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ARCHAEOZIPHIUS MICROGLENOIDEUS, A NEW PRIMITIVE BEAKED WHALE (MAMMALIA, CETACEA, ODONTOCETI) FROM THE MIDDLE MIOCENE OF BELGIUM

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ABSTRACT—Three partial skulls of odontocetes from the Miocene of Antwerp and Kessel, northern Belgium (southern North Sea Basin) are described here as a new genus and species of beaked whale (Ziphiidae), *Archaeoziphius microglenoideus*. This small new whale is one of the most archaic beaked whales, because of its low vertex, thin and laterally directed premaxillary crests, low contact between the supraoccipital and the frontals on the vertex, and its free atlas. It is also characterized by the strong transverse compression of the frontals on the vertex and a reduced glenoid surface on the squamosal; the two last characters might be considered as derived. Nasals wider than the frontals on the vertex might group *A. microglenoideus* with the extant larger genera *Berardius* and *Tasmacetus*; the nodular frontals and the premaxillary crests are more similar to the condition in *Berardius*. A sediment sample from the cetacean-bearing strata at Kessel is dated with dinoflagellate cysts as middle Miocene, tentatively late Langhian to early Serravallian, i.e., from ca. 15 Ma to ca. 13.2 Ma. *Archaeoziphius microglenoideus* is therefore the oldest reported beaked whale known by cranial material.

INTRODUCTION

Even if rostra are rather common, fossil beaked whales with cranium are rare. Extinct genera including at least parts of the cranium have been described from the Neogene of Antwerp (Belgium) (*Choneziphius* Duvernoy, 1851, *Ziphirostrum* du Bus, 1868), early Pliocene of Peru (*Ninoziphius* Muizon, 1983), late Miocene (*Messapicetus* Bianucci et al., 1992) and Pliocene of Italy (*Tusciziphius* Bianucci, 1997). *Squaloziphius* Muizon, 1991, from the early Miocene of Washington State, U.S.A., is a primitive odontocete with problematic affinities, previously placed by Muizon (1991) in the family Ziphiidae. With the exception of the Belgian genera, all the other genera are based on the description of only one skull.

Recently, three partial skulls of archaic beaked whales were found in the collections of the IRSNB. One of them (skull and partial atlas IRSNB 3856-M.1853) was listed by Abel (1905) as *Mioziphius belgicus*. Another (skull, fragments of basicranium IRSNB M.1854), found in a box labelled "*Archaeoziphius dolloi*, Et.: Anversien, Loc.: Kessel, Expl. Janvier 1910, Reg. I.G. 8243, Abel, 1910", is probably the otherwise unpublished specimen cited by Misonne (1958). Misonne placed it uncertainly as from the Miocene Antwerp Sands. A second label, also from Abel, identifies this second skull as cotype of *Archaeoziphius dolloi*. The third specimen (fragments of skull IRSNB M.1855) was found in a box labelled "*Eurhinodelphis cristatus*, Et.: Anversien. Lettre M. Loc.: Kessel. Expl. Fév., mars, 1910. Reg. I.G. 8243", and bears the label: "isolé—Terrain Bolderien—Loc. Kessel—le 18 mars 1910—I.G. n° 8243".

Those three conspecific skulls are described and figured here, and their affinities with the fossil and extant beaked whales are examined. Dinoflagellate cysts from sediment associated with the bone level at Kessel provide a relative age for the Kessel specimens.

MATERIAL AND METHODS

Institutional Abbreviations—**IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels; **M**, Fossil mammals collection of types and figured specimens from the IRSNB; **USNM**, United States National Museum, Smithsonian Institution, Washington D.C., U.S.A.; **ZMA**, Zoölogisch Museum Amsterdam, The Netherlands.

Terminology—The anatomical terminology is mainly taken from Heyning (1989), Muizon (1991), and Fordyce (1994).

SYSTEMATIC PALEONTOLOGY

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

Type Species—*Archaeoziphius microglenoideus*, nov. sp.

Etymology—*Archaeo* from *archaeus*, in Latin, ancient, old; *Ziphius*, the type genus of the family Ziphiidae.

Diagnosis—as for the only species.

ARCHAEOZIPHIUS MICROGLENOIDEUS, sp. nov.

Mioziphius belgicus: Abel, 1905:104 (in part).

Holotype—IRSNB 3856-M.1853, cranial part of the skull lacking the rostrum, teeth, parts of the supraoccipital shield, left squamosal, and ear bones; associated with a partial atlas. This skull was listed by Abel (1905) under *Mioziphius belgicus*.

Referred Specimens—IRSNB M.1854, a partial skull including the face and a short posterior portion of the rostrum, with detached fragments of the squamosals and the basioccipital; IRSNB M.1855, a fragmentary frontal part of the face, the occipital condyles, the left squamosal, and a fragment of the left exoccipital of a young individual.

Type Locality—The holotype is from an uncertain locality in the region of Antwerp. The two referred specimens are from Kessel, 18 km southeast of Antwerp (Fig. 1), where they were found during excavations for the construction of a fort (51° 8′ 58″ N; 4° 37′ 46″ E) in that locality in 1909–1910 (Rutot, 1909; Abel, 1938).

Type Horizon—Anversien following Abel's label, but without precise stratigraphic data. The referred specimens come from the Antwerp Sand Member, middle Miocene (see discussion on stratigraphy).

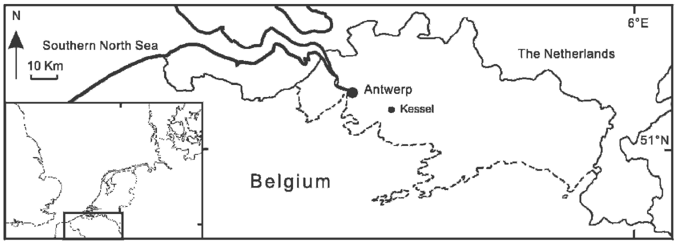

FIGURE 1. Map of northern Belgium and location of the two ziphiid localities, Antwerp and Kessel. Inset: southern North Sea Basin. Dashed line: southern limit of Neogene deposits in Belgium (modified after Tavernier and de Heinzelin, 1963).

Etymology—Micro from Greek micros, small; glenoideus, in relation to the glenoid surface of the squamosal; *microglenoideus* for the reduced glenoid surface in that species.

Diagnosis—Small ziphiid with a skull a little smaller than in extant *Mesoplodon bidens*, differing from all other ziphiids in: short zygomatic process of squamosal anteroposteriorly flattened; small semicircular glenoid surface surrounded by large tympanosquamosal recess; reduced postglenoid process of squamosal. It further differs from all other ziphiids, except *Berardius* and *Tasmacetus*, in: nasals wider than frontals on vertex; supraoccipital not reaching top of vertex (probably not derived). It differs from *Berardius* and *Tasmacetus* in its smaller size, and from *Tasmacetus* in nodular frontals on the vertex, and thinner transverse premaxillary crest (the latter probably not derived).

