First record of a platanistid (Cetacea, Odontoceti) in the North Sea Basin: a review of *Cyrtodelphis* Abel, 1899 from the Miocene of Belgium

Olivier Lambert[1]

[1] *Institut royal des Sciences naturelles de Belgique, Department of Palaeontology, Rue Vautier, 29 - 1000 Brussels, Belgium; e-mail: Olivier.Lambert@naturalsciences.be / olivierlambert78@hotmail.com.*

ABSTRACT – The systematic status of remains of odontocetes (Mammalia, Cetacea) from the Miocene of the region of Antwerp (north of Belgium, southern margin of the North Sea Basin) previously referred to the long-snouted dolphin species *Cyrtodelphis sulcatus* (Gervais, 1853) is revised. A number of the specimens, a rostrum, some rostral and mandibular fragments, probably dated from the late Early to Middle Miocene, are identified as belonging to a member of the family Platanistidae (for which the only extant genus is *Platanista* from rivers of north-eastern Asia), more precisely to the subfamily Pomatodelphininae. This is the first platanistid record from the North Sea Basin. Another fragment of skull is referred to Kentriodontidae incertae sedis. An isolated tympanic bulla belongs to a eurhinodelphinid. The palaeoecology of the pomatodelphinines is briefly discussed, comparing their palaeogeographic range and the morphology of their feeding apparatus to the eurhinodelphinids, other long-snouted dolphins mainly known from the Miocene.

Key words: *Cetacea, Odontoceti, Cyrtodelphis, taxonomy, Platanistidae, Miocene, Belgium.*

Première mention d'un platanistidé (Cetacea, Odontoceti) dans le bassin de la Mer du Nord : révision des spécimens de Cyrtodelphis Abel, 1899 du Miocène de Belgique – Le statut systématique des restes d'odontocètes (Mammalia, Cetacea) du Miocène de la région d'Anvers (nord de la Belgique, bord sud du bassin de la Mer du Nord) précédemment attribués au dauphin longirostre *Cyrtodelphis sulcatus* (Gervais, 1853) est révisé. Une partie des spécimens, un rostre et quelques fragments de rostre et de mandibule, vraisemblablement datés de la fin du Miocène inférieur-Miocène moyen, sont identifiés comme appartenant à un membre de la famille Platanistidae (pour laquelle le seul genre actuel est *Platanista*, un dauphin de rivières du nord-est asiatique), plus précisément au sein de la sous-famille Pomatodelphininae. C'est le premier platanistidé décrit dans le bassin de la Mer du Nord. Un autre fragment de crâne est placé dans Kentriodontidae incertae sedis. Une bulle tympanique isolée appartient à un eurhinodelphinidé. La paléo-écologie des pomatodelphininés est brièvement commentée, en comparant leur répartition paléo-géographique et la morphologie de leur appareil nutritif aux eurhinodelphinidés, d'autres dauphins longirostres connus essentiellement du Miocène.

Mots clés: *Cetacea, Odontoceti, Cyrtodelphis, taxinomie, Platanistidae, Miocène, Belgique.*

INTRODUCTION

The genus name *Cyrtodelphis* was first used by Abel (1899) for several long-snouted odontocetes (Mammalia, Cetacea) from the Miocene of Europe characterized by a rounded symphyseal angle of the mandible. Abel included in that genus the holotype of *Schizodelphis sulcatus* (Gervais, 1853). In his revision of the polyphyletic family Acrodelphinidae, Muizon (1988) concluded the name *Schizodelphis* had priority over *Cyrtodelphis* and placed *Schizodelphis sulcatus* in the Eurhinodelphinidae Abel, 1901. In the same paper, Muizon revised different specimens from the Miocene of Austria and Italy previously referred to the species *Cyrodelphis sulcatus* (Abel, 1899; Dal Piaz, 1903; Pilleri, 1985). He referred them to *Eoplatanista* Dal Piaz, 1917-1918, within the Eoplatanistidae, which he regarded as closely related to the Eurhinodelphinidae (Muizon, 1991).

In his study of the long-snouted odontocetes from the Miocene of Belgium, Abel (1901) related several specimens to *Cyrtodelphis sulcatus*: a roughly complete rostrum, a partial cranium, several fragments of rostra and mandibles, and an isolated tympanic bulla. The most significant specimens are re-described herein and their systematic affinities are discussed.

MATERIAL AND METHODS

Institutional abbreviations: FLG: Florida Geological Survey, Gainesville, Florida, USA; IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; M: Fossil mammals collection of types and figured specimens from the IRSNB; MCZ: Museum of Comparative Zoology, Harvard College, Cambridge, Massachussetts, USA; MGPD: Museo di Geologia e Paleontologia dell'Università di Padova, Italy; USNM: United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

List of the studied specimens: IRSNB 3246-M.291: large fragment of rostrum (Abel, 1901: fig. 10, pl. 5, fig. 1); IRSNB 3247-M.292a-b-c-d: a fragment of the cranium and palate, and two fragments of mandibular symphysis (Abel, 1901: pl. 5, figs 2-4, palate not figured); IRSNB 3566 - 3568: maxillary fragments of rostrum; IRSNB 3453-M.293: an isolated right tympanic bulla with small fragments of rostrum (Abel, 1901: figs 11-14). The fragment of rostrum IRSNB 3565, also placed in the species *Cyrtodelphis sulcatus* by Abel (1901), is probably lost.

Terminology. The terminology for the elements of the tympanic bulla follows Kasuya (1973). The orientation of the tympanic bulla is simplified in the following descriptions, relative to its anatomical position on the basicranium; the long axis is considered as anteroposteriorly oriented, and the ventral surface of the inner and outer posterior prominences indicates the horizontal plane.

SYSTEMATIC PALAEONTOLOGY

Order CETACEA Brisson, 1762
Suborder ODONTOCETI Flower, 1867
Superfamily Platanistoidea (Gray, 1863) Simpson, 1945
Family Platanistidae (Gray, 1863)
Subfamily Pomatodelphininae Barnes, 2002
Pomatodelphininae genus and species indet.

