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Systematic revision of the Miocene long-snouted dolphin *Eurhinodelphis longirostris* DU BUS, 1872 (Cetacea, Odontoceti, Eurhinodelphinidae)

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Abstract

On the basis of the redescription of Miocene Belgian specimens, the systematic status of the long-snouted dolphin genus *Schizodelphis* (Cetacea, Odontoceti, Eurhinodelphinidae) is revised. The only Belgian species previously recognized, *S. longirostris*, from the late early to middle Miocene of Antwerp (north of Belgium, southern margin of the North Sea basin), is divided here in two taxa. Some specimens are kept in that species, but re-establishing the combination *Eurhinodelphis longirostris*. The content of the genus *Eurhinodelphis* is then investigated from several Miocene localities, essentially the Calvert Formation (Virginia and Maryland, east coast of USA) and the Belluno Sandstones from north-eastern Italy. The only recognized species are *E. cocheteuxi* and *E. longirostris*, both of them only found in the Belgian Miocene. Other previously described species are placed in an unnamed new genus, in *Mycteriacetus* n. gen., and in *Ziphiodelphis*.

The other Belgian specimens are maintained in *Schizodelphis*, with the prioritary species name *morckhoviensis*. The species *S. morckhoviensis* is also identified in the Calvert Formation, while a restricted *S. barnesi* is tentatively diagnosed from American specimens.

Key words: Eurhinodelphinidae, taxonomy, Miocene, Belgium, *Schizodelphis*, *Eurhinodelphis*.

Résumé

Sur base de la redescription de spécimens du Miocène de Belgique, le statut systématique du dauphin longirostre *Schizodelphis* (Cetacea, Odontoceti, Eurhinodelphinidae) est révisé. La seule espèce belge préalablement décrite, *S. longirostris*, de la fin du Miocène inférieur-Miocène moyen d'Anvers (nord de la Belgique, bord sud du bassin de la Mer du Nord), est divisée en deux taxa. Une partie des spécimens est maintenue dans cette espèce, mais en rétablissant la combinaison *Eurhinodelphis longirostris*. Le contenu du genre *Eurhinodelphis* est ensuite investigué dans plusieurs localités du Miocène, particulièrement la Formation Calvert (Virginie et Maryland, côte est des Etats-Unis) et les Sables de Belluno (nord-est de l'Italie). Les seules espèces reconnues sont *E. cocheteuxi* et *E. longirostris*, et cela uniquement dans le Miocène belge. Les autres espèces précédemment décrites sont placées dans un nouveau genre non nommé, dans *Mycteriacetus* n. gen., et dans *Ziphiodelphis*.

Une seconde partie des spécimens belges est maintenue dans le genre *Schizodelphis*, avec le nom d'espèce prioritaire *morckhoviensis*. Cette espèce *S. morckhoviensis* est également identifiée dans la Formation Calvert, de même que l'espèce *S. barnesi* brièvement redéfinie.

Mots-clefs: Eurhinodelphinidae, taxinomie, Miocène, Belgique, *Schizodelphis*, *Eurhinodelphis*.

Introduction

DU BUS (1872) shortly described several species of long-snouted dolphins from the Miocene of Antwerp (North of Belgium), which he included in the genera *Eurhinodelphis* DU BUS, 1868 and *Priscodelphinus* (LEIDY, 1851). ABEL (1902) included in the same species *E. longirostris* individuals of the species *Eurhinodelphis longirostris*, *E. ambiguus*, *Priscodelphinus morckhoviensis*, *P. elegans*, and *P. pulvinatus sensu* DU BUS, 1972. In his unpublished revision of the eurhinodelphinids from the Calvert Formation, east coast of the USA, MYRICK (1979) noticed the presence of the species *E. longirostris* in this area, which he referred to the genus *Rhabdosteus* by comparison with the holotype of the type-species of the genus {*R. latiradix* (COPE, 1868)}, a partial rostrum also from the Calvert Formation.

However, this specimen was estimated by MUIZON (1988a) as too fragmentary, and regarded as an incertae sedis. MUIZON referred the species *E. longirostris* to the genus *Schizodelphis* GERVAIS, 1861, as well as all the *Rhabdosteus* species recognized by MYRICK (1979) in the Calvert Formation (excluding *R. latiradix*). MUIZON's conclusions were based on the study of the holotype of *Schizodelphis sulcatus* GERVAIS, 1853 (Miocene of France), the type-species of the genus. MUIZON did not recognize *S. longirostris* in the Calvert Formation, where he only identified one species, *S. barnesi*, including the individuals from the species *Rhabdosteus longirostris*, *R. barnesi* and *R. hruschkai sensu* MYRICK, 1979.

A detailed observation of the Belgian specimens of *Schizodelphis longirostris sensu* MUIZON, 1988a allows the recognition of two genera, *Eurhinodelphis* and *Schizodelphis*, for which an emended diagnosis and a redescription are presented here.

Specimens from the Calvert Formation (MYRICK, 1979), from the Belluno Sandstones (early Miocene of north-eastern Italy, PILLERI, 1985), and from several other localities, previously reported to the genus *Eurhinodelphis*, are also briefly discussed.

Material and methods

Most of the specimens used in this study are housed in the IRSNB. The main specimens are two well preserved skulls, IRSNB 3249-M.342 and IRSNB 3235-M.343, already described by ABEL (1902). Additional specimens from the IRSNB, USNM, CMM, and MGPD are more briefly discussed.

Though MYRICK's Ph. D. thesis (1979) was not published, I use it as a starting point for the systematic revision of the Calvert eurhinodelphinids.

The species *Eurhinodelphis cristatus sensu* DU BUS, 1872 and *E. bossi sensu* KELLOGG, 1925 are referred to a new eurhinodelphinid genus that will be diagnosed in a paper in preparation; those two species are cited here as *'E.' cristatus* and *'E.' bossi*. The Italian species *E. bellunensis sensu* PILLERI, 1985, included by its author in the genus *Eurhinodelphis*, is referred to a new genus, *Mycteriacetus* n. gen., diagnosed below.

Terminology. The terminology for cranial and ear bones anatomy is mainly taken from: FORDYCE (1983 and 1994); KASUYA (1973); MUIZON (1984, 1987 and 1988a). The orientations of the tympanic bulla and periotic are simplified in the following descriptions, relatively to the anatomical position on the basicranium. The long axis of the tympanic is considered as antero-posterior, with ventral surfaces of inner and outer posterior prominences indicating the horizontal plane. The anterior direction of the periotic is given by the longitudinal axis of the anterior process, and the horizontal ventral plane by the surface contacting the most ventral points of pars cochlearis and anterior process.

Abbreviations. **CMM**: Calvert Marine Museum, Solomons, Maryland, USA; **IRSNB**: Institut Royal des Sciences Naturelles de Belgique, Brussels; **M**: Fossil mammals collection of types and figured specimens from the IRSNB; **MGPD**: Museum of Geology and Palaeontology of Padova, Italy; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France; **USNM**: United States National Museum, Smithsonian Institution, Washington D.C., USA.

Explanations of the measurements. Fig. 1.