Remark—The content and the definition of the genus *Ziphirostrum* du Bus, 1868 (= *Mioziphius* sensu Abel, 1905) is revised in a work in progress. *Archaeoziphius microglenoideus* differs from the cotypes of *Mioziphius belgicus* as defined by Abel (1905), IRSNB 3845-M.536 and IRSNB 3847-M.537, in: lower vertex with thinner, laterally directed premaxillary crest, and frontals narrower than nasals; less asymmetric premaxillary sac fossae; and absence of prenarial basin.

DESCRIPTION

IRSNB 3856-M.1853 and IRSNB M.1854

The description is based on the holotype IRSNB 3856-M.1853 (Figs. 2–4, 6) and IRSNB M.1854 (Fig. 5) skulls. The third skull M.1855, because of its smaller size and fragmentary preservation, is discussed below. The state of preservation is curiously different from that of other fossil ziphiids of Antwerp; the specimens of *A. microglenoideus* lack a main part of the rostrum and show at least fragments of the basicranium, while Belgian fossils of *Ziphirostrum*, *Choneziphius*, and *Mesoplodon* are only known by rostra and rostral parts of the cranium. This perhaps indicates a less massive rostrum for *A. microglenoideus*, for which the bones of the face are also more porous. The bony surfaces of the holotype and IRSNB M.1854 are eroded in places, losing or hiding some structural details, e.g., the basicranial foramina. The skulls were at least partially disarticulated when discovered; their reconstruction, dating from that period, is roughly correct. However, we could not precisely quantify the natural lateral deviation of the bones of the vertex; it is not clear whether this asymmetry is stressed by reconstruction inaccuracies.

The cranial part of the skull (Table 1) is slightly smaller than in the extant *Mesoplodon bidens*, with a face wider and shorter.

Premaxilla—The premaxillae are only preserved on their facial part. The height of the premaxilla and mesethmoid anterior to the bony nares is sufficient to indicate the absence of a prenarial basin. The right premaxillary sac fossa is wider than the left; the ratio between the maximum width of left and right premaxillae at that level equals 0.82 for the holotype and 0.84 for IRSNB M.1854, values nearly identical to the ratios calculated on USNM specimens of *Berardius bairdii*. There is no contact between the left and right fossae anterior to the nares, and their inner margins are slightly convex, without marked prenarial corners. Posteriorly, the premaxilla rises steeply towards the vertex, with an apical slope of more than 65°, although not vertical. The widening forming the transverse premaxillary crest is slight and the crest is thin and transversely directed. The right crest is wider than the left (respectively 34 and 26 mm on IRSNB M.1854). The premaxilla roughly reaches the dorsal level of the nasal; it sends a thin posterior projection along that bone, extending the medial margin of the premaxilla on the holotype, and slightly more lateral on IRSNB M.1854.

Maxilla—The base of the rostrum is only poorly preserved on IRSNB M.1854, without palatine and pterygoid. The ventral part of the maxilla is thin and porous, not sclerotic. The outer surface of the bone is too partially preserved to assess the anterior extent of the pterygoid sinus fossa. No alveoli could be detected; if maxillary teeth were still present in *Archaeoziphius microglenoideus*, they were held in much reduced alveoli, at least posteriorly. The vomer appears between the two maxillae as a thin posteriorly thickening keel. Posterior to the antorbital notch, the maxilla is somewhat elevated relative to the premaxillae; this condition might indicate that *Archaeoziphius microglenoideus* possessed a longitudinal maxillary crest extending from the supraorbital process to the base of the rostrum.

The supraorbital process of the maxilla is short and wide; the lateral margin is rounded and it does not totally cover the frontal on the anterolateral corner of the supraorbital process. At least one large posterior infraorbital foramen pierces the supraorbital process (two on the left side of the holotype). The medial part of the maxilla applied to the vertex is steeply elevating against the frontal and the transverse premaxillary crest, where it overhangs the more lateral part of the maxilla.

Nasal—On IRSNB M.1854, the nodular, triangular nasals are wide posteriorly and pointed anteromedially, extending anteriorly beyond the premaxillary crests; the nasals are very similar to those of the extant *Berardius*. The nasals of the holotype are smaller, with roughly parallel lateral margins, and a shorter anterior projection, barely more anterior than the premaxillary crests. The suture between the nasals is distinctly deflected to the left side relatively to the longitudinal axis of the skull.

Mesethmoid—In the V-shaped wide valley formed by the vomer, the mesethmoid is ossified only from 30 mm posterior to the antorbital notch. In the bony nares, the mesethmoid is complete along the nasals of the holotype, 15 mm lower than the top of the nasals.

Frontal—The uncovered preorbital process is more lateral than the postorbital process; the orbit is therefore laterally oriented. The supraorbital process is nearly flat in lateral view; pre- and postorbital processes project weakly ventrally.

On the vertex, the frontals are narrower than the nasals, transversely compressed with a maximum width of 31–32 mm. This compression isolates the frontals; they appear nodular, with an irregular, barely distinct median suture. The compression is also important in *Squaloziphius emlongi*, but with less expanded nasals, in *Mesoplodon longirostris* (Lambert, pers. obs.), and in the extant *Berardius*.

Laterally, the frontal forms an acute crest between the supraoccipital and the maxilla. This crest goes posteriorly beyond the dorsomedian margin of the supraoccipital.

Supraoccipital—The convex supraoccipital shield is nearly vertical. Its median portion forms a narrow strip between the posterior margins of the maxillae; that strip contacts the nodular frontals at a dorsal level 25 mm below the top of the vertex occupied by the nasals and the slightly lower frontals. The wide

