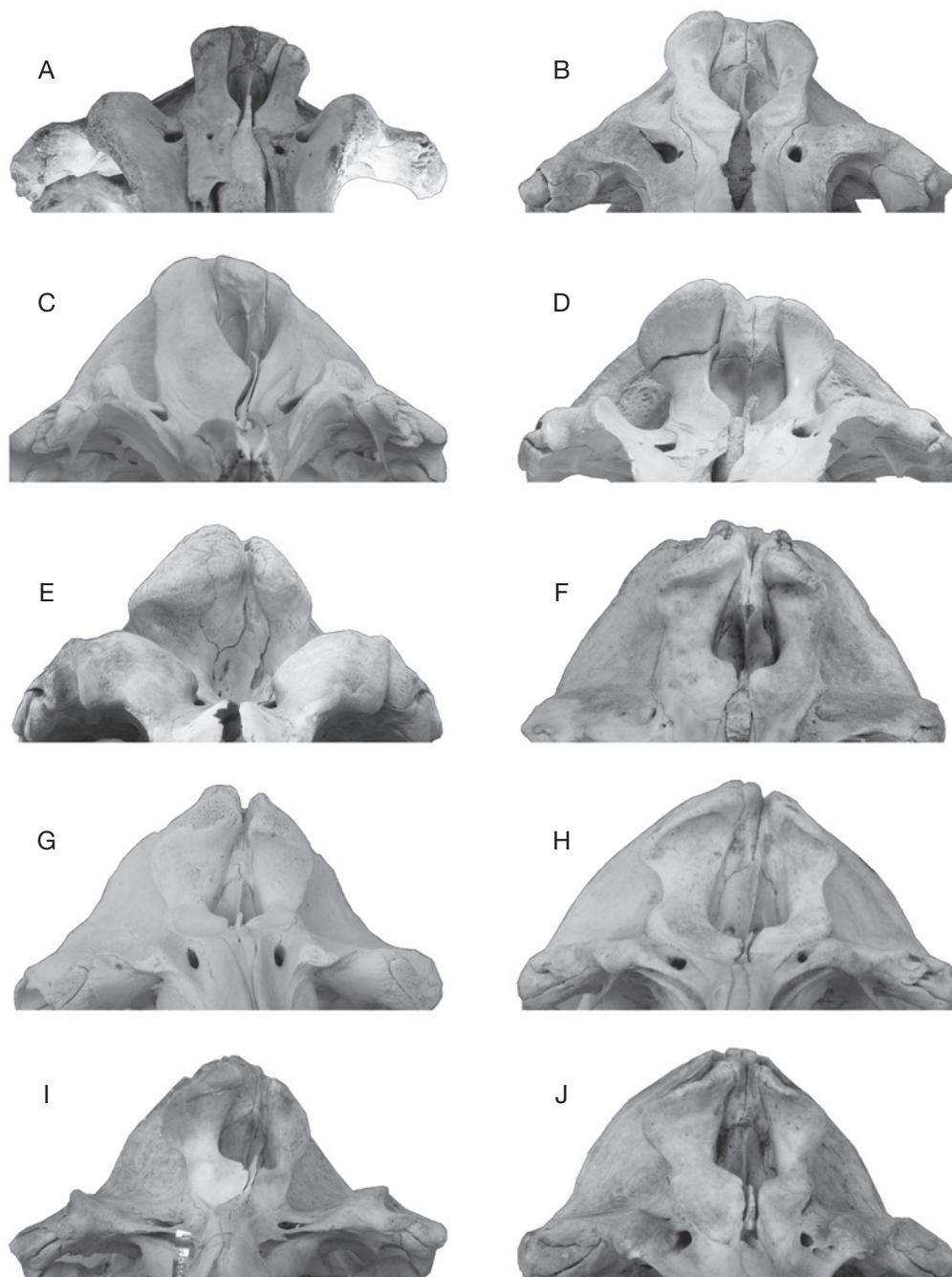
Fɪɢ. 34. — Comparison of cranium in anterior view of extant ziphiids considered in the phylogenetic analysis: **A**, *Berardius arnuxi* (ZM 39296); **B**, *Tasmacetus shepherdi* (ZM 41113); **C**, *Ziphius cavirostris* (ZM 38237); **D**, *Indopacetus pacificus* (MZUF M4854); **E**, *Hyperoodon planifrons* (ZM 41123); **F**, *Mesoplodon bidens* (IRSNB 19.822); **G**, *M. densirostris* (ZM 40713); **H**, *M. grayi* (ZM 40478) **I**, *M. layardii* (ZM 39566); **J**, *M. mirus* (ZM 39932). Reduced approximately at the same preorbital width.

a subfamily here defined by only two autapomorphies: the presence of either a nodular interparietal between frontals and supraoccipital or of nodular frontals on the vertex and the presence of two pairs of apical and sub-apical enlarged teeth on the mandible (only observed in *Berardius* because the mandible of *Microberardius* n. gen. is unknown).