Systematic palaeontology

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1867

Superfamily Eurhinodelphinoidea MUIZON, 1988a

Family Eurhinodelphinidae ABEL, 1901

Type-genus. Eurhinodelphis DU BUS, 1867

Included genera. Eurhinodelphis, *Schizodelphis* GERVAIS, 1861, *Ziphiodelphis* DAL PIAZ, 1908, *Argyrocetus* LYDEKKER, 1894, *Macrodelphinus* WILSON, 1935, and *Mycteriacetus* n. gen.

Emended diagnosis. Family of long-snouted odontocetes differing from all the other families by an edentulous premaxillary anterior part of the rostrum, longer than the mandible.

Additionally, the family differs from the probably closely related family Eoplatanisidae by: a more inclined dorsomedial portion of the supraoccipital shield, a generally lower temporal fossa, the presence of a marked median groove on the tympanic, a longer anterior process of the periotic; and from the Squalodontidae, Waipatiidae and other more primitive odontocetes by: an homodont dentition with single-rooted teeth, premaxillae widened at the level of the posterior margin of the bony nares, a higher vertex.

Eurhinodelphis DU BUS, 1867

Type species. E. cocheteuxi DU BUS, 1867

Included species. E. cocheteuxi and *E. longirostris* DU BUS, 1872. The species *E. cocheteuxi* was redescribed in a previous paper (LAMBERT, in press).

Diagnosis. The genus *Eurhinodelphis* differs from the genera *Schizodelphis* and *Ziphiodelphis* in: maxillary part of the rostrum relatively shorter (ratio between bizygomatic width of the skull and length of the maxillary part of the rostrum > 0.5); vertical medial plate of the maxilla along the vertex antero-dorsally developed; flat to convex supraoccipital shield (shield concave in the two other genera); more elevated and narrower paroccipital process of the exoccipital with occipital condyles more highly positioned (ventral margin of the condyles nearly reaching the level of the floor of the temporal fossa); less excavated premaxillary sac fossae, which are roughly flat; zygomatic process of the squamosal relatively higher in lateral view and narrower in ventral view; absence of fossa for the postorbital lobe of the pterygoid sinus on the ventral surface of the supraorbital process (that fossa is sometimes very short but nearly always present in *Schizodelphis* and *Ziphiodelphis*). The last character is probably in a primitive state, but it clearly separates the genera.

It differs from *Macrodelphinus* by: more longitudinally telescoped and more elevated vertex with frontals shorter than the nasals; flat to convex supraoccipital shield.

It differs from *Argyrocetus* (provisionally only including the species *A. patagonicus*) in: a more elevated vertex and flat to convex more vertical supraoccipital shield.

It differs from *Mycteriacetus* n. gen. in: a relatively wider and shorter face (ratio between bizygomatic width and length of the face from the antorbital notch to the occipital condyle > 0.95); a more elevated vertex with shorter frontals and wider nasals; flat to convex and more vertical supraoccipital shield.

Eurhinodelphis longirostris DU BUS, 1872

* 1872 *Eurhinodelphis longirostris* DU BUS, p. 491.
v. 1880 *Eurhinodelphis longirostris* VAN BENEDEN & GERVAIS, p. 493, pl. 58, fig. 2.
v. 1902 *Eurhinodelphis longirostris* ABEL, pl. 11, 12 and 13, pl. 17, fig. 1.
v. 1988a *Schizodelphis longirostris* MUIZON, p. 40.

Emended diagnosis. This species differs from *Eurhinodelphis cocheteuxi* by: the distinctly smaller size of the

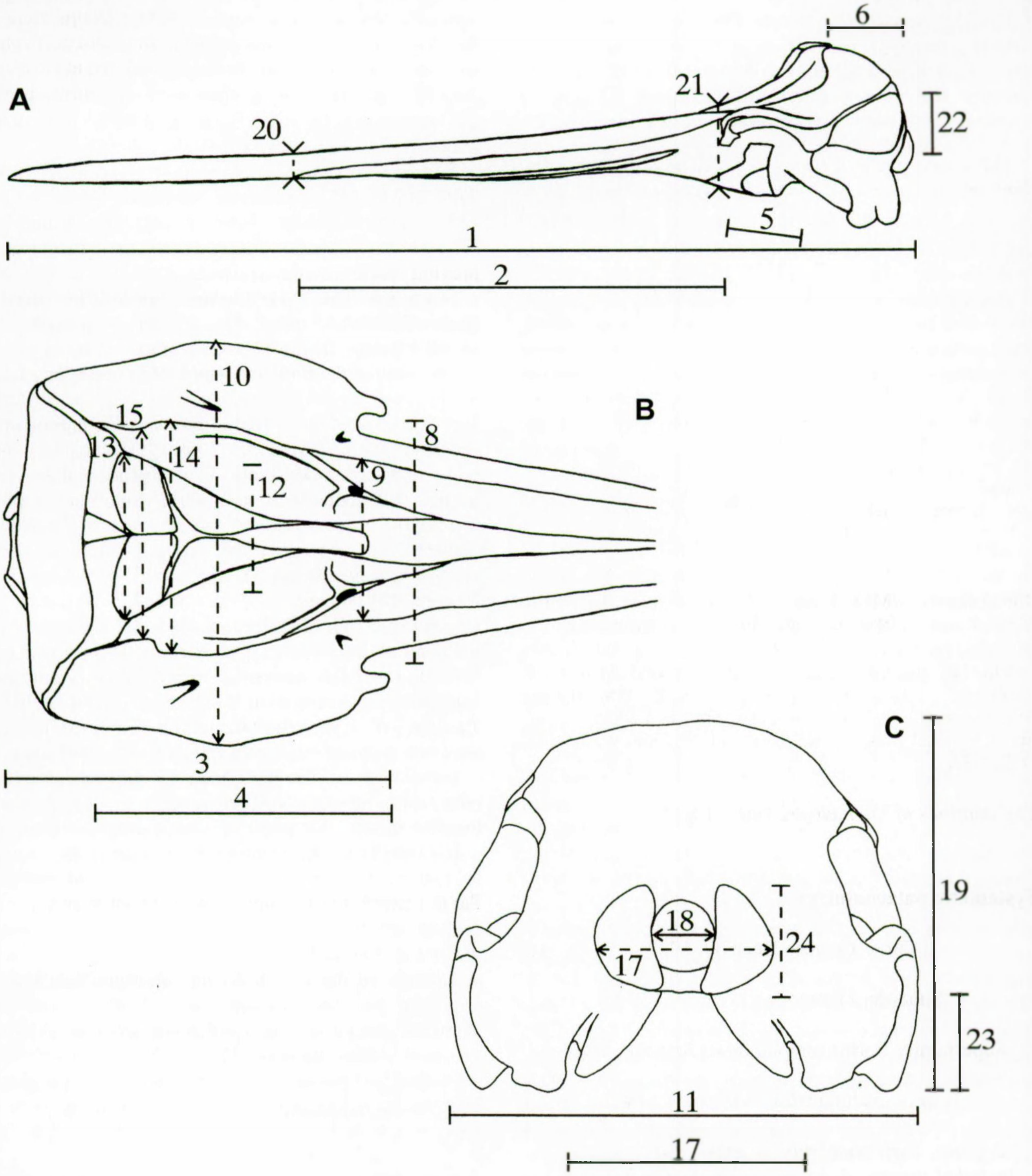

Fig. 1 – Description of the measurements on the skull of eurhinodelphinids, outlines of the holotype of *Eurhinodelphis cocheteuxi* IRSNB 3252-M.294. A. left lateral view. B. dorsal view. C. posterior view. Explanation of the measurements on Tables 1-2.

cranial skull (the general dimensions of the cranial skull of the holotype of *E. longirostris* vary between 70 and 80 % of the dimensions of the holotype of *E. cocheteuxi*); relatively longer and more slender rostrum (ratio between postorbital width of the skull and length of the rostrum < 0.25), especially the premaxillary apical part of the rostrum; narrower base of the rostrum; relatively narrower vertex with a strong compression of the frontals between the supraoccipital and the nasals (a contact between nasals and supraoccipital is present on two specimens of *E. longirostris*).