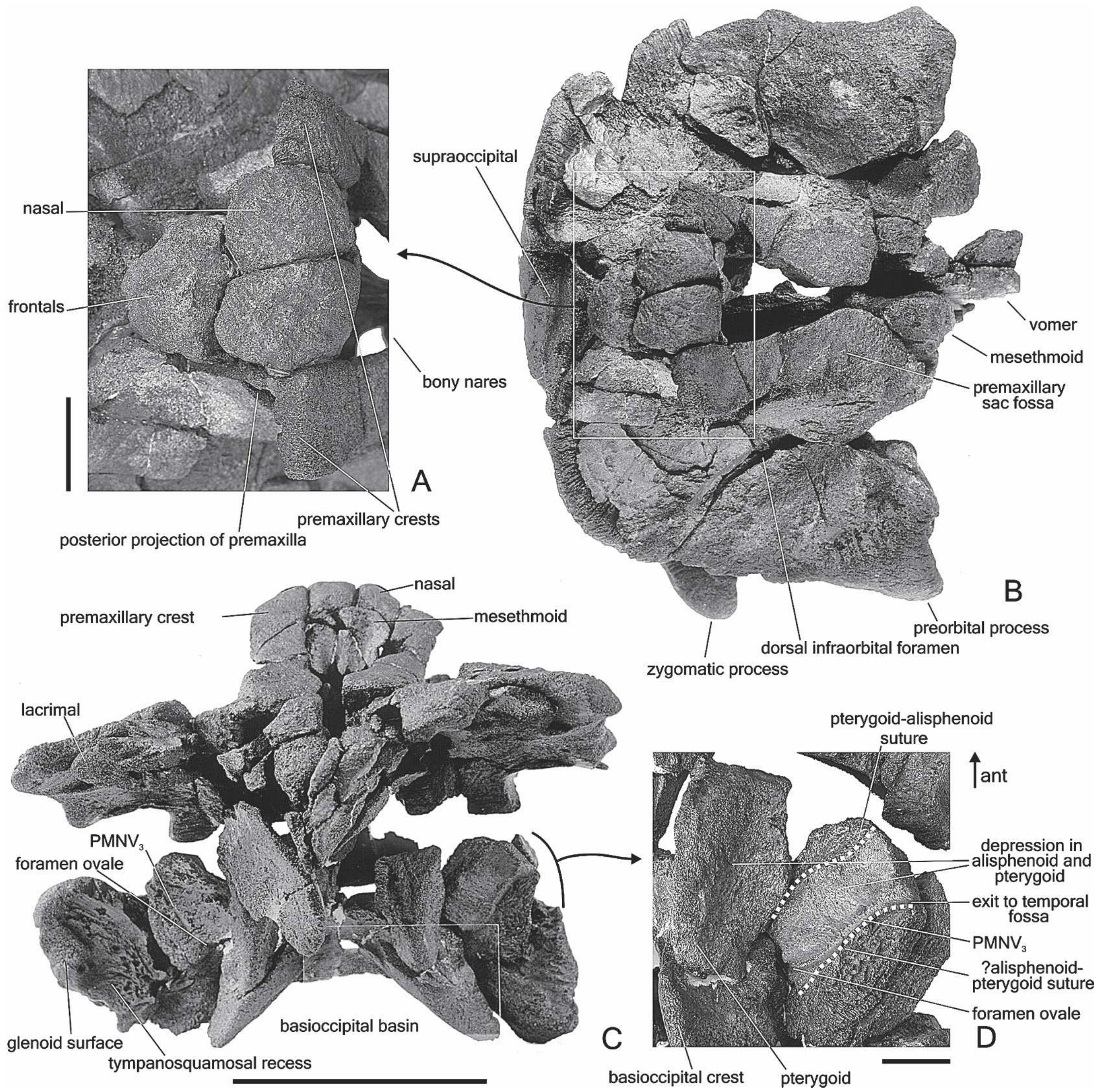

FIGURE 2. Skull of *Archaeoziphius microglenoideus*, gen. et sp. nov. IRSNB M.1853-3856 (holotype). **A**, detail of the vertex in dorsal view; **B**, dorsal view, a little more anterior than A; **C**, anteroventral view; **D**, detail of the left alisphenoid and pterygoid in ventral and slightly lateral view, broken lines indicate suture marks. PMNV$_3$, path for the mandibular nerve V$_3$. Scale bar for A, D equals 20 mm, for B, C, 100 mm.

occipital condyles are weakly posteriorly protruding, without distinct necks.

Lacrimal—A large anteromedian portion of the roof of the orbit is covered by the lacrimal, forming the anterior margin of a deep, wide optic groove. The jugal is lost on the holotype, indicating that it was not fused to the lacrimal.

Orbitosphenoid—On the ventral part of the orbitosphenoid and towards the braincase, the optic groove divides into an anterior narrower and a posterior wide foramen (Fig. 5D). Those foramina presumably correspond respectively to the optic foramen and orbital fissure described by Fordyce (2002:fig. 13) on the archaic Oligocene odontocete *Simocetus rayi*. A similar condition, with variable proportions of the two foramina, is observed in *Ziphius* and *Mesoplodon*.

Squamosal—The anterolaterally directed zygomatic process of the squamosal is widely visible in dorsal view, extending 25 mm laterally beyond the postorbital process of the frontal. In lateral view, the zygomatic process is short, anteroposteriorly flattened, with a reduced postglenoid process; that condition is even more pronounced than in the extant *Ziphius*. The postglenoid process is separated from the ventrally elongated posttympanic process (uneroded on IRSNB M.1854) by a distinct external auditory meatus. On the posterodorsal surface of the zygomatic process, the fossa for the sternomastoideus is shallow. The temporal fossa is longitudinally short, but it is dorsoposteriorly pointed, not as reduced as in *Ziphius*.

The narrow glenoid surface lies lateral to a wide tympanosquamosal recess, which hollows a large portion of the ventral face of the squamosal, with an irregular posterior portion carrying deep grooves and ridges. A small fossa excavates the surface dorsal to the spiny process of the squamosal (Fig. 5F). This fossa is larger on IRSNB M.1854 (10 mm long, 8 mm wide, and 5 mm deep; right side). It has a similar position to the deep subcircular fossa described by Muizon (1987:fig. 3) in *Notocetus*, or the posterior part of the periotic fossa sensu Fordyce (1994:fig. 8), in *Waipatia*. This portion of the basicranium is, however, too partially preserved to detect homologies with other odontocete taxa; it is also possible that the fossa seen in *Archaeoziphius microglenoideus* corresponds to the suprameatal pit (sensu Geisler and Sanders, 2003), first observed by Muizon (1987) between the