Referred specimens. IRSNB 3246-M.291, a nearly complete rostrum (discovered at 'Fort n° 4, Vieux-Dieu', Antwerp). Following du Bus (1872), this specimen comes from the 'crag inférieur'. It was first referred to *Platydelphis canaliculatus* (von Meyer, 1853) by du Bus (1872), later renamed *Platyrhynchus canaliculatus* by Van Beneden (1876), and finally referred to *Cyrtodelphis sulcatus* by Abel (1901); IRSNB 3247-M.292b-c-d, two fragments of mandible and a portion of the palate [discovered November 20 1863, in the '3^{e} section', Antwerp (from the labels on the fragments). Abel (1901) gave an other location, probably wrong: 'Fort n° 4, Vieux-Dieu', Antwerp)]. The identification on the oldest labels (probably from du Bus) is *Platydelphis canaliculatus*. The different fragments, including a partial cranium IRSNB 3247-M.292a described below and not placed in the Pomatodelphininae, were considered as one individual of *Cyrtodelphis sulcatus* by Abel (1901), though it was not possible to unite the fragments; IRSNB 3566, a rostral fragment of the left maxilla (found in August 1862 at 'Fort n° 4, Vieux-Dieu', Antwerp); IRSNB 3567, a small fragment of the maxilla at the base of the rostrum (found in August 1862 at 'Vieux-Dieu', Antwerp); IRSNB 3568, a rostral fragment of the left maxilla (found in March 1863 at 'Fort n° 4, Vieux-Dieu', Antwerp).

IRSNB 3246-M.291
Description (figs. 1-3)

This 770 mm long fragment of rostrum is preserved up to 105 mm posterior of the anterior margin of the left premaxillary foramen. Ten to 15 mm of the apex are probably missing. The rostrum is dorsoventrally compressed, distinctly wider than high, and rectilinear throughout its length.

Premaxilla. The premaxillae are narrow and rectilinear until more or less 200 mm anterior of the premaxillary foramen; at that level, they begin to widen, flatten and diverge. The premaxillae are distinctly asymmetric some centimetres anterior of the premaxillary foramen: the right is narrower than the left (18 and 24 mm wide respectively at 90 mm from the premaxillary foramen). Furthermore, the right premaxilla is thinner and slightly more concave along its preserved proximal part. The lateral margins of the premaxillae diverge strongly in that region, but rise only slightly. Thirty-five millimetres posterior of the premaxillary foramen, a thin and depressed medial plate of the premaxilla appears (well preserved on the left side only). This concave and medially sloping plate is pierced by the large premaxillary foramen (8 mm in diameter on the left side). The plate widens posteriorly, while the lateral higher part of the bone progressively narrows. That lateral part ends as a pointed apex 90 mm posteriorly to the premaxillary foramen. The distance between the right and left apices is 100 mm.

In ventral view, the premaxillae appear in the medial groove between the two maxillae more than 280 mm anterior to the preserved apex, but the anterior widening of their ventral surface is progressive. At the preserved apex, the ventral exposition of the premaxillae has a width of only 8 mm, suggesting that the maxillae are roughly as long as the premaxillae.

Maxilla. The maxillae are well exposed dorsally on the rostrum, laterally to the premaxillae. A longitudinal groove slightly hollows the maxilla along its suture with the premaxilla, from at least 200 mm anterior of the premaxillary foramen (more posteriorly, maxillae are worn). A ventrally descending lateral maxilla-premaxilla suture, characteristic of the Eurhinodelphinidae, is not discernable on this rotrum, consistent with the hypothesis of the maxillae being roughly as long as the premaxillae.

In ventral view, the surface of the maxillae medial to the alveolar groove is wide and flat. Within 580 mm of the preserved left alveolar groove, *ca.* 51 alveoli are counted. Including the missing apex, it is estimated that the total number of alveoli ranged between 57 and 65. The posterior