Holotype. IRSNB 3249-M.342, a well preserved skull, only lacking teeth and ear bones, fragments of the basicranium and of the rostrum (found in January 1862, individual 1 of the species *Eurhinodelphis longirostris* in ABEL, 1902, figured in pl. 11, 12 and 13).

Referred specimens. IRSNB 3250-M.1858, a partial skull including a part of the rostrum, the two supraorbital processes, a portion of the vertex and the basicranium (individual 3 of the species *Eurhinodelphis longirostris* in ABEL, 1902); IRSNB 3251, a part of the rostrum with the posterior part of the left maxilla (individual 7 of the species *E. longirostris* in ABEL, 1902). No skull from the Calvert Formation could be referred to this species.

Comments on the other specimens referred to E. longirostris *by ABEL (1902)*

The fragmentary rostrum IRSNB 3245, individual 17 of the species *Eurhinodelphis longirostris sensu* ABEL, 1902, shows very flattened and wide premaxillae at the base of the rostrum, and should then be reported to *'E.' cristatus* (paper in prep.).

The left side of a face IRSNB 3495 (*Eurhinodelphis ambiguus sensu* DU BUS, 1872 and individual 15 of the species *E. longirostris sensu* ABEL, 1902) is probably a part of a juvenile specimen of *'E.' bossi* (LAMBERT, in press).

The partial skull IRSNB 3238-M.344 (individual 2 of *E. longirostris sensu* ABEL, 1902, pl. 18, fig. 1, figured here in Pl. 1, Fig. 2, including the base of the rostrum, the supraorbital processes, a portion of the vertex with the nasals, a fragment of the supraoccipital, the two squamosals and the paroccipital process of the left exoccipital) shows some features that place it in the genus *Eurhinodelphis*: slightly excavated premaxillary sac fossa, flat posterior portion of the maxilla laterally to the vertex, elevated and narrow paroccipital process of the exoccipital, and absence of fossa for the postorbital lobe of the pterygoid sinus. A striking characteristic of this specimen is the strong development of the transverse premaxillary crests that are wide and thick. The measurements of the skull (see Table 1) are similar to the measured specimens of *E. longirostris*. However, it differs from these specimens in the smaller nasals less posteriorly displaced, and the more dorso-ventrally flattened zygomatic process of the squamosal. Because of those differences, and because it is fragmentary, this specimen IRSNB 3238-M.344 is referred to *Eurhinodelphis* cf. *longirostris*.

The partial rostrum IRSNB 3225 (individual 8 of the species *Eurhinodelphis longirostris sensu* ABEL, 1902) has size and proportions similarities with *E. longirostris* but no diagnostic character is observable and this fragment is referred to Eurhinodelphinidae incertae sedis.

The isolated fragments of mandible IRSNB 3258-M.347 (figured by ABEL, 1902, plate 17, fig. 4) probably belong to an eurhinodelphinid, with proportions roughly similar to *'Eurhinodelphis' bossi* USNM 167629. None of the individuals of *E. longirostris* is associated with a mandible, and the lack of diagnostic features on this mandible precludes its attribution to any eurhinodelphinid species. It is placed in Odontoceti aff. Eurhinodelphinidae.

The periotics associated with the specimen IRSNB 3447-M.351 (*Eurhinodelphis ambiguus sensu* DU BUS, 1872, figured in ABEL, 1902, p. 122, fig. 19 and plate 17, figs. 11-12) were already clearly recognized as belonging to a physeterid (KELLOGG, 1927). The erroneously associated symphyseal portion of mandible (figured by Abel, 1902, plate 17, fig. 6) is regarded as an Odontoceti aff. Eurhinodelphinidae.

The specimen IRSNB 3244-M.346 (holotype of *Priscodelphinus elegans sensu* DU BUS, 1872) is a hypothetical association of a partial small basicranium and a vertex (figured by ABEL, 1902, pl. 17, fig. 2), but without bony contact between them. The squamosal shows similarities with that of *Eurhinodelphis longirostris*, with a zygomatic process high in lateral view and narrow in ventral view. However, the vertex is close to that of several specimens of *Rhabdosteus hruschkai sensu* MYRICK (1979), e.g. USNM 187211, with an anterolateral projection of the prominent nasal along the external nare. As most of the specimens of *R. hruschkai sensu* MYRICK (1979) are probably referrable to the genus *Schizodelphis*, the association basicranium-vertex of IRSNB 3244-M.346 is regarded as doubtful and those fragments are considered as Eurhinodelphinidae incertae sedis.

Locus typicus. The holotype of *Eurhinodelphis longirostris* was found in Antwerp, in January 1862, and the locality cited by ABEL (1902) is '*4^{e} Section*'. This locality corresponds to the south-eastern portion of the city wall around Antwerp, built during fortification works in the 1860's (see VAN DEN BROECK, 1878), in Berchem. This section matches the south-eastern part of the present motorway R1, around the city.

Stratum typicum. No precise stratigraphic data are available for the holotype and referred specimens. However, the preservation and colour of those specimens are very similar to that of the skulls of *Eurhinodelphis cocheteuxi*, known from the Antwerp Sands. This strongly suggests an origin in the same member, dated from late early to middle Miocene (see LOUWYE *et al.* 2000).

Redescription of the species Eurhinodelphis longirostris (Pl. 1, Fig. 1; Pl. 2, Fig. 1; Figs. 2-4)

General morphology. Eurhinodelphis longirostris has a relatively small braincase and a very long rostrum (see measurements, Table 1), which is nearly completely preserved on the holotype. The rostrum constitutes more than 80 % of the total length of the skull, with more than 50 % of its length made by the premaxillae.

Table 1 – Measurements on the skulls of *Eurhinodelphis longirostris*. Measurements are in millimetres. (e) indicates estimate, '+' nearly complete, and '–' no data.