Our results further increase the past diversity of the subfamily Ziphiinae (two new species in the new genus *Izikoziphius* n. gen. and probably a new species of *Ziphius*), nowadays only including the species *Z. cavirostris*. The ziphiine genera considered in our cladistic analysis form a well defined clade characterized by a highly elevated vertex that partially covers the bony nares, elongated nasals anterior to the premaxillary crests, reduced contact between nasal and premaxillary crest, anterolaterally directed transverse premaxillary crest, and the moderately to highly asymmetrical premaxillary sac fossae laterally overlapping the maxillae. A less derived condition for some of the characters listed above is observed in other fossil ziphiine not addressed in our phylogenetic analysis (e.g., *Beneziphius*, *Choneziphius*, *Tusciziphius*, and *Ziphirostrum*, see Lambert 2005).

Three new genera significantly enlarge the subfamily Hyperoodontinae; two of them, *Africanacetus* n. gen. and *Ihlengesi* n. gen., are located between *Indopacetus* and *Hyperoodon* + *Mesoplodon*. This subfamily is here defined by only one clear autapomorphy: the deep anteromedian excavation of the nasals (Fig. 33). In the clade *Hyperoodon* + *Mesoplodon*, the new species *M. slangkopi* n. sp. is positioned in the subgroup of *M. bidens*, the type species of the genus *Mesoplodon*.

Finally three additional genera do not fit in any of the three subfamilies mentioned above: *Pterocetus* n. gen. and *Xhosacetus* n. gen. are more closely related to the Hyperoodontinae than to the Ziphiinae, while the position of *Nenga* n. gen. could not be resolved.

The relationships between Recent genera obtained in this analysis are consistent with the last molecular studies for the basal position of *Berardius* (van Helden *et al.* 2002; Dalebout *et al.* 2002, 2003). The clade *Indopacetus* + (*Hyperoodon* + *Mesoplodon*) is similarly found in the morphological analyses

of Moore (1968), Muizon (1991), and Lambert (2005), while *Tasmacetus* is excluded from the Berardiinae, contrary to Muizon (1991) and Lambert (2005). The unresolved position of *Tasmacetus* can be explained by its mix of seemingly archaic (mainly the retention of a large number of functional mandibular and maxillary teeth) and more derived characters (constriction of the ascending process of the premaxilla, anteromedian depression of the nasals). *Hyperoodon* is here nested within the species-rich *Mesoplodon*. The limited amount of morphological characters prohibited the inclusion of more species in our analysis; we suspect that the possible paraphyly of *Mesoplodon* may only be dealt with in combination with molecular data. Until now, however, molecular analyses could not provide better-supported trees (van Helden *et al.* 2002; Dalebout *et al.* 2002, 2003).

STRATIGRAPHY

Phosphorites are rocks of sedimentary origin containing more than 18% P_2O_5. More generally, any rock or grain formed by direct precipitation or by replacement of calcium carbonate containing over 5% P_2O_5 may be called a phosphorite (Birch 1977).

After the *Challenger* expedition – during which the first phosphorites were dredged in 1873 from the Agulhas Bank off the coast of South Africa – research on these sediments started, inspired by scientific and economic interests alike. It soon became apparent that large volumes of phosphorites were and are appearing on or near the seabed of the continental margin off the South African coast from 25°E to as far north as 30°S (Birch 1973; Dingle 1975). During 1959 the South African research vessel *Africana* proved that phosphorites also appear on the deeper slopes of the continental shelf to depths of 2716 to 3383 m (R. Leslie pers. comm. 2005) and recent studies (Bremner 1981; Baturin 2000) and catches of Namibian commercial fishermen indicated more northwards existence of phosphatic conglomerates and fossils off the Namibian coast (25°S, 13°14'W, W. Hart pers. comm. 2005).

These offshore phosphatic sediments appear in many forms (small round grains, cobbles, large flat slabs of over 1 m, conglomerates, etc.) and are divided into various types by their genesis and diagenetic origin (Parker 1971; Birch 1973; Compton *et al.* 2002). One of the types is a phosphatic conglomerate characterised by an inhomogeneous mixture of pebbles with macrofossils (frequently with microfossil-rich infilling) and bone debris set in a grain- or cement-supported matrix of glauconite, microfossils and quartzite-sand sealed by a carbonate fluor-apatite cement (Parker 1971). We observed a special variation within this type, which obviously appears quite frequently in South African waters; it consists of large and often rounded or somewhat polished macrofossils of marine mammals (up to 1 m long and weighting over 15 kg), saturated with francolite (carbonate fluor-apatite, main mineral of phosphorite), either without any of the original conglomerate attached or with only minor adherent phosphatic debris remaining. The abundance of fossils of this type may be illustrated by the catch of 18 fairly complete ziphiid rostra at a depth of 914 m by the South African research vessel *Africana* on 4 may 1993 (deepwater trawls demersal cruise, voyage 111, station A14840-111D002, R. Leslie pers. obs. 2005).