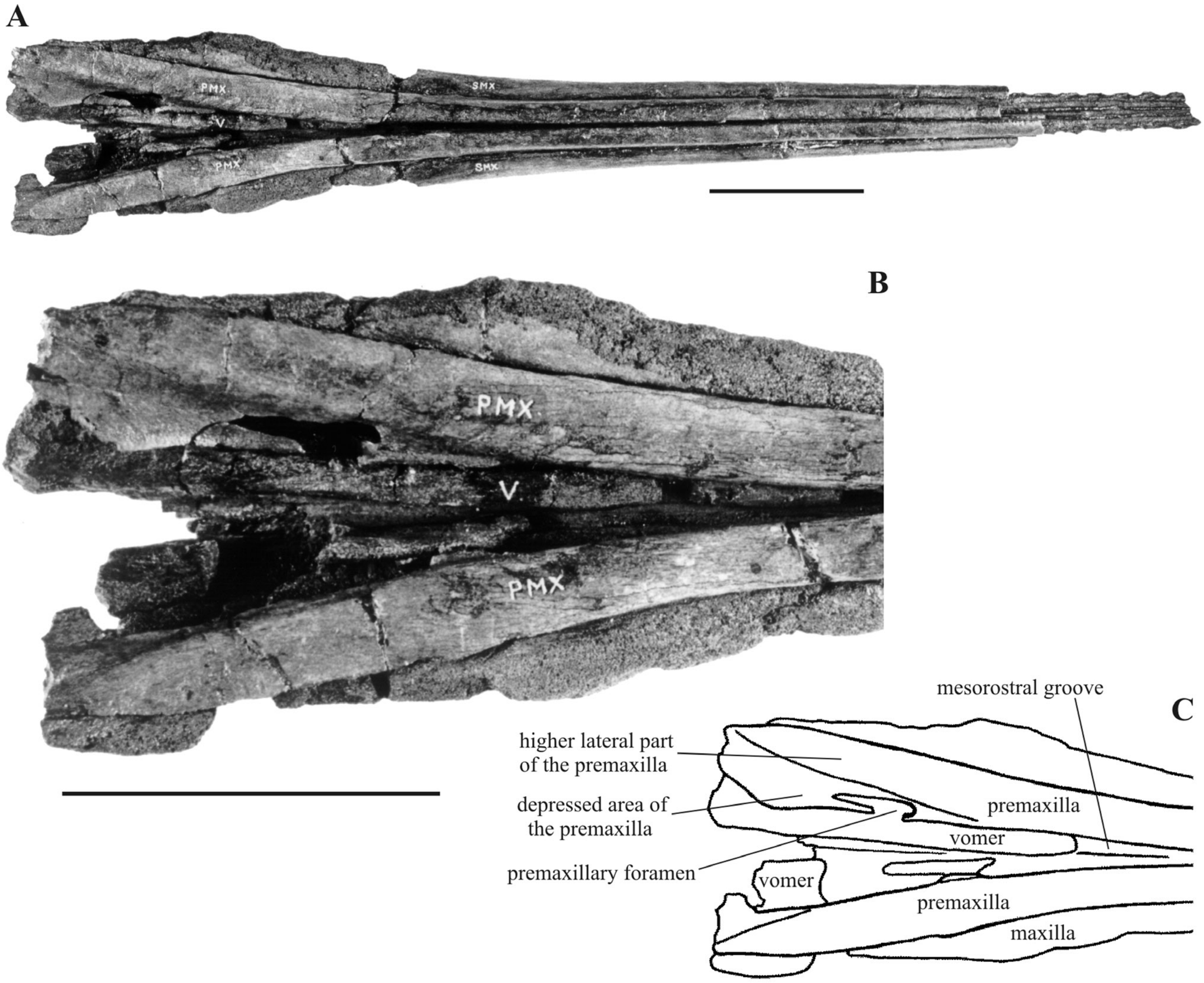

Figure 1 – Rostrum IRSNB 3246-M.291, Pomatodelphininae genus and species indet., Antwerp Sands, late Early to Middle Miocene, Antwerp, Belgium. A: dorsal view. B: detail of the base of the rostrum and the anterior part of the cranium. Scale bars = 100 mm. C: line drawing illustrating the figure 1B. The abbreviations on the specimen were written before Abel (1901). pmx: premaxilla; smx: maxilla; v: vomer.

alveoli are small, close to each other, and posteromedially excavated. Groups of two or three alveoli are separated by more reduced interalveolar septa; this condition might let suggest there may have been some small posterior teeth with two (? or three) roots (fig. 3). A few centimetres anterior to these, the alveoli become more regular, roughly circular, with a diameter of 4 mm and interalveolar septa of 4-5 mm. The diameter of the alveoli increases anteriorly, as does their spacing. Two hundred millimetres anterior of the posterior end of the alveolar groove, their diameter is 6-7 mm and the septa are 9-10 mm long, with much shallower alveoli. Around 45 mm anterior of that level, the alveoli deepen again, with roughly constant diameters, but with more variable interalveolar septa (4-11 mm). The last apical alveoli have a diameter of 6-7 mm and septa of 10-11 mm. On the right side, 80 mm anterior of the start of the alveolar groove, 6-7 shallow pits excavate the surface of the maxilla medial of the alveoli, corresponding to impressions of mandibular teeth. These occlusal pits are somewhat wider spaced than the corresponding maxillary alveoli, and are absent on the left side.

Vomer. The mesorostral groove is widely open dorsally. It is lateroventrally walled by the thickened vomer; the left and right walls are only separated by a few millimetres some centimetres anterior of the premaxillary foramen. Ventrally, the vomer appears between the pterygoids and, for several centimetres anteriorly, between the maxillae.

Palatine-pterygoid. The palate is poorly-preserved and the sutures of that area are difficult to identify. Nevertheless, the two palatines seem to be separated

Figure 2 – Rostrum IRSNB 3246-M.291, Pomatodelphininae genus and species indet., in left lateral view. Scale bar = 100 mm.

medially, dorsolaterally positioned relative to the longer medial pterygoids (fig. 3).

Discussion

The first point to discuss is the proposition of Abel (1901) to refer this specimen to the species *Cyrtodelphis sulcatus*, including the holotype of *Schizodelphis sulcatus* and an Austrian specimen from Eggenburg (figured in Abel, 1899: pl. 1-3), later related to *Eoplatanista gresalensis* by Muizon (1988). The specimen IRSNB 3246-M.291 differs radically from *Schizodelphis sulcatus*, now referred to the family Eurhinodelphinidae (Muizon, 1988). It is larger, with a wider and more dorsoventrally compressed rostrum; the depressed medial surface of the premaxillae around the premaxillary foramen and the transversely expanded premaxillae of IRSNB 3246-M.291 are not present in *S. sulcatus* and in other known eurhinodelphinids, which have a thick elevated anterior portion of the premaxillary sac fossa in that area, and posteriorly tapering premaxillae; and the vomerian gutter is wider in IRSNB 3246-M.291 than in *S. sulcatus* and other eurhinodelphinids.

The monogeneric family Eoplatanistidae was defined by Muizon (1988) as possessing a triangular unflattened section of the rostrum, much unlike the low and wide rostrum of IRSNB 3246-M.291, excluding this specimen from that family. Species of *Eoplatanista* are also much smaller, and the morphology of the posterior part of their premaxillae is closer to *Schizodelphis*. Therefore, this specimen is related neither to the eurhinodelphinids nor to the eoplatanistids.

Apart from the eurhinodelphinids and eoplatanistids, a pronounced longitudinal groove along the lateral premaxilla-maxilla suture is present in the platanistids and in *Pontoporia*. It might be correlated to the elongation of the rostrum and an important innervation of its apex in different lineages of odontocetes. Following Muizon (1987), the laterodorsal migration of the palatines, medially overlapped by the elongated pterygoids, is a synapomorphy of the family Platanistidae. This feature is likely to be present, even if obscured by the type of preservation, on the specimen IRSNB 3246-M.291, in a way similar to *Pomatodelphis* cf. *inaequalis* Allen, 1921 USNM 187414.

Among the platanistids, Barnes (2002) separates the Miocene subfamily Pomatodelphininae (including *Zarhachis* Cope, 1868, east coast of the USA, *Pomatodelphis* Allen, 1921, east coast of the USA and France, and *Prepomatodelphis* Barnes, 2002, Austria) from the subfamily Platanistinae (only including the extant fresh water *Platanista* from rivers of south-eastern Asia) by several characters, which concern anatomical regions not preserved on IRSNB 3246-M.291, but also by the dorsoventrally flattened rostrum, and transversely expanded premaxillae in their posterior portion. These latter two characters are clearly present on IRSNB 3246-M.291.