Measurements on the skulls of *E. longirostris*	Holotype IRSNB 3249-M.342	IRSNB 3250-M.1858	IRSNB 3238-M.344 *E.* aff. *longirostris*
1. total length skull	+1018	–	–
2. length base rostrum-anterior maxilla	390	–	–
3. length anterior orbit-posterior skull	214	190	–
4. length anterior supraoccipital-anterior orbit	114	117	e125
5. length orbit	86	82	66
6. length temporal fossa	e75	–	–
7. width rostrum anterior maxillae	29	–	–
8. width base rostrum	103	e96	e105
9. width premaxillae base rostrum	67	–	e64
10. width skull postorbital processes	199	–	e198
11. width skull zygomatic processes	210	197	–
12. width bony nares	44	–	32
13. width nasals	68	–	34
14. maximal posterior premaxillary width	97	–	e98
15. minimal posterior distance between maxillae	65	–	–
16. width medio-ventral margins exoccipitals	98	85	–
17. width lateral margins occipital condyles	+80	76	–
18. width inner margins occipital condyles	34	34	–
19. height cranium	146	–	–
20. height rostrum at anterior maxillae	30	–	–
21. height base rostrum	57	e49	69
22. height temporal fossa	e58	–	–
23. height ventral margin occipital condyles	48	44	–
24. height occipital condyles	43	43	–

Dorsal view. The dorsal surface of the premaxilla is convex and prominent until the base of the rostrum, with a slight narrowing and lowering just anterior to that level. The triangular elongated surface antero-medial to the premaxillary foramen is nearly smooth and partially lower than the thick and rounded lateral part of the premaxilla at that level. The premaxillary sac fossa is thick, roughly flat and progressively raising towards the vertex, lacking the deeper concavity and the more abrupt posterior elevation of *Schizodelphis morckhoviensis* (see below). The posterior extremity of the premaxilla contacts the antero-lateral angle of the nasal and is longitudinally incised by the erected median edge of the maxilla. The contact between premaxilla and frontal is probably absent on the holotype but it is present on IRSNB 3250-M.1858, depending upon the shape and position of the nasals on the vertex.

The lateral margin of the maxilla exhibits a very weak swelling about 100 mm anterior to the antorbital notch. Several dorsal infraorbital foramina pierce the maxilla along its suture with the premaxilla, at the level and anterior to the shallow and antero-laterally open antorbital notch. The preorbital process is narrow in dorsal view and its lateral margin diverges posteriorly. A distinct elevation of the maxilla is present above the orbit. It is separated from the premaxillary sac fossa by a narrow longitudinal depression. The posterior portion of the maxilla is roughly flat and slopes antero-laterally. It is only slightly concave at the level of its overhanging median edge along the vertex. The posterior margin of the maxilla extends posteriorly 20 mm beyond the antero-median margin of the supraoccipital.

The shape of the nasals strongly varies between the two skulls on which it is preserved. On the holotype, those bones are somewhat eroded. They are wider than long and exhibit a wide contact with the supraoccipital. The frontals are reduced on the vertex to three small triangles between the nasals and the supraoccipital. This special morphology was correctly recognized by ABEL (1902), but KELLOGG (1932) erroneously identified the two wide and short bones as the frontals. On IRSNB 3250-M.1858, with only the right part of the vertex preserved, the nasal

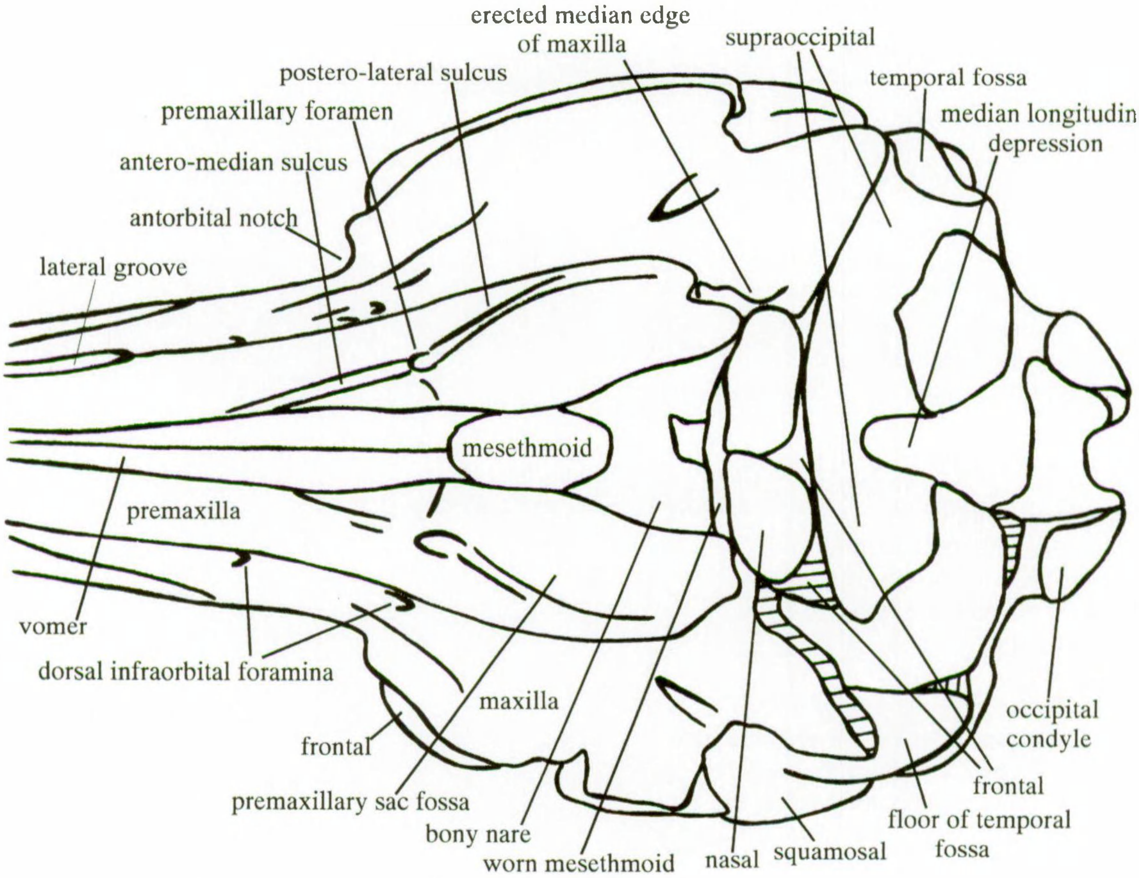

Fig. 2 – Schematic drawing of the dorsal view of the skull of *Eurhinodelphis longirostris* IRSNB 3249-M.342 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene.

also contacts the supraoccipital on most of its width. However, the nasal is narrower than on the holotype, and a wide part of the frontal is dorsally exposed, lateral to the nasal (see Fig. 3a). The trend to a posterior shift of the nasals towards the supraocipital is present on both specimens, but variably modelling the bones of the vertex. The sagittal section of the vertex of the skull IRSNB 3250-M.1858 allows the observation of the posterior part of the mesethmoid. This bone deeply penetrates the frontal posteriorly below the nasal, nearly reaching the suture with the supraoccipital (see Fig. 3b).

The supraoccipital shield is convex, only hollowed by a median longitudinal depression ending 15 mm before its anterior margin. This rounded shield is regularly sloping posteriorly, with a mean slope of ca. 35°.

Posterior view. The paroccipital process of the exoccipital is high and narrow. As a consequence, the occipital condyles are elevated, with a ventral margin nearly reaching the level of the floor of the temporal fossa. The basioccipital crests are sharp and ventrally shorter than the exoccipitals.

Lateral view. The lateral groove of the rostrum starts 180 mm anteriorly to the antorbital notch. It is deep and widens over 100 mm forwardly. Then it progressively shallows and disappears more than 100 mm posteriorly to the apex of the rostrum. The maxilla-premaxilla suture leaves the floor of the groove 250 mm anteriorly to the antorbital notch, 140 mm posteriorly to the apex of the maxilla.