The age of the phosphatic nodules and pebbles is difficult to determine. There seems to be consensus that the phosphorites must have been formed by a sudden regression of the sea just after or during a period of massive and intense upwelling; debris of large amounts of phosphatic biomass fed by the rich nutrients of the upwelling sea and available mud seem essential elements in the genesis of phosphorites, and polishing of phosphorites and fossils might be caused by the transgressing seas. Research has established that there were periods of upwelling and sudden sea regressions followed by erosion in South African coastal waters within late Eocene, late Oligocene to early Miocene, middle Miocene to early Pliocene, and late Pliocene to Pleistocene epochs (Dingle 1975; Udeze *et al.* 2005; Wigley & Compton 2006). Haughton (1956) postulated an early Miocene origin for the phosphorites based on some trawled specimens of fossil nautiloid found (on land) in the lower Miocene Bogenfels Formation.

Birch (1973) mentioned a conglomeratic phosphorite off the north-west coast containing abundant benthic foraminiferan *Nummulites* sp. and stated that on-land rocks with similar fossils were dated to the upper middle Miocene. In a later publication, Birch (1977) confirmed a middle Miocene origin as most probable for all the South African types of phosphorites (both on land and offshore). Extensive recent research using vibracores and dating of Sr isotopes confirmed the stratigraphical complexity of the South African western continental shelf, but also dated and quantified the phosphogenic epochs (Compton *et al.* 2002, 2004; Wigley & Compton 2006); the most prevalent period of phosphogenesis occurred during the latest Oligocene (26.1-23.6 Ma); the next significant formation of phosphorites followed in the late early Miocene (19-16 Ma) and less predominantly in the middle to early late Miocene (15-10 Ma). Proof of late Pliocene and Pleistocene grains genesis is found, but all large and solid phosphatic pebbles and slabs seem to have Miocene backgrounds (or at least possess cores dating to the Miocene); this relative paucity of phosphorite younger than the middle Miocene might be related to lack of time to develop sufficiently hard layers for surviving the more vigorous currents, sea-level fluctuations and tectonic uplift later in the Neogene (Compton 2002).

Considering the preservation state of the fossil ziphiid skulls described above and the localised concentration of a part of them on the sea floor, we believe that most of them underwent at least one phase of reworking. The similar rounded aspect of the phosphorite concretions attached to some skulls indicates a common reworking of skulls and phosphorites. As few or no unquestionable ziphiids are known from layers older than middle Miocene (e.g., early-middle Miocene of Ecuador, Bianucci *et al.* 2005), the most probable age for these skulls would be middle to early late Miocene, but we cannot completely exclude older ages. Because more reduced phosphogenic phases occurred later in the Miocene and Pliocene, some specimens might even prove to be younger. Taking into account the relatively short fossil history of Recent cetacean genera and the attribution of some fossil specimens to the Recent genera *Mesoplodon* and *Ziphius* (*Mesoplodon slangkopi* n. sp. and *Ziphius* sp.) these specimens
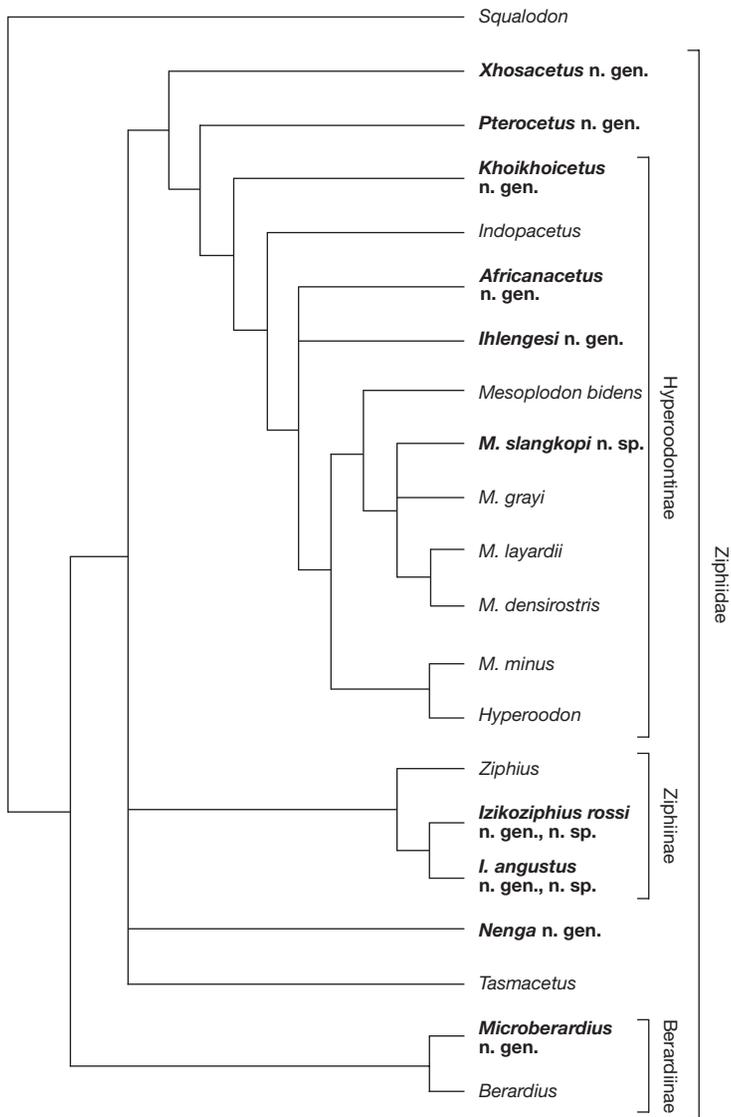
FIG. 35. — Consensus tree of four equally parsimonious cladograms showing the relationships of the fossil ziphiids from South African (in bold) and the extant genera. Tree length: 53; CI: 0.623; RI: 0.847. See text for discussion, data matrix in Appendix 3 and description of characters in Appendix 2.

might originate from post-Miocene strata. This leaves unsolved the question whether or not all the fossils belong to one and the same fauna. A possible way to clarify this question might be to undertake Sr isotopes dating of phosphorite concretions attached to ziphiid skulls (see Compton *et al.* 2004).