The asymmetry of the premaxillae anterior of the premaxillary foramen is decribed by Allen (1921) in *Pomatodelphis inaequalis* Allen, 1921, in which the right premaxilla is narrower. This feature is also present in *Pomatodelphis* cf. *inaequalis* USNM 299695 and in *Zarhachis flagellator* Cope, 1868 (only the right premaxilla is preserved in that area in the holotype of *Prepomatodelphis korneuburgensis* Barnes, 2002). The shape of the premaxillae of the Belgian specimen around the premaxillary foramen shows similarities with *Zarhachis*, *Pomatodelphis* and *Prepomatodelphis*, with a median depressed area and a posteriorly narrowing lateral part of the bone. The depressed surface is convex in *Zarhachis*, and partially concave in *Pomatodelphis*; the concave plate of IRSNB 3246-M.291 therefore seems closer to *Pomatodelphis*. That area is described by Barnes (2002) in *Prepomatodelphis* as rough, with a depression for the premaxillary foramen, while the surface is smooth on IRSNB 3246-M.291. The posterior divergence of the premaxillae is less pronounced in *Pomatodelphis* relative to *Zarhachis* and IRSNB 3246-M.291.

The estimated number of maxillary alveoli is close to *Pomatodelphis inaequalis* MCZ 4433 (52 on the nearly complete left side, Kellogg, 1959), smaller than in *Zarhachis flagellator* (more than 80 alveoli by side) and *Prepomatodelphis korneuburgensis* (nearly 75 teeth, Barnes, 2002). The alveoli are more rounded than in *Pomatodelphis inaequalis*, closer in this respect to *Zarhachis flagellator*. Shallow pits made by mandibular teeth medial of the maxillary alveolar groove are also observed on the right side in *Pomatodelphis inaequalis* FGS 5834 and USNM 20738, but over a more extended area (see Allen, 1921: pl. 10, fig. 7; Kellogg, 1959: pl. 5, fig. 3). This implies the mandibular tooth rows converge more posteriorly than the maxillary tooth rows, and in consequence no contact between mandibular and maxillary teeth in the posterior portion of the jaws.

IRSNB 3246-M.291 probably had a total skull length of around one metre. This may be somewhat smaller than *Zarhachis flagellator*, close to *Pomatodelphis*

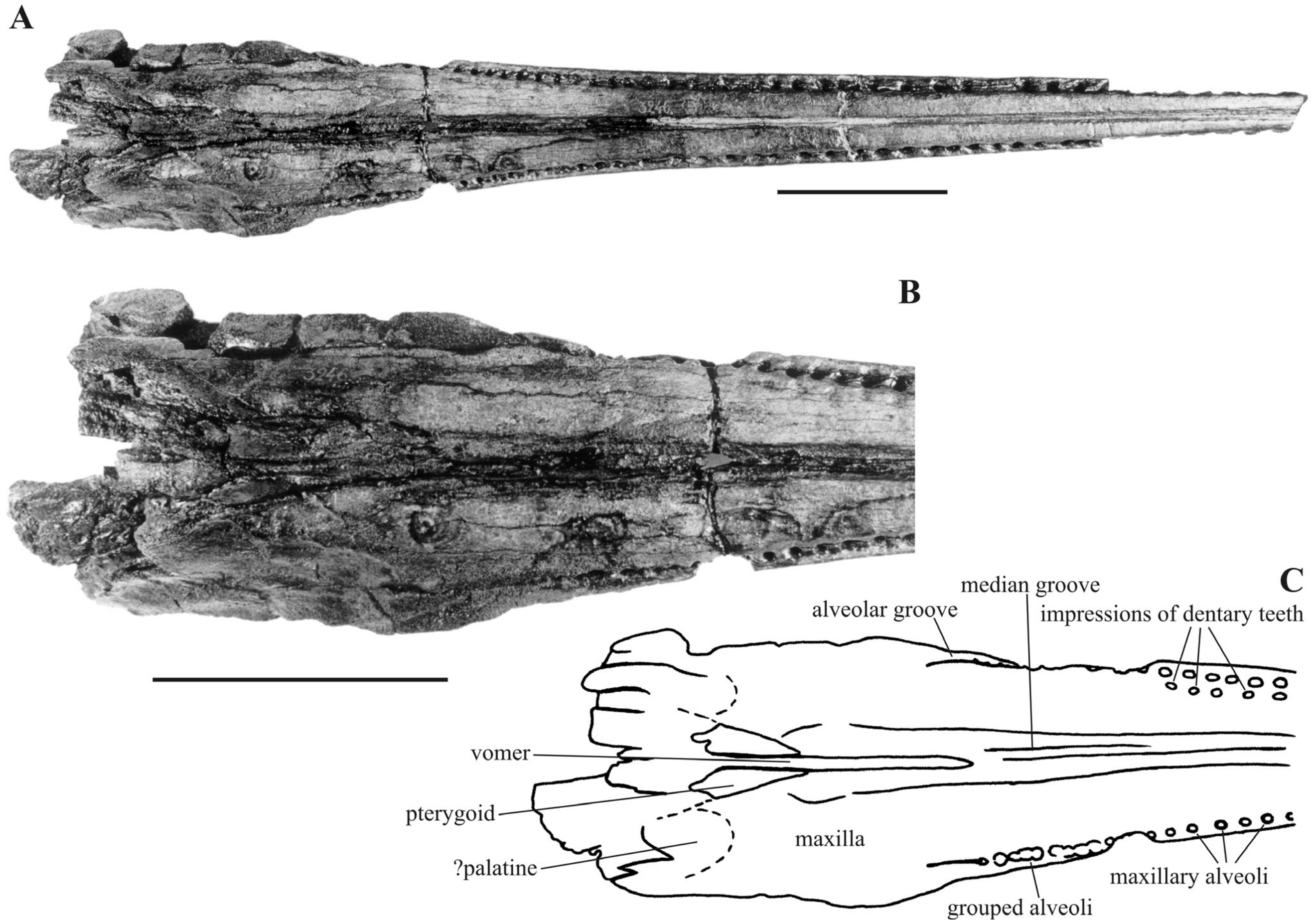

Figure 3 – Rostrum IRSNB 3246-M.291, Pomatodelphininae genus and species indet. A: ventral view. B: detail of the palate and the base of the rostrum in ventral view. Scale bars = 100 mm. C: line drawing illustrating the figure 3B.

bobengi (Case, 1934) (the largest Floridan species of *Pomatodelphis*, sizes given by Morgan, 1994), and larger than *Prepomatodelphis*.