The roof of the orbit is long and lower than the top of the temporal fossa. The frontal is roughly as thick as the maxilla. The lacrymal-jugal complex is visible in lateral view for a short length antero-ventral to the preorbital process of the frontal. The elevated zygomatic process of the squamosal is stronger than the rounded postglenoid process.

Ventral view. The premaxillary part of the rostrum does not bear alveoli; the alveolar groove of the maxilla extends in the premaxilla as a thin groove with rectilinear edges precluding the presence of teeth inserted in the bone. The maxillary alveoli are eroded on the holotype, but are preserved on the proximal part of the rostrum of IRSNB 3250-M.1858. The first alveolus is 30 mm anterior to the antorbital notch. Forty-two deep alveoli are present on the first 243 mm of the right side of the rostrum and 40 on the left side. The average diameter is 4-5 mm and the septa are less than 3 mm thick. Considering the length of the maxilla on the rostrum of the holotype, the total number of alveoli on each side should be around 60. On the right alveolar row of IRSNB 3250, the 14th alveolus is distinctly shifted laterally and the 15th, medially, as if the posterior part of the row was pushed against the anterior part (see Pl. 2, Fig. 1c). This might indicate a trend towards an increase in the number of maxillary teeth, or more simply a pathology.

The palatines are short; their apex extends until 10 mm beyond the level of the antorbital notches. The thin lateral plate of the palatine contacts the large infraorbital foramen. This part of the palatine was erroneously identified as part of the pterygoid by Abel (1902). The condition of *Eurhinodelphis longirostris* is similar to that observed in *E. cocheteuxi* (see Lambert, in press). As in this species, the palatine plate is crossed by a longitudinal crest, which disappears anteriorly before reaching the palatine-maxilla suture. Only small fragments of the pterygoid are preserved anteriorly. The anterior pterygoid fossa clearly excavates the palatine anterior to the choana, on a short distance (10 to 25 mm).

The jugal-lacrymal complex is only preserved as a small eroded knob in the bottom of the antorbital notch. The ventral face of the roof of the orbit is hollowed by a shallow sulcus which runs from the large infraorbital foramen towards the antorbital notch. There is no fossa for the postorbital lobe of the pterygoid sinus, as in *Eurhinodelphis cocheteuxi*, and contrary to *Schizodelphis morckhoviensis* (see below).

The zygomatic process of the squamosal is anteriorly pointed, with a ventral apical projection for the contact with the missing jugal. The ventral apex of the postglenoid process is transversely flattened. The tympanosquamosal recess is deep, laterally extending for a short distance dorsal to the glenoid surface. The recess does not have a clear anterior limit, extending on the medial side of the zygomatic process. The falciform process of the squamosal is not completely preserved. On the holotype, it takes an anterior direction, and is interrupted by a transverse canal, very likely the path for the mandibular nerve V3, exiting in the temporal fossa through the foramen 'pseudo-ovale' (see Fordyce, 1994). As the falciform process is incomplete, the presence or absence of a lateral lamina of the pterygoid can not be asserted. On the skull IRSNB 3250-M.1858, the anterior part of the falciform process is more clearly antero-laterally deflected, along a well developed pterygoid sinus fossa on the alisphenoid. This condition, observed on every skull of *Eurhinodelphis cocheteuxi*, is probably related to the loss or the important reduction of the lateral lamina of the pterygoid (Lambert, in press). The foramina of the basicranium are poorly preserved. On the holotype, only the carotid foramen and the anterior margin of the foramen ovale can be observed. On the skull IRSNB 3250-M.1858, the posterior lacerate foramen has an elongated shape, with a maximal length of 18 mm and a small median constriction. There is no posterior sinus fossa,

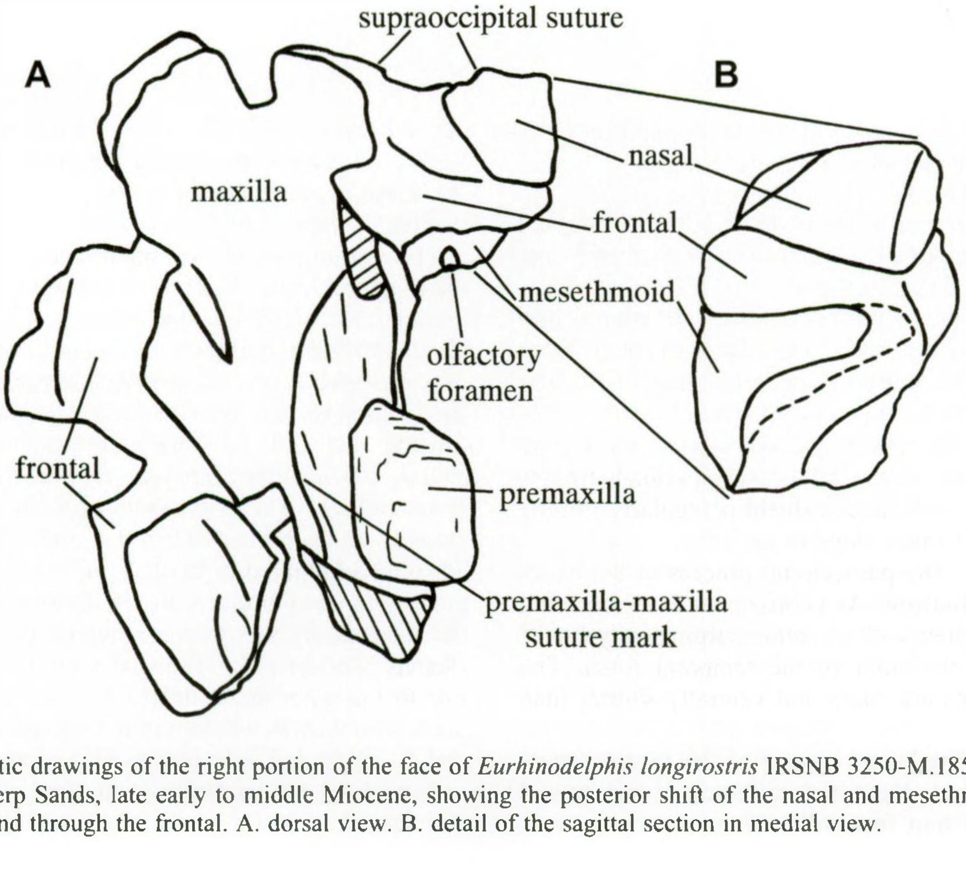

Fig. 3 – Schematic drawings of the right portion of the face of *Eurhinodelphis longirostris* IRSNB 3250-M.1858, from Antwerp, ? Antwerp Sands, late early to middle Miocene, showing the posterior shift of the nasal and mesethmoid, respectively above and through the frontal. A. dorsal view. B. detail of the sagittal section in medial view.