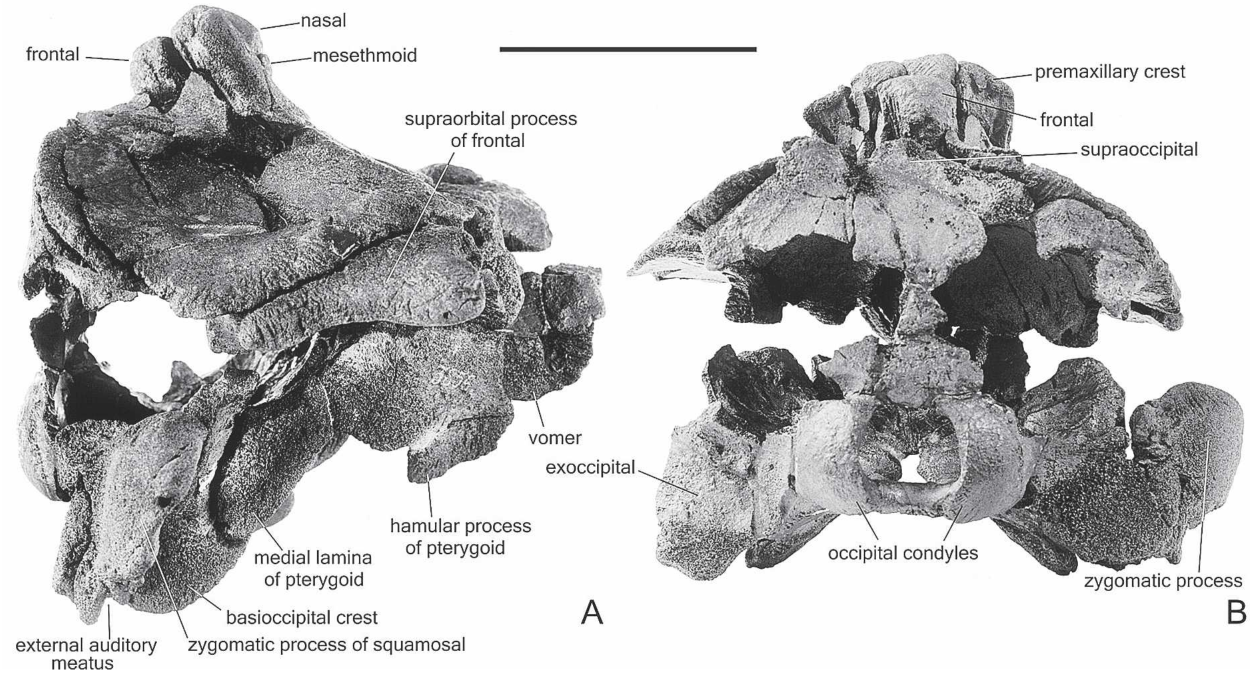

FIGURE 3. Skull of *Archaeoziphius microglenoideus*, gen. et sp. nov. IRSNB M.1853-3856 (holotype) in (**A**) right lateral, (**B**) posterior view. Scale bar equals 100 mm.

spiny process and the subcircular fossa in *Notocetus* and the platanistids. The medial margin of the tympanosquamosal recess is at least partially missing; the important reduction of the falciform process of the squamosal seen in extant ziphiids is, therefore, only suspected.

Pterygoid Sinus Fossa—Keeping in mind that the correlation between the sinus and the corresponding fossa is not always obvious in extant odontocetes (e.g., Fraser and Purves, 1960), the pterygoid sinus fossa occupies most of the wide and smooth ventral surface of the alisphenoid; laterally, the fossa extends beyond the level of the medial limit of the tympanosquamosal recess, a feature observed in the other ziphiids, and nearly achieved on *Squaloziphius*. Medially, the pterygoid sinus fossa excavates the pterygoid from its posterior contact with the basioccipital crest. Anteriorly to the alisphenoid, the superior lamina of the pterygoid is not preserved; nevertheless, considering the extent of the fossa on the alisphenoid and the mark of the anterolaterally directed alisphenoid–pterygoid suture, we suggest that a well-developed superior lamina of the pterygoid formed the roof of the anterior part of the fossa, laterally limited by a subtemporal crest (Fig. 4). That hypothetical subtemporal crest and the lack of a fossa for the pre- or postorbital lobe of the pterygoid sinus on the orbit roof are arguments indicating that the sinus did not spread in the orbit.

Alisphenoid—Posterolateral to the concave area of the pterygoid sinus fossa, the alisphenoid is crossed by a narrow groove, anterolaterally directed; this groove is interpreted as the path for the mandibular nerve (PMN) V_3 (sensu Fordyce, 1994), from the small foramen ovale towards the temporal fossa (Fig. 2D). In *Ziphius*, the $PMNV_3$, sometimes as marked as in *A. microglenoideus*, roughly follows the squamosal–alisphenoid suture; the squamosal is lost at that level in *A. microglenoideus* but suture marks indicate a similar condition. The posterior lacerate foramen is divided in two branches, the anterior larger than the posterior.

Pterygoid—Medial to the partially preserved foramen ovale, the carotid foramen pierces the medial lamina of the pterygoid at its posterior contact with the basioccipital crest. The incomplete hamular process of the pterygoid is thick along the outer margin of the choana. Even if it is not possible to estimate the length of the missing ventral portion, the bone is more ventrally than ventromedially directed, suggesting an important ventral development (the reconstruction in Figure 4 only gives the minimum size of the hamular process). The smooth and slightly concave lateral surface of the preserved part stresses the presence of the hamular fossa.

Basioccipital—Bounding a wide basioccipital basin, the basioccipital crests diverge strongly ventroposteriorly; the angle between them reaches 70º, a value lower than in the larger ziphiids *Berardius*, *Tasmacetus*, and *Ziphius*, and closer to that in, e.g., *Mesoplodon* and *Tursiops*.

Atlas—The ventral part of the atlas of the holotype is preserved (Fig. 6), perfectly matching the occipital condyles. The ventral transverse processes are well developed; the neural canal, slightly ventrally pointed, has a maximal width of 40 mm. The anterior articulation facets are poorly medially limited, roughly continuous from one side to the other. The posterior surface of the bone is partially eroded, but fragments of the articulation facets with the axis indicate that the two bones were freely articulated, without fusion. In lateral view, the bone is short (ca. 28 mm). Extant ziphiids have three to seven cervical vertebrae fused, and in *Ninoziphius*, the only fossil ziphiid described with associated cervical vertebrae, atlas and axis are fused (Muizon, 1984). The free atlas of *Archaeoziphius microglenoideus* indicates a wider range of movements of the neck, an argument further supported by anterior articulation facets less medially delimited than in *Ninoziphius*, more similar to the condition in eurhinodelphinids, for example.

IRSNB M.1855

The third specimen, IRSNB M.1855, is more fragmentary. It includes parts of the frontals and supraoccipital, the occipital condyles, and the left squamosal, with fragments of the left ex-