The geographically closest pomatodelphinine is the poorly known *Pomatodelphis stenorhynchus* Holl, 1829 from the Miocene of Maine-et-Loire (France). It is smaller than IRSNB 3246-M.291 and no depression is visible posterior of the premaxillary foramen on the figure of Van Beneden & Gervais (1880: pl. 57, fig. 9 = '*Delphinus renovi*').

IRSNB 3246-M.291 is probably too incomplete to allow precise placement within the Pomatodelphininae. This would require information about the supraorbital process, the posterior extremity of the premaxillae, and the zygomatic process of the squamosal, all parts included in the diagnoses of the pomatodelphinine genera. IRSNB 3246-M.291 probably represents a new species of pomatodelphinine but it is referred to Pomatodelphininae genus and species indet. This specimen comes from the same locality as most of the specimens of *Eurhinodelphis cocheteuxi* du Bus, 1867 and shows the same kind of preservation. For these reasons, it was very likely collected from the same member, the Antwerp Sands, late Early to Middle Miocene (Louwye *et al.* 2000, Lambert, 2005b). It is the first platanistid described from the North Sea Basin.

IRSNB 3247-M.292b-c-d (excluding the partial cranium IRSNB 3247-M.292a)

The first fragment of mandible is a 413 mm long ventral surface of a long, flattened symphysis and the distal region of the rami (fig. 4A). The angle between the rami is rounded and widely open (*ca.* 55 degrees). This is a wider angle than in the holotype of *Zarhachis flagellator*, which unfortunately has distorted rami, probably artificially decreasing the opening of the symphyseal angle. The dorsal part of the angle is more anterior than the ventral part, forming a triangular cavity. A deep sulcus extends along the ventrolateral surface of the symphysis. No traces of the alveoli are preserved.

The second fragment of mandible is a 26 mm long portion of the dorsal surface of the symphysis between the alveoli (fig. 4B). This flat surface possesses a median groove, which is medially divided by a thin crest, much like the ventral face of the rostrum of IRSNB 3246-M.291.

The fragment of palate is broken just anterior

Figure 4 – Rostral and mandibular fragments IRSNB 3247-M.292b-c-d, Pomatodelphininae genus and species indet. The three fragments are considered to belong to the same individual. A: ventral surface of a symphyseal portion of mandible IRSNB 3247-M.292b, in ventral view. B: fragment of the dorsal surface of a symphyseal portion of mandible IRSNB 3247-M.292c, in dorsal view. C: fragment of the maxillary part of the palate IRSNB 3247-M.292d, in ventral view. Scale bar = 50 mm.

of the apex of the pterygoids and palatines (fig. 4C). The vomer is observed between the two maxillae only anterior of the pterygoids, unlike IRSNB 3246-M.291. Nevertheless, the inclination of the ventrolateral surfaces is similar; the distance between the vomerian keel and the alveolar groove is only slightly smaller here; the first small alveoli have the same orientation; and the posterior region of the median ventral groove is similar.

Even if we cannot be sure that these three fragments belong to a same individual, the similarities with the first specimen IRSNB 3246-M.291 at the level of the palate and the resemblance of the dorsal part of the symphysis with the ventral surface of the rostrum of the latter lead us to consider both specimens as the same taxon.

IRSNB 3566 - 3568

The rostral fragment of the left maxilla IRSNB 3566, with 21 alveoli developed over a total length of 291 mm, is similar to IRSNB 3246-M.291, except for the smaller size of the anterior alveoli (transverse diameter of 2-3 mm); and that they are more anteriorly directed.

The alveoli are more numerous and distinctly smaller on the small maxillary fragment of the base of the rostrum IRSNB 3567 (found in August 1862 at ‘Vieux-dieu’, Antwerp). Eighteen alveoli with a mean diameter of 2.5 mm are counted over a length of 118 mm. It might represent a different taxon in the Pomatodelphininae, although the number and size of the alveoli seems variable among the species of that subfamily.

The same argument is suggested for the slightly more anterior fragment of left maxilla IRSNB 3568 (found in March 1863 at ‘Fort 4, Vieux-Dieu’, Antwerp) that includes 10 alveoli over a length of 90 mm, with a mean diameter of 3 mm.

Family Kentriodontidae *incertae sedis*

Referred specimen. IRSNB 3247-M.292a, a partial cranium mainly comprising the frontals, including the vertex and the left supraorbital process, fragments of the posteromedian plates of the maxillae, an eroded fragment of the left premaxilla along the bony nares, the vertical plate of the mesethmoid posterior of the bony nares, and a small fragment of the supraoccipital. The specimen was discovered November 20 1863, in the ‘3^{e} section’, Antwerp (from the labels on the fragments). Abel (1901: p. 52) gave another location, probably wrong: ‘Fort n° 4, Vieux-Dieu’, Antwerp.

Description (fig. 5)

The cranium is relatively short and wide. The longitudinal distance between the preorbital process of the frontal and the anterior margin of the supraoccipital is *ca.* 128 mm and the postorbital width is estimated at 230 mm.

Frontal. The preorbital process of the frontal is a short anterolateral projection, only weakly ventrally directed, and medially shifted relative to the postorbital process. The dorsal surface of the supraorbital process is flat and was completely covered by the maxilla. The ventral surface of the preorbital process shows a wide and long suture with the lacrimal. The roof of the temporal fossa is not totally preserved, but considering the thickness of the bone, the missing portion seems small. This margin was therefore posteromedially directed, probably not completely covering the temporal fossa.