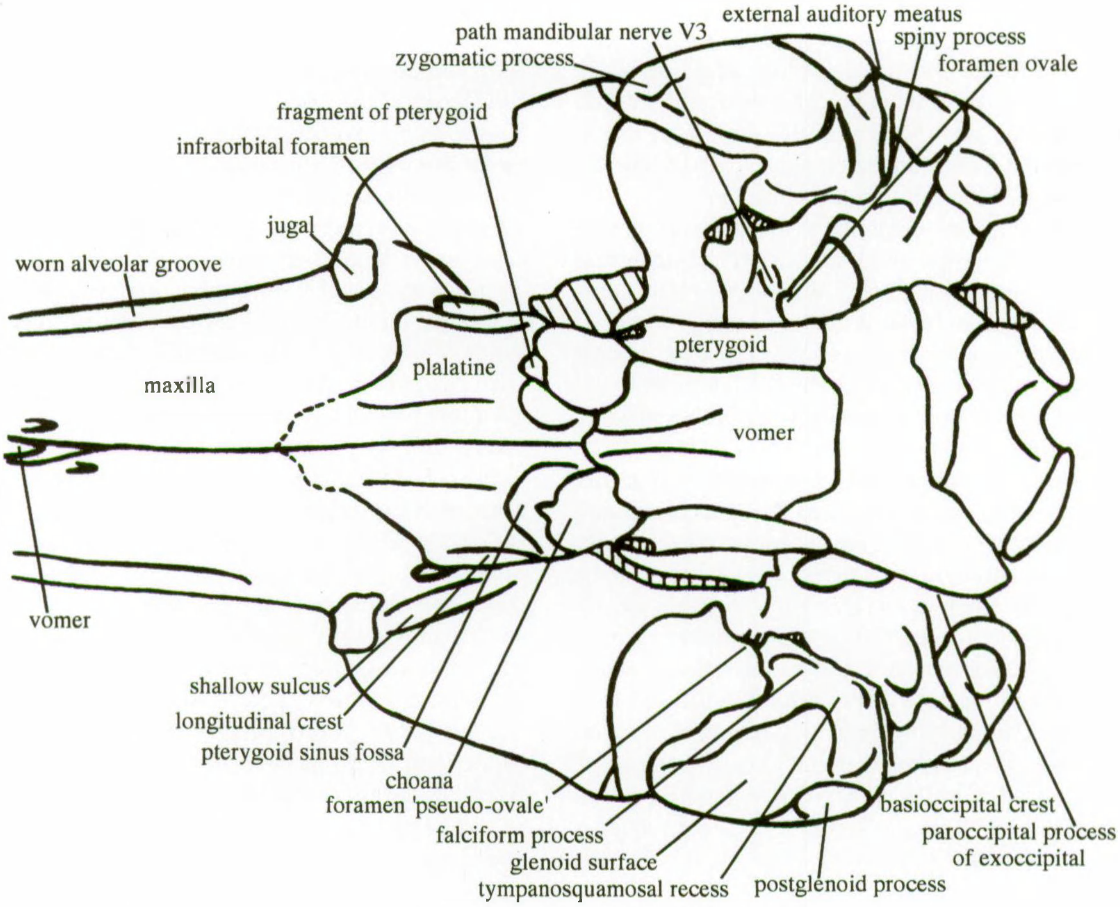

Fig. 4 – Schematic drawing of the ventral view of the skull of *Eurhinodelphis longirostris* IRSNB 3249-M.342 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene.

and the surface dorso-medial to the spiny process is smooth and unexcavated.

Comments on specimens from the Calvert Formation referred to Eurhinodelphis *by Myrick (1979, unpublished thesis)*

The only previously published eurhinodelphinid from the Calvert Formation (early to middle Miocene of Maryland and Virginia) is the species *'Eurhinodelphis' bossi* Kellogg, 1925. In his unpublished thesis, Myrick (1979) also recognized the species *'E.' cristatus* in the Calvert Formation, and described four additional new species: *'E.' vaughni*, *'E.' ashbyi*, *'E.' whitmorei* and *'E.' morrisi*. It is outside the scope of the present study to carry out a complete systematic revision of the high number of eurhinodelphinid specimens from the Calvert Formation, but the different species of *Eurhinodelphis* erected by Myrick (1979) are briefly discussed here.

After *'E.' cristatus*, *Eurhinodelphis vaughni sensu* Myrick, 1979 is the most common species of the genus, with seven skulls identified from the Calvert Formation. In the diagnosis of the species, Myrick (1979, p. 222) gave few characters differentiating it from *'E.' cristatus*, *'E.' whitmorei* and *'E.' ashbyi*: lack of fold on the posterior margin of the maxilla along the transverse crest, premaxillae not mesially sloping at the level of the antorbital notches and supraorbital processes slightly elevated. Those characters roughly consist in the main features of *'E.' bossi* as defined relatively to *'E.' cristatus*. And Myrick (1979) could not give differences with *'E.' bossi*, probably because of '*the great disparity in morphologic features and morphometrics among the four specimens* (of *'E.' bossi*)'. Actually, the measurements on the skulls of *'E.' vaughni* are globally close to *'E.' bossi*, and no clear separation could be found for any measurement. The large width of the rostrum at its base suggested by Myrick (1979) is only measured in one specimen that slighly exceeds in this respect the largest *'E.' bossi*. Furthermore, the morphology of the face is very similar in both groups. I suggest therefore to include the specimens identified by Myrick (1979) as *Eurhinodelphis vaughni* in *'E.' bossi*.

It should be noticed that the four specimens identified as *'E.' bossi* by Kellogg (1925) were found in three different stratigraphic levels of the Calvert Formation, the beds 3, 5 and 10 of Shattuck (1904), and that the seven specimens of *'E.' vaugni sensu* MYRICK 1979 come from the beds 12 (six of them) and 13. Supposing a highly speculative uniform rate of deposition along the two million years duration of the Calvert Formation, MYRICK (1979) suggested an average time of 120.000 years for the deposition of each of the 15 beds of the formation. The morphological variability among *'E.' bossi* as defined here might then be partially explained by, on one side, the difference of age between the beds containing the different specimens of *'E.' bossi sensu* KELLOGG, 1925, and on the other side the younger age of the beds providing the specimens of *'E.' vaughni sensu* MYRICK, 1979.

The species *'Eurhinodelphis' ashbyi sensu* MYRICK, 1979 is based on two partial skulls USNM 244401 and USNM 244411. It is diagnosed by MYRICK (1979, p. 249) as somewhat similar to *'E.' cristatus*, with the following differences: probably smaller maximum adult size; pentagonal frontals with apex pointed forward between nasals; larger nasals; more pronounced overhanging of the maxillary plate by the supraoccipital crest; supraorbital processes thick but not protuberant or abruptly elevated. However, the morphology of the vertex is only observable in one of the specimens and it could easily be explained by individual variation. Actually, the shape of the frontals and nasals is close to the Belgian *'E.' cristatus* IRSNB 3237 for instance. The longitudinal telescoping of the face is also variable, giving a more or less pronounced elevation of the transverse supraoccipital crest. The elevation of the supraorbital protuberance was shown to be variable in *'E.' cristatus* (e.g. ABEL, 1905, p. 118). Furthermore, the size of the face, even if smaller than the average for *'E.' cristatus* fits the smaller specimens of the species, including the Belgian ones. As most of the diagnostic characters of *'E.' cristatus* are observed in the two specimens of *'E.' ashbyi sensu* MYRICK, 1979, I propose to synonymize this species with *'E.' cristatus*.