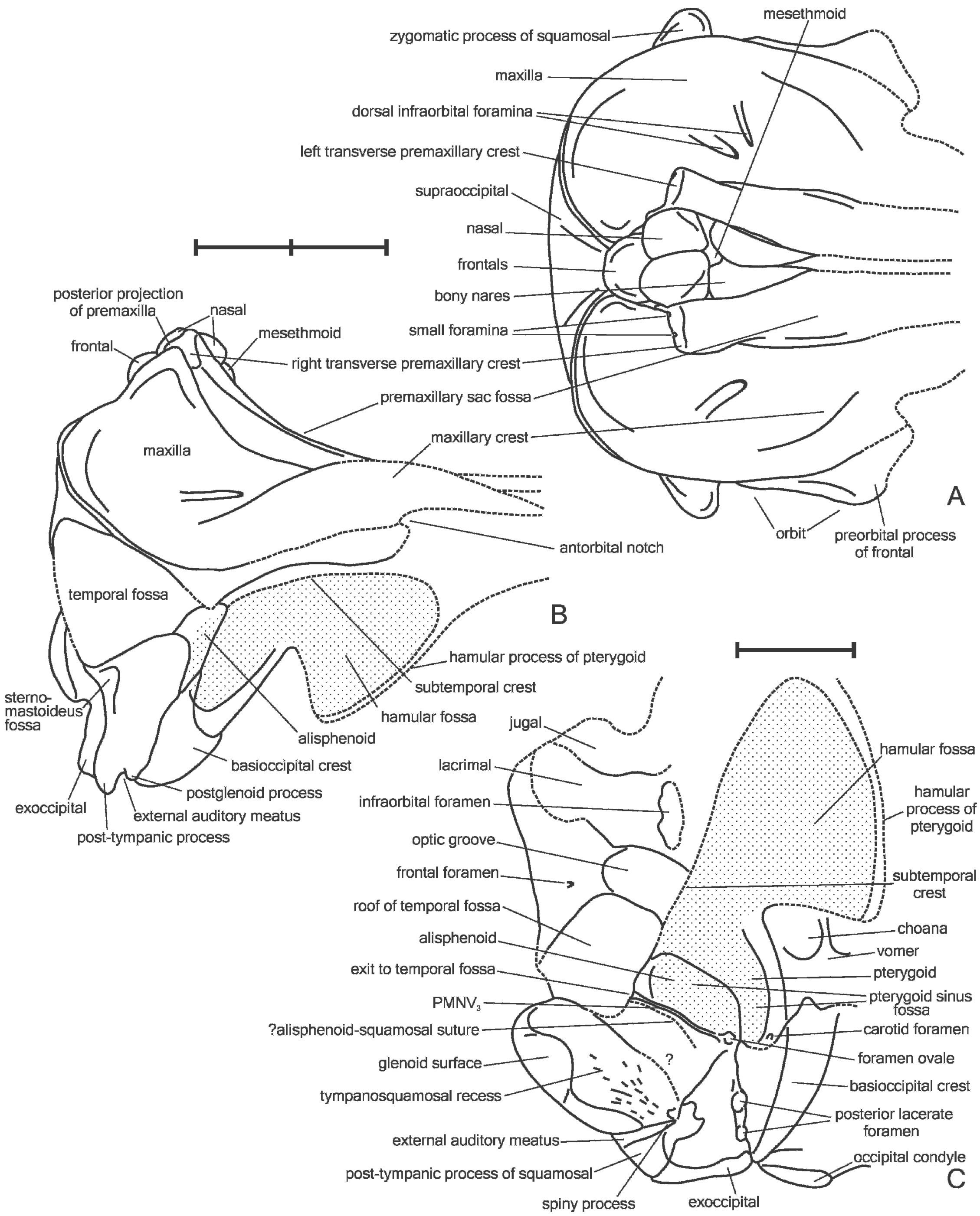

FIGURE 4. Hypothetical reconstruction of the skull of *Archaeoziphius microglenoideus*, gen. et sp. nov., mainly based on the holotype IRSNB 3856-M.1853, in (**A**) dorsal, (**B**) right lateral view; **C**, detail of the right part of the basicranium in ventral view. Broken lines indicate unpreserved structures; stippled area indicates the supposed extension of the anterior portion of the pterygoid sinus. PMNV$_3$, path for the mandibular nerve V$_3$. Scale bar for A, B equals 100 mm, for C, 50 mm.

occipital (Fig. 7). The strong lateral compression of the frontals on the vertex, more elevated than the supraoccipital, the flat supraorbital part of the frontal with a preorbital process anterolaterally directed, and the morphology of the squamosal with a very small glenoid surface and a wide tympanosquamosal recess are strong similarities with the two skulls described above. Several arguments indicate that this specimen is a younger individual from the same species: it is smaller (Table 1; for example, the lateral margin of the supraorbital process is roughly 30 mm more medial than on the holotype); the bones are much thinner (the supraorbital process of the frontal has a maximum thickness of 7 mm, vs. more than 20 mm on the holotype); the sutures are widely open and no fragment of maxilla is preserved on the supraorbital processes of the frontals. The width of the foramen magnum is roughly the same as for the holotype, but the occipital condyles are smaller in IRSNB M.1855 (total width: 61 mm for IRSNB M.1855, 86 mm for the holotype). The same kind of process occurs during the ontogeny of, e.g.,

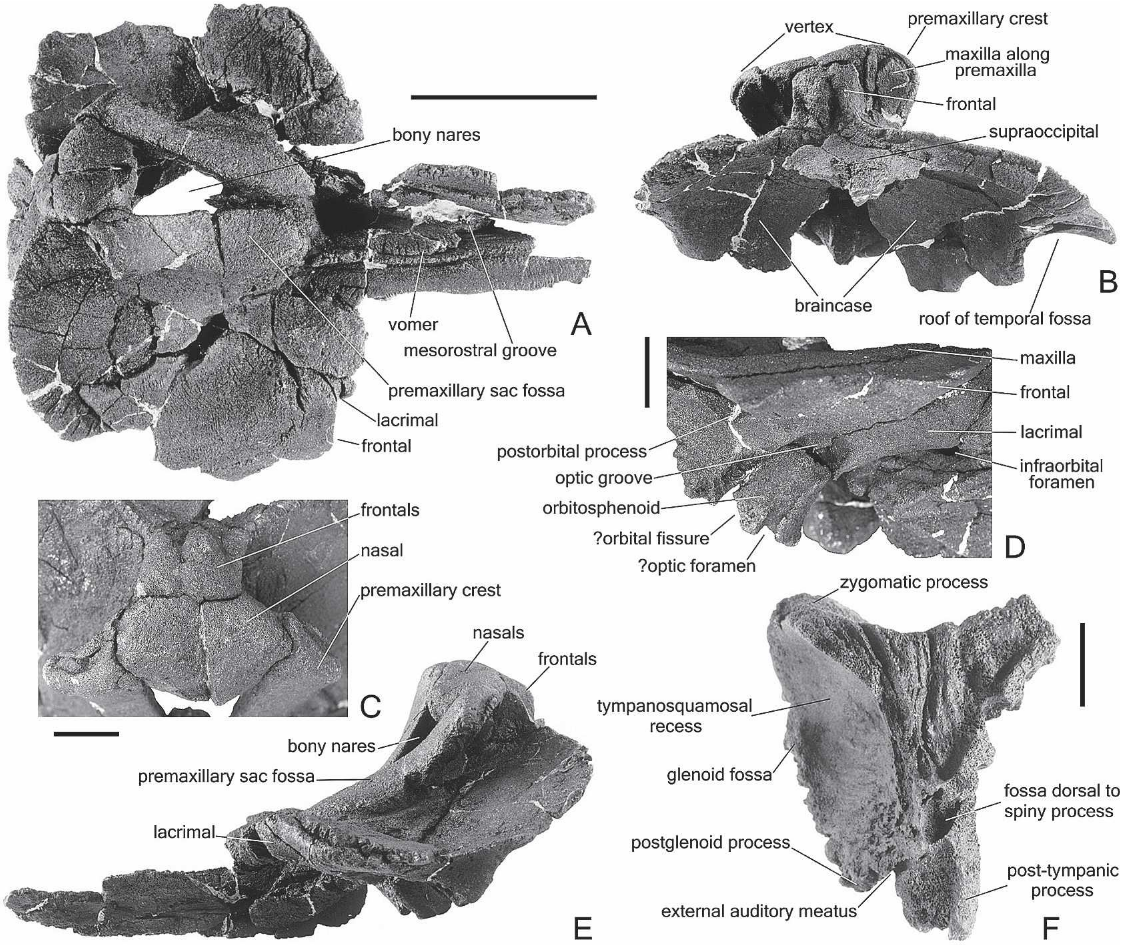

FIGURE 5. Skull of *Archaeoziphius microglenoideus*, gen. et sp. nov. IRSNB M.1854 in (**A**) dorsal, (**B**) posterior, and (**E**) left lateral views; **C**, detail of the vertex in dorsal view; **D**, detail of the right orbit in lateral view; **F**, detached right squamosal of IRSNB M.1854 in ventromedial view. Scale bar for A, B, E equals 100 mm, for C, D, F, 20 mm.