DISCUSSION

Until now, besides anecdotal records based on non-diagnostic specimens (e.g., Mead 1975; Glaessner 1947), *Ninoziphius platyrostris* was the only fossil ziphiid described from the southern hemisphere.

This article presents the description of 10 new species in nine genera (eight of these genera are new to science). The multiplicity of undescribed fragmentary specimens (34 isolated rostra) suggests an even more significant number of taxa along the coasts of South Africa. None of the described taxa could be definitely attributed to any northern hemisphere fossil ziphiid genus. In particular, none of them exhibits the characteristic dorsomedian elevation of the premaxillae above the mesorostral groove seen in most of the North Sea and Mediterranean late Miocene-early Pliocene ziphiid genera (*Aporotus*, *Beneziphius*, *Choneziphius*, *Messapicetus*, and *Ziphirostrum*).

As demonstrated above, several of the new taxa are closely related to Recent genera and even a new species of *Mesoplodon* is described. Other taxa are more distantly related, and might correspond to other extinct lineages. Although we cannot estimate the interval of time that might separate the specimens of this study, we observe that a high number of ziphiid species from several lineages was present during Miocene-early Pliocene along the coasts of South Africa and that most of them do not belong to Recent genera. Moreover, considering that most of the new described species are based on only one or two specimens, it is highly probable that future fossils will further increase the high diversity of this (these) fossil fauna(s).

Nowadays, the South African waters constitute the occasional or more permanent habitat of at least nine ziphiid species, namely *Berardius arnuxii*, *Hyperoodon planifrons*, *Indopacetus pacificus*, *Mesoplodon densirostris*, *M. grayi*, *M. hectori*, *M. layardii*, *M. mirus*, and *Ziphius cavirostris* (Ross 1984; Mead 1989; Dalebout *et al.* 2003). Ross (1984) divides the ziphiids from the south-east coast into different ecological groups: 1) tropical/subtropical: *M. densirostris*, associated with the Agulhas Current; 2) temperate/subantarctic: *M. layardii*, *H. planifrons*, *B. arnuxii* (with probably more accidental records of *M. hectori* and *M. grayi*), cool inshore water of the Agulhas Current; 3) more cosmopolitan: *Z. cavirostris*; and 4) mixed cool and warm waters: *M. mirus*. The high diversity of fossil forms that we observe for

the Neogene, even if we cannot be sure that all the specimens are contemporary, might suggest a similar division in several ecological niches. Among Recent ziphiids, all generalists probably feeding at or close to the bottom, local co-existence of several species is allowed by dietary (different prey size), temporal or fine-scale geographic segregation (Waring *et al.* 2001; McLeod *et al.* 2003). Considering the general size and rostrum shape differences between the above described taxa, different dietary niches may logically be proposed. More detailed information about the oral apparatus, for example the shape of the mandible and teeth, and precise stratigraphic data would however be necessary to formulate more thorough ecological hypotheses.

To explain the high concentration of specimens recovered by trawling off the south-west coast of South Africa, from Cape Columbine to the area of Cape Town, a relation with the Benguela Current and related coastal upwelling area must be suspected. Nannofossil and sedimentary studies indicate that this upwelling system, due to the entry of the northward running cool oceanic Benguela current into the shallower waters off the south-west coast of South Africa and Namibia, was at least intermittently established from the middle Miocene (± 15 Ma, Wigley & Compton 2006) and more firmly present during the late Miocene (10 Ma, Krammer *et al.* 2006). Periods of intensified upwelling are recognized during the late Miocene and the early to early late Pliocene (Udeze & Oboh-Ikuenobe 2005). Several studies on Recent ziphiid habitats indicate strong links between feeding areas and the interaction of submarine topography with marine currents (Waring *et al.* 2001; McLeod & Zuur 2005).

CONCLUSIONS

Our study of a series of 32 partial skulls of fossil ziphiids dredged from the sea bottom along the coasts of South Africa, most of them preserved at the SAM, leads to the description of 10 new species in nine genera (number of specimens for each species indicated between brackets):

Africanacetus ceratopsis n. gen., n. sp. (10)
Ihlengesi saldanhae n. gen., n. sp. (2)
Izikoziphius rossi n. gen., n. sp. (2)
I. angustus n. gen., n. sp. (1)
Khoikhoicetus agulhasis n. gen., n. sp. (1)
Mesoplodon slangkopi n. sp. (2)
Microberardius africanus n. gen., n. sp. (1)
Nenga meganasalis n. gen., n. sp. (4)
Pterocetus benguelae n. gen., n. sp. (3)
Xhosacetus hendeysi n. gen., n. sp. (1)

The more fragmentary specimens were referred to Berardiinae indet. (1), *Pterocetus* aff. *benguelae* (2), *Ziphius* sp. (1), and Odontoceti *incertae sedis* (2). Finally a series of non-diagnostic fragments (34) suggests an even higher number of taxa.