'Eurhinodelphis' whitmorei sensu MYRICK, 1979, based on the skull USNM 25666, was diagnosed in MYRICK (1979, p. 254) by: a smaller maximum size relatively to *'E.' cristatus*, thicker nasals, premaxillae not mesially sloping at the level of the antorbital notches and anterolateral curve of the dorsal margin of the maxilla not as marked. The skull USNM 25666 presents all the features differentiating *'E.' cristatus* from *'E.' bossi*, except its face which is longer relatively to its width than on specimens of *'E.' cristatus*. That peculiarity, also present on some specimens of *'E.' bossi* does not seem sufficient to create a new species. Because the characters given by MYRICK (1979) are variable within *'E.' cristatus*, USNM 25666 is referred here to that species.

The last species of *Eurhinodelphis* described by MYRICK (1979), *E. morrisi*, is also based on a single specimen, USNM 167622. The diagnosis given by MYRICK (1979, p. 270) mainly differentiates it from *'E.' cristatus*. This seems correct as the derived characters of *'E.' cristatus* are absent on the skull. But here again, there is no comparison with *'E.' bossi*. The dimensions of the skull are globally at the lower limit of the interval for *'E.' bossi* (including *'E.' vaughni sensu* MYRICK, 1979), and are very close to the skull USNM 171103 (= *'E.' vaughni sensu* MYRICK, 1979). Several differences with *'E.' bossi* appear: lower and flatter supraorbital process; more concave and erected medial plate of the maxilla along the vertex; absence of medio-anterior point of the frontals on the vertex. It seems, however, difficult to build a new species on so few characteristics, observed in only one specimen. Therefore, the holotype of *'E.' morrisi sensu* MYRICK, 1979 is provisionally referred to *'E.' bossi*.

To summarize, the list of species from the genus *'Eurhinodelphis'* proposed by MYRICK (1979) is restricted to two species: *'E.' bossi* (including *'E.' vaughni* and *'E.' morrisi sensu* MYRICK, 1979) and *'E.' cristatus* (including *'E.' ashbyi* and *'E.' whitmorei sensu* MYRICK, 1979). Because those two species are referred here to a new genus described in work in progress, no species of the genus *Eurhinodelphis* – restricted to the species *E. cocheteuxi* and *E. longirostris* – is recognized in the Calvert Formation.

Comments about specimens from the Belluno Sandstones (north eastern Italy) referred to Eurhinodelphis *by* PILLERI *(1985)*

In 1985, PILLERI described *Eurhinodelphis sigmoideus* on the basis of a well preserved skull MGPD 26396 from the Belluno Sandstones (lower Miocene of northeastern Italy), lacking the apex of the rostrum, the mandible and teeth, but with one tympanic *in situ* and associated with five cervical vertebrae and two thoracics. PILLERI gave the following short justification for the attribution of the species to *Eurhinodelphis*: '*Taxonomically speaking, this is a new species, which in view of the essential morphological features of the skull and the spinal column belongs to the genus* Eurhinodelphis... .' First, it should be noticed here that the schematic drawing of the dorsal view of the skull of *Eurhinodelphis sigmoideus sensu* PILLERI, 1985 presented by PILLERI (1985, fig. 21) bears some important mistakes: the posterior apex of the premaxillae is much too long and wide, the nasals are too nodulous, narrower than in reality, and the nasals are too short on the vertex (see corrected drawing, Fig. 5).

When considering the genus *Eurhinodelphis* only including the species *E. cocheteuxi* and *E. longirostris*, *E. sigmoideus sensu* PILLERI, 1985 is closer to members of the genus *Schizodelphis* than to members of the genus *Eurhinodelphis*, with a stronger longitudinal compression of the vertex correlated to a more erected supraoccipital shield. But the most striking similarities are in fact observed when comparing *E. sigmoideus sensu* PILLERI, 1985 with *Ziphiodelphis abeli*, as suggested by BIANUCCI & LANDINI (2002). Those two species share the following characters, absent in *Eurhinodelphis* and *Schizodelphis*:

- Wide and flattened surface of the premaxilla at the level of the antorbital notches with a median portion regularly laterally sloping. In *Eurhinodelphis* and *Schizodelphis*, this area medial to the antero-medial sulcus is narrower, thicker and less medially elevated, with a more regular triangular shape.

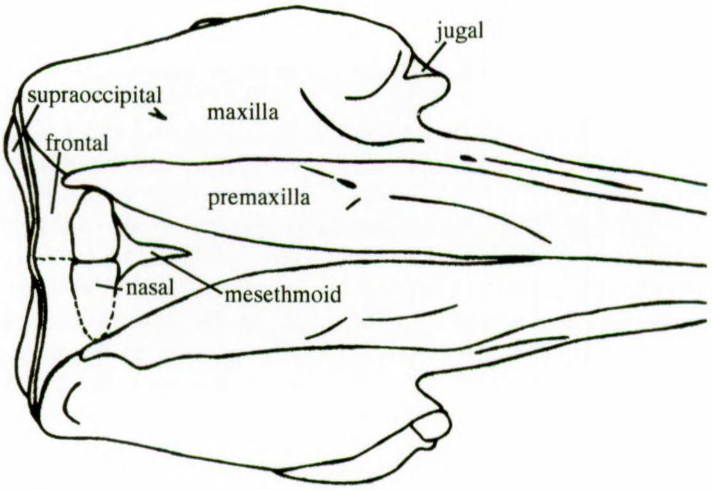

Fig. 5 – Corrected schematic drawing of the dorsal view of the skull of *Ziphiodelphis sigmoideus* (PILLERI, 1985), from Belluno, north-eastern Italy, Belluno Sandstones, early Miocene.

- Thickened antero-dorsal portion of the nasals constituting the highest surface of the vertex.
- Medial plate of the maxilla against the vertex keeping an elevated dorsal margin in a postero-lateral direction, giving the postero-dorsal corner of the skull a more angular aspect in lateral view.
- The ventral view of the right tympanic preserved *in situ* on the basicranium of the type of *E. sigmoideus sensu* PILLERI, 1985 (see PILLERI, 1985, Plate 45) has proportions and size close to the tympanic of the holotype of *Ziphiodelphis abeli* MGPD 26194 (see DAL PIAZ, 1977, Plate 3, Fig. 9), anteriorly wider than the more pointed tympanic of *Eurhinodelphis cocheteuxi* IRSNB M.1856 (see LAMBERT, in press), *'E.' bossi* USNM 16581 and *Schizodelphis barnesi* USNM 24413 (both figured in MUIZON, 1988a, Fig. 6).

The holotype of *Eurhinodelphis sigmoideus sensu* PILLERI, 1985 is clearly smaller than the holotype of *Ziphiodelphis abeli*, with a general size of the facial skull close to the smallest individuals of *'Eurhinodelphis' cristatus*. Its face is relatively longer than that of *Z. abeli*. The vertex is slightly more elevated. A small fossa for the postorbital lobe of the pterygoid sinus nearly reaches the ventral face of the roof of the orbit in *E. sigmoideus sensu* PILLERI, 1985, while it is dorsally shorter in the holotype of *Ziphiodelphis abeli*. The most striking difference is the dorsal elevation of the premaxillae, forming an elongated bulge with a maximal height of 28 mm at a level 80-90 mm anteriorly to the antorbital notches. This median prominence gives the base of the rostrum a sigmoid profile (inspiring the species name *sigmoideus* to PILLERI, 1985). Those differences seem sufficient to exclude *Eurhinodelphis sigmoideus sensu* PILLERI, 1985 from the species *Ziphiodelphis abeli*, and I suggest to place it in the same genus, as *Ziphiodelphis sigmoideus*.