Mesoplodon densirostris (see the measurements of Ross, 1984: 220).

The left squamosal of this specimen is more finely preserved (Fig. 7C) than on the two other skulls, allowing a better observation of the glenoid surface, which is a smooth, slightly concave, semicircular facet surrounded by the large tympanosquamosal recess, at mid-length of the lateral margin of the bone. The short and narrow glenoid surface is close to, but even more reduced than in *Ziphius*; *Berardius*, *Hyperoodon*, *Mesoplodon*, *Tasmacetus*, and the fossil *Messapicetus*, *Ninoziphius*, and *Ziphirostrum* (skull from the late Miocene of Antwerp; Lambert, pers. obs.) have a wider and longer glenoid surface with a strong curvature, extending from the postglenoid tip to the zygomatic process. The reduced glenoid fossa might be related to a different feeding process. The suction feeding, proposed by Heyning and Mead (1996) to explain the reduction of the number of teeth and the anatomy of the throat of the extant ziphiids, might allow a less robust articulation for the mandible. The small glenoid surface is nevertheless also related to the enlargement of the tympanosquamosal recess; this recess, occupied by the middle air sinus (Fraser and Purves, 1960), is particularly wide in *Ziphius* and *Archaeoziphius microglenoideus*.

The ventral margin of the paroccipital process of the exoccipital is excavated, and thinner than in odontocetes characterized by a small posterior process of the tympanic bulla (e.g., *Delphinus*, the eurhinodelphinid *Schizodelphis*); this feature, close to that in, e.g., *Mesoplodon*, suggests an enlarged posterior process of the tympanic bulla in *A. microglenoideus*, as in most of the known ziphiids. The irregular ventromedial surface of the post-tympanic process of the squamosal likely corresponds to the suture of that large posterior process of the tympanic to the squamosal, unfused because of the young age of the individual.

SYSTEMATIC DISCUSSION

Archaeoziphius microglenoideus is allocated to the family Ziphiidae because of the presence of an elevated vertex, with well-developed transverse premaxillary crest and the medial plate of the maxilla strongly overhanging the lateral part of the bone (Figs. 2A, B, 5B, C). Furthermore, the zygomatic process of the squamosal of *A. microglenoideus* is anterolaterally directed (Fig. 2B, C), and a large posterior process of the tympanic bulla might be present (Fig. 7C; no tympanic bulla of the species is known, but the morphology of the exoccipital and the squamosal in the area of the ear bones likely indicates a large posterior process). Those two features are also known in physeteroids (Physeteridae + Kogiidae), which lack an elevated vertex with transverse premaxillary crests.

The elevated vertex of the Pliocene delphinid *Australodelphis mirus* Fordyce et al., 2002, is very similar to the ziphiid condition, with laterally compressed frontals and transverse premaxillary

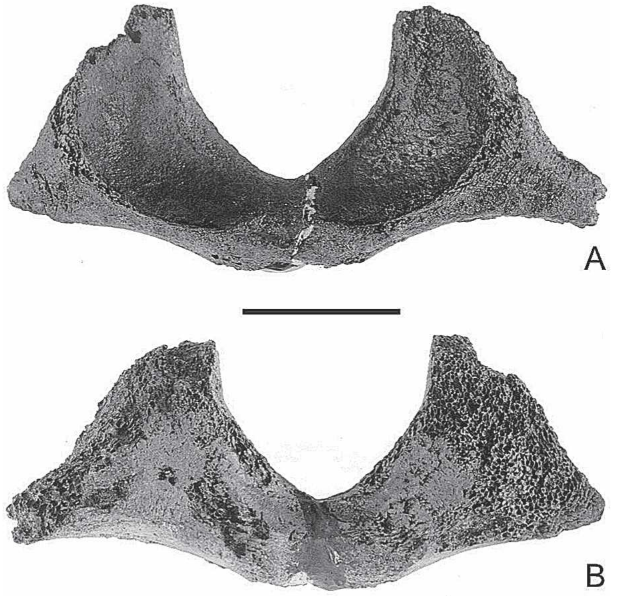

FIGURE 6. Atlas of *Archaeoziphius microglenoideus*, gen. et sp. nov. IRSNB M.1853-3856 (holotype) in (**A**) anterior and (**B**) posterior view. Scale bar equals 30 mm.

crests. However, *A. mirus* differs from *Archaeoziphius microglenoideus* and the other ziphiids in: premaxillary crests distinctly lower than nasals (specially the left crest), absence of posterior projection of premaxilla between nasal and maxilla, and short posterior process of tympanic bulla. Furthermore, delphinid odontocetes do not possess a laterally enlarged pterygoid sinus fossa anterior to the ear bones and a long post-tympanic process of the squamosal.

The attribution of *Squaloziphius emlongi* to the family Ziphiidae (Muizon, 1991) was debated by Fordyce and Barnes (1994), considering its primitive morphology as more reminiscent of the Eurhinodelphinidae. As suggested by Geisler and Sanders (2003), the elevation of the vertex and the development of the transverse premaxillary crests are probably not enough pronounced in *S. emlongi* to allow its inclusion in the family Ziphiidae; those features are not more developed than in, e.g., the eurhinodelphinid *Eurhinodelphis cocheteuxi*. Furthermore, *S. emlongi* lacks the extension of the supraoccipital between the posterior margins of the maxillae towards the vertex. The morphological phylogenetic analysis of Geisler and Sanders (2003) resulted in a sister-group relationship between *S. emlongi* and the odontocete crown group. Contrary to the opinion of those authors, we do not see any fundamental difference between the morphology of the hamular process of *Ziphius–Tasmacetus* and of the other ziphiids; the pterygoid sinus fossa of *S. emlongi* is nearly as wide as in *Archaeoziphius microglenoideus* and other ziphiids anterior to the ear bones; and its basioccipital basin is much enlarged. Those features might suggest a sister-group relationship of *S. emlongi* and the ziphiids.

Archaeoziphius microglenoideus is relatively archaic among the ziphiids. The slope of the premaxillae along the vertex does not reach the vertical; the transverse premaxillary crests are thin, narrow, and laterally directed, differing from the thicker crests of *Tasmacetus*, the thickened posterolaterally directed crests of *Hyperoodon*, *Indopacetus*, and *Mesoplodon*, and the more anterolaterally directed crests of *Choneziphius*, *Messapicetus*, *Ziphirostrum*, and *Ziphius*; the anterodorsal extension of the supraoccipital does not reach the top of the vertex, as in *Berardius* and *Tasmacetus*; the atlas is free, contrary to the condition in the early Pliocene *Ninoziphius* and all the extant genera.