A phylogenetic analysis reveals the relationships of the new taxa with Recent ziphiids; several genera are referred to the following subfamilies: Berardiinae (*Microberardius* n. gen.), Hyperoodontinae (*Africanacetus* n. gen., *Ihlengesi* n. gen.*,* and *Khoikhoicetus* n. gen.), and Ziphiinae (*Izikoziphius* n. gen.), while the other genera might belong to different extinct lineages.

The association of most of the fossils with phosphorite concretions allows us to suggest a middle to early late Miocene, or even slightly older, age for them. As phosphorites also formed, though in much lower quantities, later in the Miocene and Pliocene along the coasts of South Africa, we cannot exclude the possibility of younger ages for some specimens.

Although we cannot be sure that all species were contemporary, their high number and their assignment to different lineages indicates a significant diversity of fossil ziphiids along the coasts of South Africa during the Miocene-Pliocene. These species could have occupied various niches, as for Recent ziphiids, and their local diversity might have been related to the development of the Benguela upwelling system, which is known to have existed off the south-west coast of South Africa from the middle Miocene to present.

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TABLES

TABLE 1. — Measurements (in mm) of the skulls of Berardiinae from the Neogene of South Africa, *Microberardius africanus* n. gen., n. sp. and Berardiinae indet. Abbreviations: **e**, estimate; **+**, nearly complete; **-**, no data.

		Microberardius africanus n. gen., n. sp. SAM PQ 3003	Berardiinae indet. SAM PQ 2198
6.	Maximum opening of mesorostral groove	25	26
8.	Width of rostrum base at antorbital notch	e165	e257
9.	Width of premaxillae at rostrum base (anterior notch)	e67	e83
10.	Distance rostrum base-anterior apex palatine	-	e125
11.	Preorbital width of skull	+255	-
15.	Longitudinal distance premaxillary foramen-antero-median corner of naris	e69	116
16.	Width of premaxillary sac fossae	116	146
17.	Width of right premaxillary sac fossa	57	76
18.	Width of left premaxillary sac fossa	45	62
19.	Width of bony nares	53	73
20.	Minimum width of ascending process of premaxilla	31	41
21.	Width of premaxillary crests	107	+134
22.	Width of right premaxillary crest	30	-
23.	Width of left premaxillary crest	22	-
24.	Minimum distance between premaxillary crests	52	52
25.	Maximum width of nasals	60	73
26.	Length of medial suture of nasals on vertex	e43	84
27.	Minimum posterior distance between maxillae	e46	79
28.	Vertical distance between terminal foramen and top of vertex	+77	e108

TABLE 2. — Measurements (in mm) of the skulls of Ziphiinae from the Neogene of South Africa, *Izikoziphius rossi* n. gen., n. sp., *I. angustus* n. gen., n. sp., and *Ziphius* sp. Abbreviations: **e**, estimate; **+**, nearly complete; **-**, no data.

		Izikoziphius rossi n. gen., n. sp. PEM N 3265	*Izikoziphius rossi* n. gen., n. sp. SAM PQ 2086	*I. angustus* n. gen., n. sp. SAM PQ 3004	*Ziphius* sp. SAM PQ 2826
1.	Rostrum length	+490	e530	597	-
2.	Length of maxilla on rostrum	450	465	520	-
3.	Length of premaxillary portion of rostrum	+40	e65	83	-
4.	Width of rostrum at mid-length	115	94	76	-
5.	Height of rostrum at mid-length	+100	84	111	-
6.	Maximum opening of mesorostral groove	20	30	38	-
8.	Width of rostrum base at antorbital notch	-	e205	239	-
9.	Width of premaxillae at rostrum base (anterior notch)	100	110	104	-
10.	Distance rostrum base-anterior apex palatine	170	e116	160	-
12.	Postorbital width of skull	-	-	+395	-
14.	Longitudinal distance apex of rostrum-antero-median corner of naris	+645	e690	722	-
15.	Longitudinal distance premaxillary foramen-antero-median corner of naris	-	115	e96	-
16.	Width of premaxillary sac fossae	145	155	165	-
17.	Width of right premaxillary sac fossa	75	80	90	+141

		Izikoziphius rossi n. gen., n. sp.		*I. angustus* n. gen., n. sp.	*Ziphius* sp.
		PEM N 3265	SAM PQ 2086	SAM PQ 3004	SAM PQ 2826
18.	Width of left premaxillary sac fossa	55	62	+60	-
19.	Width of bony nares	56	73	83	-
20.	Minimum width of ascending process of premaxilla	-	45	44	-
21.	Width of premaxillary crests	129	+126	161	-
22.	Width of right premaxillary crest	71	-	e40	79
23.	Width of left premaxillary crest	32	-	30	74
24.	Minimum distance between premaxillary crests	-	69	59	-
25.	Maximum width of nasals	39	e88	58	76
26.	Length of medial suture of nasals on vertex	66	86	91	149
27.	Minimum posterior distance between maxillae	+39	82	68	-
28.	Vertical distance between terminal foramen and top of vertex	-	177	171	-

TABLE 3. — Comparison of measurements (in mm) of the vertex of *Ziphius* sp. from the Neogene of South Africa and of a Recent adult male *Ziphius cavirostris* Cuvier, 1823. Abbreviation: +, nearly complete.