Maxilla. The maxilla is pierced on the supraorbital

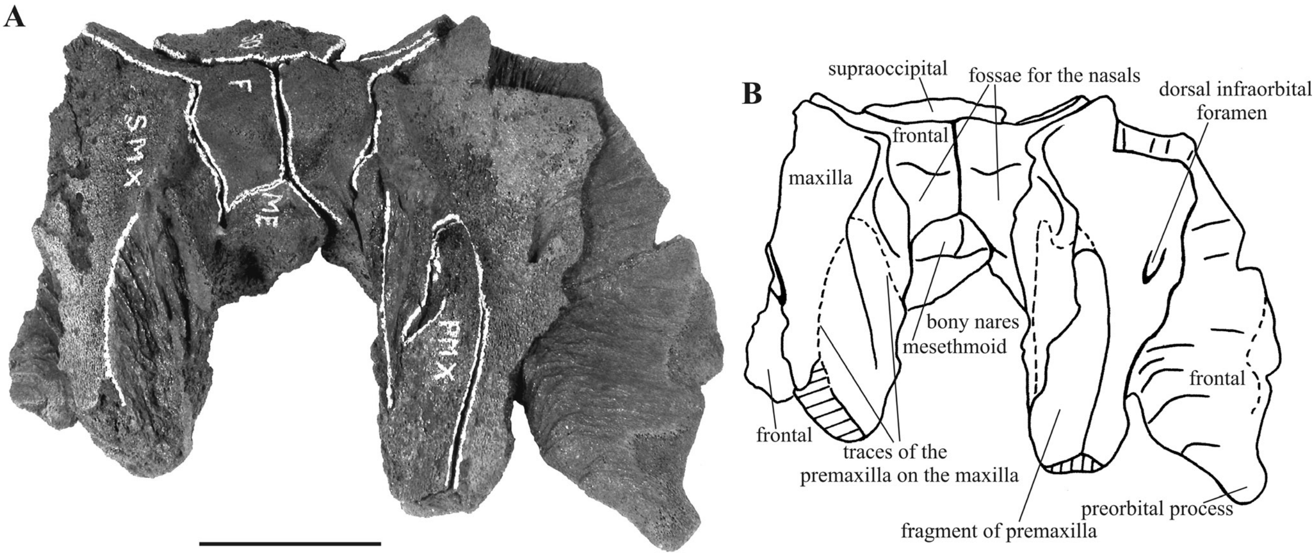

Figure 5 – Facial part of the skull IRSNB 3247-M.292a, Kentriodontidae *incertae sedis*. A: dorsal view. The abbreviations on the specimen were written before Abel (1901). f: frontal; me: mesethmoid; pmx: premaxilla; smx: maxilla; so: supraoccipital. Scale bar = 50 mm. B: line drawing clarifying fig. 5A.

process by a dorsal infraorbital foramen 15 mm lateral of the premaxilla. The posteromedial margin of the maxilla is abruptly elevated, forming an anterolaterally curved crest that divides the posterior apex of the premaxilla in two branches.

Premaxilla. The apex of the partially preserved premaxilla, even if divided in two laminae by the underlying maxilla on the left side, clearly tapers posteriorly, ending roughly at the anterolateral corner of the missing nasal. The maximum distance between the lateral margins of the premaxillae is 94 mm, roughly at the level of the postorbital processes; from that level, the lateral margins of the premaxillae converge anteriorly. That distance is shorter than the 108 mm separating the lateral margins of the premaxillae on IRSNB 3246-M.291 (described above), 50 mm posterior of the premaxillary foramen.

Frontal. On the low vertex, the frontals are two small rectangular surfaces, with a common anteriorly convex anterior margin. The left frontal is somewhat shorter and wider than the right. The minimum distance between the maxillae lateral of these rectangles is 43 mm.

Nasal. The nasals are lost but their cavity is well delimited, posteriorly by the frontals, laterally by the erected medial plate of the maxilla, anterolaterally by the apex of the premaxilla and ventrally by the mesethmoid. The relatively low mesethmoid did probably not border the nasals anteriorly. The nasals were clearly wider than the frontals on the vertex, with lateral margins anteriorly divergent; it is probable that they possessed a short posterolateral projection.

Supraoccipital. The supraoccipital shield, with a slope < 20 degrees, does not reach the dorsal level of the frontals; its surface is actually nearly continuous with the sub-horizontal dorsal surface of the frontals. The supraoccipital-frontals suture is strongly and regularly anteriorly convex.

Discussion

This fragment of cranium IRSNB 3247-M.292a differs from known members of the Pomatodelphininae by several characters. The posterior extremity of the premaxilla is shorter, and not transversely expanded, a synapomorphy of *Prepomatodelphis*, *Pomatodelphis* and *Zarhachis* following Barnes (2002). The proportions of the nasals and frontals also differ from *Pomatodelphis* and *Zarhachis* (not preserved in *Prepomatodelphis*); here the nasals are equal or larger in size to the frontals, whereas in *Pomatodelphis* and *Zarhachis*, the frontals are much longer and slightly wider than the nasals, probably representing a primitive condition (present for example in *Waipatia* Fordyce, 1994, a primitive odontocete from the Oligocene of New Zealand, and in *Squalodon*).

As mentioned above, the specimens studied here were placed by Abel (1899) in the species *Cyrtodelphis sulcatus* because of similarities with the holotype of *Schizodelphis sulcatus* and with an Austrian skull from the Miocene of Eggenburg. The vertex of the holotype of *S. sulcatus* is completely eroded, but this skull, reported as an eurhinodelphinid by Muizon (1988), is comparable, at least at the level of the genus, with several American and Belgian specimens displaying a well preserved vertex (Lambert, 2004). All of them differ from IRSNB 3247-M.292a in: the cranium relatively narrower; longer premaxilla contacting the frontal; and a higher supraoccipital shield relatively to the frontals. The Eggenburg skull, revised as *Eoplatanista gresalensis* by Muizon (1988), has wider and much longer frontals, with reduced nasals, and it retains a contact between premaxilla and frontal.

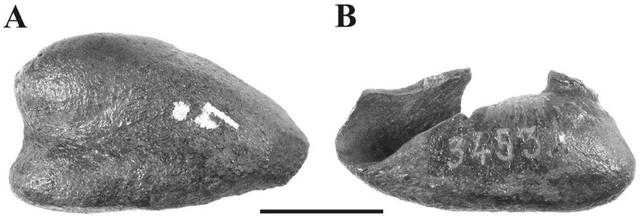

Figure 6 – Right tympanic bulla IRSNB 3453-M.293, Eurhinodelphinidae aff. *Eurhinodelphis* in ventral (A) and medial (B) views. Scale bar = 20 mm.