For the slope of the premaxilla, the shape of the premaxillary crest and the strong lateral compression of the nodular frontals on the vertex, *Archaeoziphius microglenoideus* is more similar to *Berardius* (Fig. 8) than to any other known ziphiid. A well-supported basal position of *Berardius* in a phylogenetic tree of the extant ziphiids was obtained in several molecular studies (Dalebout et al., 1998, 2002; Van Helden et al., 2002). *Archaeoziphius microglenoideus* shares with *Berardius* and *Tasmacetus* nasals wider than the frontals. This feature is better developed on the second specimen IRSNB M.1854, but it might constitute a synapomorphy for a clade *Archaeoziphius* + *Berardius* + *Tasmacetus*.

With the width of the skull at the level of the zygomatic processes estimated for the holotype as 286 mm, *Archaeoziphius microglenoideus* is much smaller than *Berardius* spp.; adults of *B. arnuxii* and *B. bairdii* have a width of the skull at that level ranging respectively from 489 to 565 mm and from 471 to 520 mm, for a total length of the body that can go respectively beyond 9 and 12 m (Ross, 1984); *Archaeoziphius microglenoideus* was probably not larger than 3.5–4 m (by comparison with specimens of *Mesoplodon* of similar cranial size).

STRATIGRAPHY

For the cetaceans of the Neogene from the area of Antwerp found during the nineteenth century and the beginning of the twentieth century, the stratigraphic data are often sparse or absent (Misonne, 1958). This is also the case for these skulls; the holotype lacks any indication of origin, while the labels of the other two skulls (from Kessel) indicate 'Et. : Anversien', which does not necessarily correspond to the Antwerp Sands, late early Miocene–middle Miocene. Actually, Abel (1901) divided the fos-

TABLE 1. Measurements (mm) on the skulls of *Archaeoziphius microglenoideus* gen. et sp. nov. (e) indicates estimation and '—' no data.

	IRSNB 3856-M.1853	IRSNB M.1854	IRSNB M.1855
Length between anterior preorbital process and occipital condyles	182	—	—
Length of orbit	77	(e)61	—
Width of skull at level of postorbital processes	237	—	—
Width of skull at level of zygomatic processes	(e)286	—	—
Maximum width of right premaxillary sac fossa	39	37	—
Maximum width of left premaxillary sac fossa	32	31	—
Width of bony nares	38	37	—
Width of nasals	44	54	—
Width of synvertex at level of premaxillary crests	87	95	—
Minimum distance between maxillae across vertex	28	31	(e)20
Distance between ventromedian margins of exoccipitals	(e)157	—	—
Distance between lateral margins of occipital condyles	86	—	61
Width of foramen magnum	38	—	37
Height of cranium	210	—	—
Height of temporal fossa	63	—	—

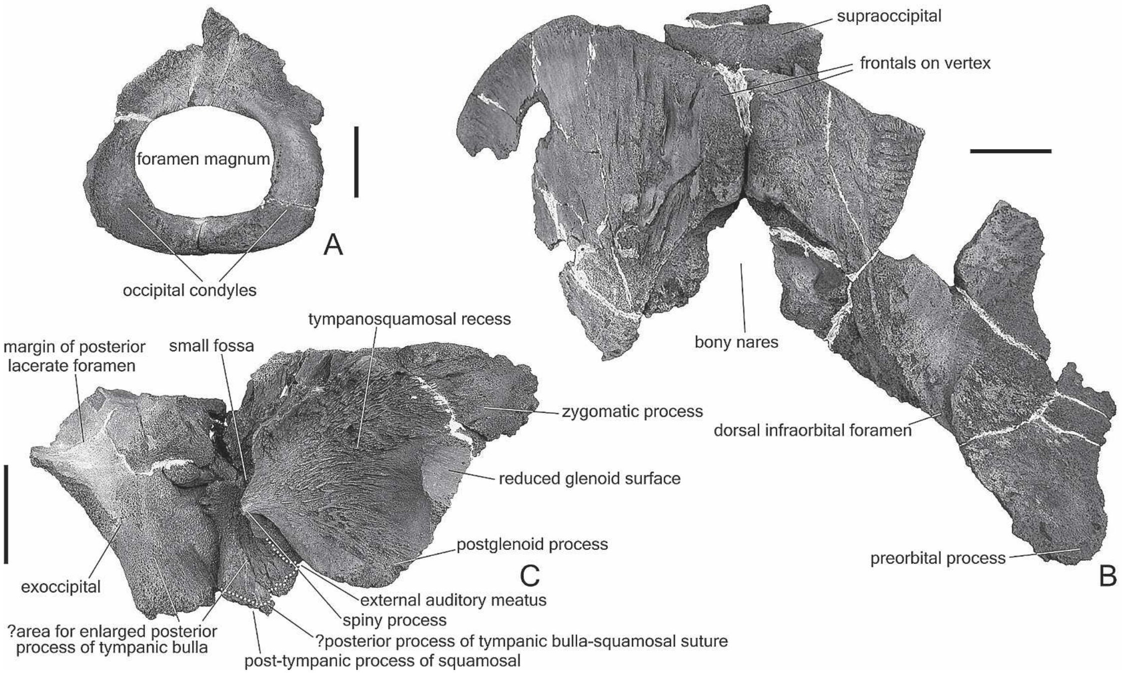

FIGURE 7. Fragmentary skull of *Archaeoziphius microglenoideus*, gen. et sp. nov. IRSNB M.1855. **A**, posterior view of the occipital condyles; **B**, dorsal view of the frontals on the face and the vertex with a fragment of supraoccipital, lacking the maxillae, nasals and mesethmoid; **C**, left squamosal and exoccipital in ventral view, slightly anteromedial. Scale bars equal 20 mm.

sil cetaceans from Antwerp in two stratigraphic groups: the 'Sables Inférieurs' for all the odontocetes and a few mysticetes, and the 'Sables Moyens' for most of the mysticetes; in his later citations, the 'Sables Inférieurs' are a synonym for 'Anversien'. Because odontocetes are found in more than three Miocene and several Pliocene levels in the Antwerp area, this classification is a huge simplification of the real situation.

In a study of the teleostean otoliths from the Zonderschot Sands, Huyghebaert and Nolf (1979:figs. 1, 3) provided a geological map and sections indicating that the only Neogene deposits found under the Quaternary cover in the area of Kessel (near GD 11, Huygebaert and Nolf, 1979:fig. 1) belong to the Antwerp Sands, dated from the late early to middle Miocene (Louwye et al., 2000).