	Ziphius sp. SAM PQ 2826	*Ziphius cavirostris* SAM ZM 39369
Width of right premaxillary sac fossa	+141	120
Width of right bony naris	68	41
Width of right premaxillary crest	79	117
Width of left premaxillary crest	74	64
Maximum width of nasals	76	81
Maximum length of nasals	149	148

TABLE 4. — Measurements (in mm) of the skulls of Hyperoodontinae from the Neogene of South Africa, *Khoikhoicetus agulhasis* n. gen., n. sp., *Ihlengesi saldanhae* n. gen., n. sp., *Africanacetus ceratopsis* n. gen., n. sp., and *Mesoplodon slangkopi* n. sp. Abbreviations: **e**, estimate; **+**, nearly complete; **-**, no data.

		K. agulha-sis n. gen., n. sp.	*Ihlengesi saldanhae* n. gen., n. sp.		*Africanacetus ceratopsis* n. gen., n. sp.			*Mesoplodon slangkopi* n. sp.	
		SAM PQ 2678	SAM PQ 2792	SAM PQ 69673	NMR 9991-00001993	SAM PQ 2162	SAM PQ 3002	SAM PQ 2069	SAM PQ 35107
2.	Length of maxilla on rostrum	-	-	-	475	-	-	-	-
6.	Maximum opening of mesorostral groove	24	-	-	38	31	40	-	-
7.	Width of rostrum base at prominental notch	-	108	104	-	-	-	93	-
8.	Width of rostrum base at antorbital notch	120	-	-	198	196	184	156	-
9.	Width of premaxillae at rostrum base (anterior notch)	49	-	-	106	-	93	42	44
10.	Distance rostrum base -anterior apex palatine	78	-	-	196	e175	e119	87	-
11.	Preorbital width of skull	-	-	-	+500	-	-	-	-

	K. agulha-sis n. gen., n. sp.	*Ihlengesi saldanhae* n. gen., n. sp.		*Africanacetus ceratopsis* n. gen., n. sp.			*Mesoplodon slangkopi* n. sp.	
	SAM PQ 2678	SAM PQ 2792	SAM PQ 69673	NMR 9991-00001993	SAM PQ 2162	SAM PQ 3002	SAM PQ 2069	SAM PQ 35107
12. Postorbital width of skull	-	-	-	-	-	-	223	-
13. Length of orbit	-	-	-	-	-	-	74	-
15. Longitudinal distance premaxillary foramen -antero-median corner of naris	54	31	-	84	-	-	57	49
16. Width of premaxillary sac fossae	106	105	101	161	-	-	93	87
17. Width of right premaxillary sac fossa	50	51	e52	78	-	-	44	41
18. Width of left premaxillary sac fossa	48	46	44	61	-	-	40	32
19. Width of bony nares	43	49	-	72	-	-	48	38
20. Minimum width of ascending process of premaxilla	25	25	-	77	-	-	-	24
21. Width of premaxillary crests	100	103	-	187	-	-	86	87
22. Width of right premaxillary crest	33	47	-	83	-	-	53	48
23. Width of left premaxillary crest	30	38	-	52	-	-	40	
24. Minimum distance between premaxillary crests	34	34	-	63	-	-	9	9
25. Maximum width of nasals	45	52	-	70	-	-	38	-
26. Length of medial suture of nasals on vertex	32	e45	-	60	-	-	23	-
27. Minimum posterior distance between maxillae	38	32	-	63	-	-	29	-
28. Vertical distance between terminal foramen and top of vertex	77	85	-	143	-	-	93	-

TABLE 5. — Measurements (in mm) on the skulls of Ziphiidae *incertae sedis* from the Neogene of South Africa. Abbreviations: **e**, estimate; **+**, nearly complete; **-**, no data.