The enlargement of the nasals relative to the frontals is observed in most of the kentriodontids and several ziphiids (e.g. *Berardius*, *Tasmacetus*). The loss of contact between premaxillae and frontals is a feature also present in kentriodontids. The vertex is low, and the frontals less compressed transversely, similar to the kentriodontine *Kampholophos serrulus* Rensberger, 1969, from the Miocene of California.

To summarize, the partial cranium IRSNB 3247-M.292a was probably erroneously associated with IRSNB 3247-M.292b-c-d. The shortened and posteriorly tapering apex of the premaxillae not contacting the reduced frontals, and the enlarged nasals lead to provisional referral of that specimen to Kentriodontidae *incertae sedis*.

Family Eurhinodelphinidae Abel, 1901
Eurhinodelphinidae aff. *Eurhinodelphis*

Referred specimen. IRSNB 3453-M.293, a right tympanic bulla, found with six non-diagnostic small fragments of rostrum in 1861-63 in Antwerp. The location given by Abel (1901) is '? Quatrième section'. The tympanic bulla was identified as *Cyrtodelphis sulcatus* by Abel (1901), because of its similarities with that of the Eggenburg skull.

Description (fig. 6)

This large tympanic bulla lacks a part of the outer lip and the posterior process. It seems roughly complete anteriorly, with a total length of 50 mm and a maximum width of 30 mm. In ventral view, the inner posterior prominence is considerably narrower than the outer one, and somewhat posteriorly longer. The medial groove rapidly shallows and widens anteriorly, and exhibits slight laterally-directed curvature. There is no apical spine. The convex dorsal margin of the involucrum shows an anterior descent cut only by a small notch. In dorsal view, the anterior thinning of the involucrum is more abrupt, the wall becoming narrow at the level of this small notch.

Discussion

Even if the drawings of the Eggenburg specimen in Abel (1899: pl. 3, figs 2-4; fig. 7 in this work) lack detail, several differences with the Belgian tympanic bulla are apparent. First, the Eggenburg tympanic bulla is relatively shorter (total length of *ca.* 43 mm; maximum width of *ca.* 30 mm). The widths of the outer and inner posterior prominences differ less. Furthermore, the medial groove is much longer, deeper and narrower, roughly reaching the more pointed anterior apex. In dorsal view, the involucrum has a less rectilinear anterior portion.

Remark on the Eggenburg specimen. The Eggenburg tympanic bulla (fig. 7A-C) is actually very different from the known tympanics of Italian *Eoplatanista* (e.g. Muizon, 1988: fig. 11), which are somewhat smaller and narrower and, more importantly, have a much more reduced medial groove, a character defining the family Eoplatanistidae following Muizon (1988). The developed anterolateral convexity seen on the Eggenburg specimen characterizes the group Platanistidae + Squalodelphinidae in the superfamily Platanistoidea *sensu* Muizon, 1987. Among this group, the medial groove is longer in the squalodelphinids, which possess posterior prominences less asymmetrical than in platanistids, two features present on the Eggenburg specimen (see *Notocetus*, *Phocageneus* in Muizon, 1987: fig. 17). However, the skull associated to the tympanic differs significantly from the known squalodelphinids; the vertex is wider and narrower than in *Notocetus vanbenedeni* Moreno, 1892 and *Squalodelphis fabiani* Dal Piaz, 1917-1918, the zygomatic process of the squamosal seems much less developed, and the supraorbital process is likely not thickened. The large surface of the frontals on the vertex is somewhat similar to *Eoplatanista gresalensis* (e.g. MGPD 26409), but also to the eurhinodelphinid *Macrodelphinus kelloggi* Wilson, 1935 and the archaic odontocete *Waipatia maerewhenua* Fordyce, 1994. Because the characters of the tympanic more likely represent apomorphies, squalodelphinid affinities are suggested for the Eggenburg specimen. Nevertheless, it seems wiser to wait for direct observations of that specimen for a more definitive systematic attribution.

The Belgian tympanic IRSNB 3453-M.293 may not be related to a platanistid taxon; it lacks the reduction in length and transverse thickness of the inner posterior prominence characterizing the family, and the long, narrow, and sharp anterior spine associated with a salient anterolateral convexity of the group Platanistidae + Squalodelphinidae (Muizon, 1987). Actually, this bone shows better similarities with eurhinodelphinid tympanics. It is for instance close to *Eurhinodelphis cocheteuxi*, the largest described eurhinodelphinid from Antwerp. That bone is however several millimetres longer and wider than the tympanics of *E. cocheteuxi* IRSNB M.1856; its inner posterior prominence is posteriorly longer; and it lacks the distinct indentation of the dorsal margin of the