Furthermore, old sediment samples from a skull of the mysticete *Isocetus depauwi* (IRSNB 4018-M.399; Abel, 1938:fig. 4), found in the same level at the fort of Kessel as IRSNB M.1854, were discovered in the collection of the IRSNB. An analysis of marine organic-walled phytoplankton has been carried out for the assessment of the stratigraphic position of the specimen.

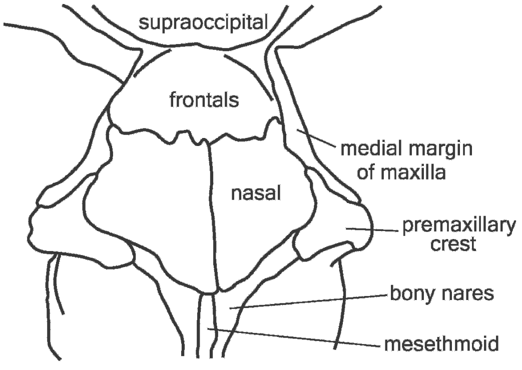

FIGURE 8. Schematic drawing of the vertex of *Berardius arnuxii* in dorsal view (modified after Moore, 1968:fig. 19).

Material and Methods

The palynological preparation of the sample followed standard maceration techniques involving demineralization with HCl and HF. No oxidation or alkali treatments were applied in order to avoid damage of the cysts. A short ultrasound treatment of about 15 s was used to disperse fine-grained palynodebris and amorphous organic matter. First, 250 marine palynomorphs were recorded systematically; the rest of the slide was then scanned for rare specimens. The 282 specimens recorded comprise 33 dinoflagellate species, five marine algae incertae sedis and one Tasmanites (Appendix 1). The preservation of the marine palynomorphs is poor to moderate and the diversity low. The low number of protoperidinioid cysts, and their poor preservation (loss of pigment, thinning of cyst wall), indicate that the deposits were mildly oxidized after deposition. All *Spiniferites* and *Achomosphaera* species have been grouped together because of their limited biostratigraphic value. All recorded marine palynomorphs are listed in Appendix 1. The taxonomy follows De Schepper et al. (2004), Louwye et al. (2000), Strauss et al. (2001), and Williams et al. (1998).

Results

The Miocene dinoflagellate cyst biozonations defined by Verteuil and Norris (1996) in the Salisbury Embayment, USA, and by Strauss et al. (2001) in the Nieder Ochtenhausen Research Well in northern Germany can be readily applied to the studied sample from Kessel.

The DN5 *Batiacasphaera sphaerica* Interval Zone of Verteuil and Norris (1996) is defined as the interval from the highest occurrence (HO) of *Distatodinium paradoxum* to the HO of *Systematophora placacantha*. Common species in this zone are *B. sphaerica*, *Labyrinthodinium truncatum*, *Sumatradinium soucouyantiae*, and *Sumatradinium druggii*. The latter species was not recorded in the studied sample. *Unipontedinium aquaeductum* occurs throughout the zone, while *Apteodinium tectatum* disappears within the zone and *Habibacysta tectata* has its lowest occurrence (LO) within this zone. The dinoflagellate cysts from our studied sample are characteristic of the DN5 Zone. Since *A. tectatum* is present and *H. tectata* not, a more tentative correlation with the lower part of the DN5 Zone may be proposed. According to Verteuil and Norris (1996), the interval assigned to the DN5 Zone overlaps with calcareous nannofossil Zones NN5 and NN6 and has a middle middle Miocene age (late Langhian to middle Serravalian), i.e., from ca. 15 Ma to ca. 13.2 Ma.

The dinoflagellate cyst assemblage allows a correlation with the middle Miocene Naq (*Nematosphaeropsis aquaeducta*) Interval Zone of Strauss et al. (2001), defined as the strata between the LO of the eponymous species and the LO of *Cannosphaeropsis passio*. Additional diagnostic events for this zone are the HO of *S. placacantha* and the HO of *Palaeocystodinium miocaenicum*. The Naq Zone has been calibrated against the middle and higher part of calcareous nannoplankton Zone NN5.

In summary, the marine palynomorphs from the Kessel sample indicate a late Langhian to middle Serravalian age (middle Miocene) given a comparison with the biozonation of Verteuil and Norris (1996). If, as suggested above, we consider the early Miocene *Squaloziphius* out of the family Ziphiidae, *Archaeoziphius microglenoideus* is the oldest known reliably dated member of that family.

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APPENDIX 1

Recorded organic-walled palynomorphs from the Kessel sample. The number of specimens recorded and the relative abundance (between brackets) is given for each species. Reworked species are scarce; an asterisk indicates possible reworking.

Dinoflagellate Cysts—*Apteodinium tectatum* 2 (0.7); *Batiacasphaera micropapillata* 13 (4.6); *Batiacasphaera minuta* 14 (5.0); *Batiacasphaera sphaerica* 13 (4.6); *Cerebrocysta poulsenii* 2 (0.7); *Cousteaudinium aubryae** 2 (0.7); *Dapsilidinium pseudocolligerum* 1 (0.4); *Hystrichokolpoma rigaudiae rigaudiae* 1 (0.4); *Hystrichosphaeropsis obscura* 1 (0.4); *Invertocysta lacrymosa* 1 (0.4); *Labyrinthodinium truncatum modicum* 1 (0.4); *Labyrinthodinium truncatum truncatum* 2 (0.7); *Lejeunecysta* sp. A Louwye (2001) 1 (0.4); *Lejeunecysta* sp. ind. 1 (0.4); *Lingulodinium machaerophorum machaerophorum* 10 (3.5); *Melitasphaeridium choanophorum* 4 (1.5); *Operculodinium*? *borgerholtense* 1 (0.4); *Operculodinium centrocarpum centrocarpum* 4 (1.4); *Operculodinium longispinigerum* 2 (0.7); *Operculodinium* sp. ind. 2 (0.7); *Palaeocystodinium miocaenicum* 1 (0.4); *Pentadinium laticinctum laticinctum* 2 (0.7); *Polysphaeridium zoharyi zoharyi* 3 (1.1); *Pyxidinopsis psilatum* 2 (0.7); *Reticulatosphaera actinocoronata* 4 (1.4); Round brown protoperidinioid cysts 1 (0.4); *Selenopemphix brevispinosa* 1 (0.4); *Spiniferites* / *Achomosphaera* spp. indet. 101 (35.8); *Sumatradinium soucouyantiae* 1 (0.4); *Systematophora placacantha* 61 (21.6); *Tectatodinium pellitum* 2 (0.7); *Tuberculodinium vancampoae* 2 (0.7); *Unipontedinium aquaeductum* 1 (0.4).

Marine Algae Incertae Sedis—Small spiny acritarchs 1(0.4); Acritarch sp. 2 Head et al. 1989 1 (0.4); *Cyclopsiella granosa* / *elliptica* 2 (0.7); *Cyclopsiella*? *trematophora* 1 (0.4); *Paralecaniella indentata* 16 (5.7).

Green Algae—Tasmanites 1 (0.4).