		Nenga meganasalis n. gen., n. sp.		*Xhosacetus hendeysi* n. gen., n. sp.	*Pterocetus benguelae* n. gen., n. sp.		*Pterocetus* aff. *benguelae*	
		SAM PQ 69675	SAM PQ 2339	SAM PQ 2082	SAM PQ 2803	SAM PQ 69684	SAM PQ 1770	SAM PQ 2751
1.	Rostrum length	e477	-	-	-	-	+480	e430
2.	Length of maxilla on rostrum	+530	-	+435	-	-	390	-
3.	Length of premaxillary portion of rostrum	-	-	-	-	-	+90	-
4.	Width of rostrum at mid-length	92	-	-	-	-	70	59
5.	Height of rostrum at mid-length	80	-	-	-	-	57	58
6.	Maximum opening of mesorostral groove	30	-	33	31	35	30	25
8.	Width of rostrum base at antorbital notch	-	-	187	e174	215	e136	-
10.	Distance rostrum base -anterior apex palatine	e100	-	103	140	-	156	e110
11.	Preorbital width of skull	-	-	e330	e366	-	-	-
14.	Longitudinal distance apex of rostrum-antero-median corner of naris	575	-	-	-	-	+538	-
15.	Longitudinal distance premaxillary foramen-antero-median corner of naris	93	101	56	104	-	82	-
16.	Width of premaxillary sac fossae	156	147	119	138	-	128	-
17.	Width of right premaxillary sac fossa	80	78	59	69	79	59	-
18.	Width of left premaxillary sac fossa	64	58	51	57	-	50	-
19.	Width of bony nares	69	66	61	78	-	50	-
20.	Minimum width of ascending process of premaxilla	38	-	29	31	-	36	-
21.	Width of premaxillary crests	+140	+133	138	171	-	+114	-
22.	Width of right premaxillary crest	-	+35	43	62	-	43	-
23.	Width of left premaxillary crest	39	-	40	46	-	26	-
24.	Minimum distance between premaxillary crests	69	64	53	70	-	39	-
25.	Maximum width of nasals	92	93	65	84	-	59	-
26.	Length of medial suture of nasals on vertex	73	66	58	58	-	40	-
27.	Minimum posterior distance between maxillae	93	102	61	60	-	55	-
28.	Vertical distance between terminal foramen and top of vertex	98	103	90	116	-	97	-

APPENDIX 1

List of specimens directly studied (see text for abbreviations).

Extinct species
Aporotus dicyrtus: IRSNB M.541
A. recurvirostris: IRSNB M.1887, IRSNB M.1888
Archaeoziphius microglenoideus: IRSNB M.1853, IRSNB M.1854, IRSNB M.1855
Beneziphius brevirostris: IRSNB M.1885, IRSNB M.1886
Caviziphius altirostris: NNML 447230
Choneziphius planirostris: IRSNB M.1881, IRSNB M.1882, IRSNB M.1883, IRSNB 3767-3773, IRSNB 3776, IRSNB 3779, IRSNB 3780, IRSNB 3790
Choneziphius macrops: IRSNB M.1884
Messapicetus longirostris: holotype, Lecce
Ninoziphius platyrostris: MNHN SAS 941
Tusciziphius crispus: IGF 1594V
Ziphirostrum marginatum: IRSNB M.1874, IRSNB M.1875, IRSNB M.536, IRSNB M.537, IRSNB M.1876, IRSNB M.1877, IRSNB M.1878, IRSNB M.1879
Z. turniense: IRSNB M.539, IRSNB M.1880
Z. recurvus: IRSNB M.544

Recent species
Berardius arnuxii: SAM ZM 39296, SAM ZM 37404, MNHN holotype
Hyperoodon ampullatus: IRSNB 18027, IRSNB 1503, MSNTUP 268

H. planifrons: SAM ZM 41123, SAM ZM 41263
Indopacetus pacificus: MZUF M4854
Mesoplodon bidens: IRSNB 19822, MNHN 1975-112
M. bowdoini: MSNTUP 269
M. densirostris: SAM ZM 40836, SAM ZM 40858, SAM ZM 4013, SAM ZM 40905, SAM ZM 40663
M. europaeus: NMR 9990-00001379, ZMA 25.735, ZMA 25.736, ZMA 25.750
M. grayi: SAM ZM 40622, SAM ZM 40478, SAM ZM 40473, SAM ZM 36839, SAM ZM 41391, SAM ZM 36846, SAM ZM 11476, SAM ZM 19470
M. layardii: SAM ZM 38236, SAM ZM 38235, SAM ZM 40051, SAM ZM 35450, SAM ZM 40479, SAM ZM 39566, SAM ZM 39779, SAM ZM 22408, SAM ZM 39786, SAM ZM 35540, SAM ZM 19932
M. mirus: SAM ZM 39932, SAM ZM 39840, SAM ZM 38219
M. peruvianus: IRSNB 4036
Tasmacetus shepherdi: USNM 484878, SAM ZM 41116, SAM ZM (no number)
Ziphius cavirostris: IRSNB 4027, IRSNB 1504, MSNTUP 270, MSNTUP 271, SAM ZM 35797, SAM ZM 36836, SAM ZM 36837, SAM ZM 36838, SAM ZM 37120, SAM ZM 38237, SAM ZM 38951, SAM ZM 39369, SAM ZM 40712, SAM ZM 40856, SAM ZM 41120

APPENDIX 2

List of characters used in the cladistic analysis. See the tables for the meaning of measurements numbers.