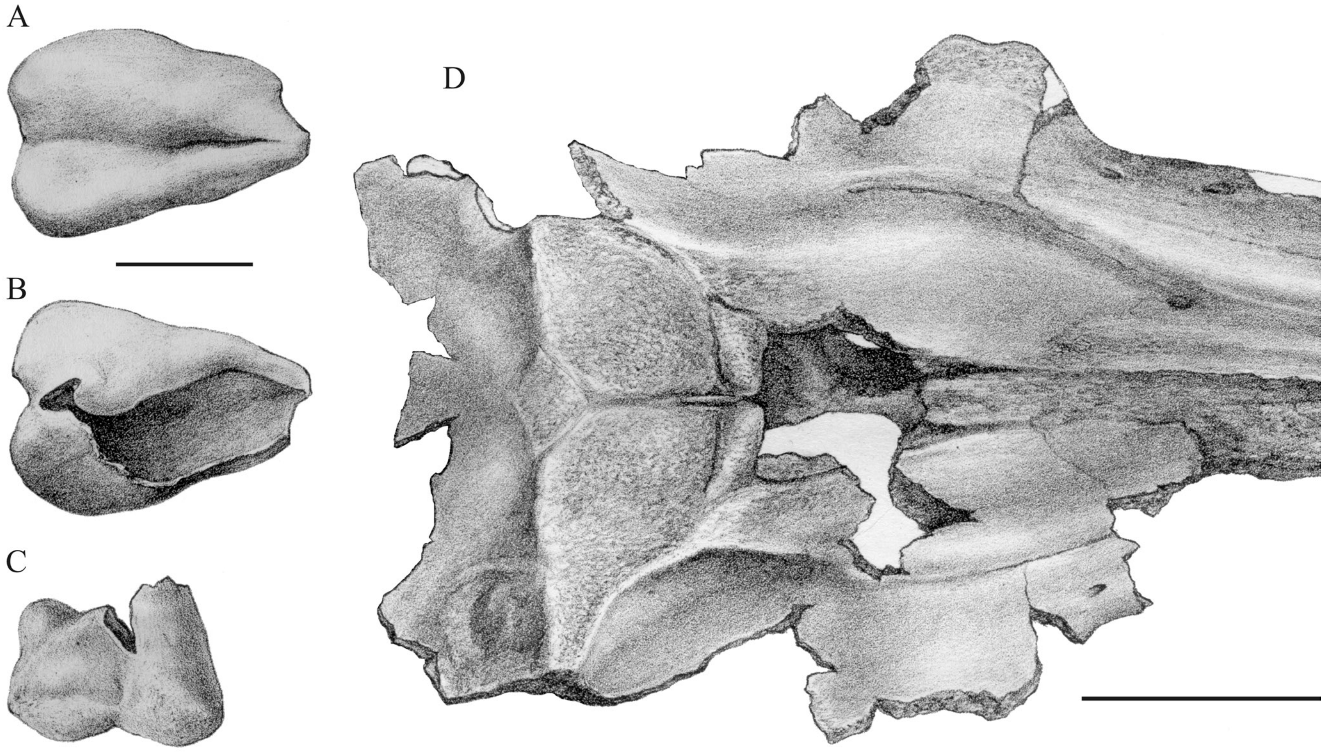

Figure 7 – *Cyrtodelphis sulcatus* sensu Abel, 1899, specimen from Eggenburg, Austria. A-C: right tympanic bulla in ventral (A), dorsal (B), and posterior (C) view. Scale bar for A-C = 20 mm. D: dorsal view of the cranium of the same individual. Scale bar = 50 mm. (Mod. from Abel, 1899: pl. 1, 3, the scales were taken directly from those figures.)

involucrum (see Lambert, 2005b). It is therefore referred to Eurhinodelphinidae aff. *Eurhinodelphis*. Among the fragments of skull associated with this tympanic IRSNB 3453-M.293, at least two fragments of premaxilla are similar to specimens of *E. cocheteuxi* and do not show any similarity with the other Belgian specimens of *Cyrtodelphis sulcatus sensu* Abel (1901).

COMMENTS ON THE PALAEOECOLOGY OF POMATODELPHININES

This first platanistid record from the North Sea Basin, probably from the late Early to Middle Miocene Antwerp Sands, confirms the presence of members of the subfamily Pomatodelphininae in the Miocene of Europe [previous records from France (Allen, 1921; Ginsburg & Janvier, 1971) and from Austria (Barnes, 2002)]. This subfamily is presently limited to the North Atlantic realm, while members of the other subfamily Platanistinae (Gray, 1863) are suspected in the Miocene of the North Pacific (Barnes, 2002) and are extant in river systems of south eastern Asia (*Platanista gangetica* and *P. minor*) (for comments on the evolutionary history of the family see Cassens *et al.* 2000; Hamilton *et al.* 2001).

Apart from *Pomatodelphis inaequalis*, which might be present in Miocene sediments of Florida and Maryland (Muizon, 1987; Morgan, 1994), other pomatodelphinine species are recorded from a relatively reduced area. The latter feature, added to the morphology of the skull of pomatodelphinines with a much elongated rostrum, might indicate that members of the subfamily were coastal dwellers, in a way similar to eurhinodelphinids (Lambert, 2005a).

It is interesting to note that, in two major deposits where both groups of long-snouted dolphins are found (i.e. Calvert Formation, Maryland-Virginia and Antwerp Sands, north of Belgium), the collections of eurhinodelphinids are far larger than the pomatodelphinines, both in number of species and in number of specimens. The discrepancies in preservation of the taxa might be explained in various ways, keeping in mind that collections are inherently biased by collectors and varying preservation conditions. (1) In these deposits, some of the eurhinodelphinid species have a size roughly similar to the pomatodelphinines. A local competition for food might have forced the pomatodelphinines in other environmental areas, less well recorded than the very shallow nearshore deposits of the Antwerp Sands (Bastin, 1966) and the inner shelf to marginal marine deposits of the Calvert Formation (Vogt & Eshelman, 1987). By contrast pomatodelphinines are common in the more tropical predominantly nearshore Middle to early Late Miocene marine units of the Bone Valley Formation, central Florida, with at least two species of *Pomatodelphis* represented by several specimens, while no eurhinodelphinid is recorded there (Morgan, 1994). (2) The morphological differences at the level of the feeding apparatus - mandible shorter than the slightly transversely compressed rostrum with an edentulous anterior portion in eurhinodelphinids against mandible as long as the rostrum and both dorsoventrally flattened in pomatodelphinines - might, however, also indicate a different type of prey selection. Variable levels of prey availability could therefore explain the recorded differences in the local diversity of the two groups. The absence of extant analogous feeding apparatus precludes a more detailed comparison: no extant dolphin possesses the unusual elongated edentulous premaxillae longer than the mandible characterizing the eurhinodelphinids, and the only extant platanistid, the fresh water *Platanista*, has a transversely compressed rostrum with enlarged anterior teeth (e.g. Reeves & Brownell, 1989), considerably differing from pomatodelphinine morphology.

CONCLUSIONS

To summarize, systematic revision of the Belgian specimens of *Cyrtodelphis sulcatus sensu* Abel (1901) gives the following results:

1. The rostrum IRSNB 3246-M.291, together with the rostral and mandibular fragments IRSNB 3247-E.F.M.292b-c-d, are placed in the platanistid subfamily Pomatodelphininae; they probably represent a new species, not defined because of the lack of available information.
2. The partial cranium IRSNB 3247-M.292a does not belong to the same specimen than IRSNB 3247-M.292b-d, contradicting the opinion of Abel (1901). It is neither a platanistid, a eurhinodelphinid nor an eoplatanistid, and is provisionally referred to Kentriodontidae *incertae sedis*.
3. The tympanic bulla IRSNB 3453-M.293 is referable to a eurhinodelphinid.

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