1. Mesorostral ossification of the vomer filling the meso-rostral groove: (0) no; (1) ossification median, not showing a median suture between the lateral walls of the vomer in the rostrum base area; (2) ossification lateral or lateral and median, in any case showing a median suture between the lateral walls of the vomer in the rostrum base area.
2. Acute ventral margin of the alveolar groove posteriorly reaching the antorbital notch and visible in dorsal view as a strengthening of the rostrum base: (0) no; (1) yes.
3. Asymmetry of the premaxillary sac fossae: (0) absent or weak, ratio between measurements 18 and 17 > 0.70; (1) moderate, ratio from 0.70 to 0.40; (2) high, ratio < 0.40.
4. Premaxillary sac fossa laterally overhanging the maxilla: (0) no; (1) yes.
5. Ascending process of the premaxilla in lateral view: (0) rectilinear; (1) slightly concave; (2) concave with posterodorsal portion vertical; (3) concave with posterodorsal portion partly overhanging the bony nares.
6. Constriction on the ascending process of the right premaxilla (between premaxillary sac fossa and premaxillary crest): (0) roughly absent, ratio between measurements 20 and 22 > 0.80; (1) moderate constriction, ratio from 0.80 to 0.61; (2) strong constriction, ratio < 0.61.
7. Elliptical fossa on the anterior surface of the ascending process of the premaxilla: (0) no; (1) yes.
8. Vertex elevation: (0) absent to weak, ratio between measurements 28 and 16 < 0.50; (1) moderate, ratio from 0.50 to 1.0; (2) strong, ratio > 1.0.
9. Premaxillary crest direction (taken on the anterior edge in dorsal view): (0) no crest or crest transversely directed; (1) crest anterolaterally directed; (2) crest posterolaterally directed.
10. Width of the premaxillary crests: (0) small, ratio between measurements 21 and 16 < 1.0; (1) moderate, ratio from 1.0 to 1.25; (2) large, ratio > 1.25.
11. Distance between premaxillary crests: (0) large, ratio between measurements 24 and 16 > 0.25; (1) reduced, ratio ≤ 0.25.
12. Nasal elongation: (0) anterior tip of nasal posterior to or in-line with the premaxillary crest; (1) anterior tip of nasal anterior to the premaxillary crest.
13. Anteromedian excavation of the dorsal surface of the nasal: (0) no; (1) slight anteromedian concavity; (2) well defined anteromedian depression; (3) deep excavation.
14. Inclusion of the nasal in the premaxillary crest: (0) no; (1) for a short distance along the posteromedian angle of the premaxillary crest; (2) until about half-way along the median margin of the crest; (3) reaching the anteromedian margin of the crest.
15. Contact between nasal and premaxillary crest: (0) Wide, on the whole length of the premaxilla on the vertex; (1) reduced, on the posterior half of the nasal.
16. Interparietal as an isolated rounded protuberance on the posterior of the vertex: (0) no; (1) yes.
17. Anteromedian projection of the supraoccipital between the posterior margins of the maxillae: (0) no; (1) yes, lower than the vertex; (2) yes, roughly reaching dorsally the level of the vertex.
18. Number of alveoli on the mandible bearing teeth, erupted in adult males: (0) more than two pairs, associated with functional maxillary teeth; (1) two enlarged pairs, apical to sub-apical; (2) one enlarged pair, apical; (3) one enlarged pair, not apical.

APPENDIX 3

Data-matrix of 18 characters for one outgroup *Squalodon* and 20 analysed taxa. All characters with multiple states are treated as ordered; 0, primitive state; 1, 2, 3, derived states; ?, missing character. See Appendix 2 for explanation of the characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Squalodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xhosacetus n. gen.	2	0	0	0	2	1	0	1	0	1	0	0	0	1	0	0	2	?
Pterocetus n. gen.	2	0	0	0	2	2	0	1	0	1	0	0	1	1	0	0	2	?
Khoikhoicetus n. gen.	2	0	0	0	2	?	0	1	0	0	0	0	3	1	0	0	2	?
Indopacetus	?	0	0	0	2	2	0	1	2	2	0	0	2	1	0	0	2	2
Africanacetus n. gen.	2	0	0	0	3	2	0	1	2	1	0	0	3	2	0	0	2	?
Ihlengesi n. gen.	2	0	0	0	3	2	0	1	2	0	0	0	3	2	0	0	?	?
Mesoplodon bidens	2	0	0	0	3	2	0	1	2	1	1	0	3	1	0	0	2	3
M. slangkopi n. sp.	2	1	0	0	3	2	0	1	2	0	1	0	3	2	0	0	2	?
M. grayi	2	1	0	0	3	2	0	1	2	1	1	0	3	2	0	0	2	3
M. layardi	2	1	1	0	3	2	0	1	2	2	1	0	3	2	0	0	2	3
M. densirostris	2	1	0	0	3	2	0	1	2	2	1	0	3	2	0	0	2	3
M. mirus	2	0	0	0	3	2	0	1	2	2	1	0	3	2	0	0	2	2
Hyperoodon	2	0	2	0	3	2	0	2	2	2	1	0	3	3	0	0	2	2
Ziphius	1	0	2	1	3	0	0	2	1	0	0	1	0	0	1	0	2	2
Izikoziphius rossi n. gen., n. sp.	1	0	1	1	3	0	1	2	1	0	0	1	0	0	1	0	2	?
I. angustus n. gen., n. sp.	1	0	1	1	3	0	1	2	1	0	0	1	0	0	1	0	2	?
Nenga n. gen.	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	2	?
Tasmacetus	0	0	0	0	2	2	0	1	0	0	0	0	1	0	0	0	2	0
Microberardius n. gen.	?	0	0	0	1	0	0	1	0	0	0	0	?	0	0	1	1	?
Berardius	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1