An additional observation can be made on that skull: the descent of the suture between premaxilla and maxilla on the lateral surface of the rostrum far before the apex, characteristic of at least the genera *Eurhinodelphis*, *Schizodelphis*, and the species *'E.' cristatus*, *'E.' bossi*, and *Ziphiodelphis abeli*, is visible on the type of *Z. sigmoideus*. The maximal length of the maxilla on the rostrum is estimated to 510 mm. The ratio between the width of the skull at the level of the zygomatic processes and that length is close to the ratio calculated for an undescribed Belgian skull of *'E.' cristatus*, and smaller than the ratio for *E. cocheteuxi* and *E. longirostris*. The maxillary part of the rostrum is then relatively longer in *Eurhinodelphis* when compared to *'E.' cristatus* and *Ziphiodelphis*.

The second *'Eurhinodelphis'* species from the Belluno Sandstones, *E. bellunensis sensu* PILLERI, 1985, is based on the skull MGPD 26404, only lacking the very apical portion of the rostrum, with the two tympanics *in situ*, several teeth, and associated with its roughly complete mandible. Here again, the attribution by PILLERI (1985) to the genus *Eurhinodelphis* is not supported by characters.

The most striking differences between *E. bellunensis sensu* PILLERI, 1985 and the species of the revisited genus *Eurhinodelphis* are given here. First, the face of *E. bellunensis sensu* PILLERI, 1985 is relatively longer than that of *E. longirostris* and clearly longer than that of *E. cocheteuxi*, with a ratio between bizygomatic width of the skull and length of the face from the antorbital notch to the occipital condyle < 0.9. The maximal width of the premaxillae on the face is smaller, but with closer median margins just anteriorly to the external nares. The postero-lateral surface of the maxilla is much less laterally inclined, with a posterior portion narrower. The nasals are narrower (relatively to their length) and the frontals are longer. The occipital shield is strongly concave, while it is roughly flat in *E. cocheteuxi* and slightly convex in *E. longirostris*. The ventral margin of the occipital condyles is relatively lower, because of the lower paroccipital process of the exoccipital.

Taken separately, some of the differences here above are found in *Ziphiodelphis*: e.g. the shape of the premaxillae anteriorly to the external nares, the concavity of the supraoccipital shield, or the low paroccipital process of the exoccipital. But the face of *Eurhinodelphis bellunensis sensu* PILLERI, 1985 is proportionally longer than that of *Ziphiodelphis abeli* and *Z. sigmoideus*, and the proportions of the nasals and frontals are very different on its lower vertex.

In his discussion of the genus *Dalpiazina*, MUIZON (1988a, p. 73) briefly suggested that the holotype of *Eurhinodelphis bellunensis sensu* PILLERI, 1985 probably belongs to the genus *Argyrocetus*. It is also probably to that specimen that COZZUOL (1996) referred when he identified a species of the genus *Argyrocetus* from northern Italy. When restricting the genus *Argyrocetus* to its fragmentary known Argentinian type-species *A. patagonicus*, some similarities appear between this species and the holotype of *Eurhinodelphis bellunensis sensu* PILLERI, 1985: a low vertex, with the nasals higher than the frontals; a weakly erected concave supraoccipital shield; a general lateral view of the mandible roughly similar; most of the measurements relatively close. However, a part of those features are linked to the low rate of longitudinal telescoping of the skull. And this is clearly a primitive character, placing *E. bellunensis sensu* PILLERI, 1985 and *Argyrocetus patagonicus* in a basal position in the phylogenetic tree of the eurhinodelphinids. Actually, the only portion of the skull of *A. patagonicus* which can be more precisely compared with *Eurhinodelphis bellunensis sensu* PILLERI, 1985 is the vertex. On this area, the nasals are more dorso-anteriorly elevated and relatively wider in *Argyrocetus patagonicus*, and the frontals shorter. The anterior portion of the face seems also relatively shorter in *A. patagonicus*. Actually, this type-species of the genus *Argyrocetus* seems too fragmentarily known to allow the inclusion of other species.

Because the holotype skull of *Eurhinodelphis bellunensis sensu* PILLERI, 1985 is nearly complete, I suggest its inclusion in a new genus, *Mycteriacetus* n. gen. This name is chosen in reference to *Mycteria ibis*, the African yellow-billed stork, characterized by a long and robust beak similar in lateral view to the rostrum of the eurhinodelphinids.

Mycteriacetus n. gen. is diagnosed by: longer and narrower supraorbital process of the maxilla, lower vertex and less erected supraoccipital shield relatively to *Eurhinodelphis*, *Schizodelphis*, and *Ziphiodelphis*; longer anterior part of the face, vertex more elevated, narrower nodular nasals not antero-dorsally projecting, and longer frontals on that vertex relatively to *Argyrocetus*; smaller size, more excavated premaxillary sac fossae, longer nasals and shorter frontals on the vertex relatively to *Macrodelphinus*.

Comments about other specimens referred to Eurhinodelphis

The brief review of FORDYCE (1983) is discussed here, in addition to comments about more recently described specimens.

The fragment of rostrum constituting the holotype of the Miocene Sardinian species *Eurhinodelphis sassariensis sensu* CAPELLINI, 1887 is undiagnostic as suggested by ABEL (1931), MYRICK (1979), and BIANUCCI *et al.* (1994). The palate seems flatter than in eurhinodelphinids, with a rostrum relatively wider at its base and a faster anterior narrowing.

The holotype of *E. pacificus sensu* MATSUMOTO, 1926, Middle Miocene of Japan, is an anterior fragment of rostrum with the corresponding mandible *in situ*. The author justified the attribution to the genus *Eurhinodelphis* by the fact that the premaxillae are longer than the maxillae and do not bear teeth. The anterior lowering of the maxilla in lateral view is much stronger than in *Eurhinodelphis* and other eurhinodelphinids for which this area is known. This feature gives the ventral margin of the maxilla on the rostrum a very convex shape, and allows to suggest that the premaxilla was not much longer than the maxilla. Actually, the mandible fragment might have been anteriorly shifted relatively to the rostrum, giving the impression of premaxillae much longer anteriorly. This undiagnostic fragment shows more similarities with delphinoids than with eurhinodelphinids, according to the opinion of ABEL (1931) who excluded it from the genus *Eurhinodelphis*.

The holotype of *E. salentinus* ZEI, 1950, from the Miocene of Pietra leccese (Apulia, Italy), is a skull too fragmentary at the level of the face to give a generic attribution. ZEI (1950) described the maxillae as occupying 3/5 of the length of the rostrum. This character is sufficient to place the specimen in the family Eurhinodelphinidae. It was placed by BIANUCCI & LANDINI (2002) in cf. *Argyrocetus salentinus* but no common diagnostic feature could be noticed from the figures of ZEI (1950) with the type-species of the genus *Argyrocetus*, *A. patagonicus*.

Another partial skull from the Pietra leccese was identified by BIANUCCI *et al.* (1994) as *Eurhinodelphis cristatus sensu* ABEL, 1902. This skull lacks the thickening of the maxilla on the roof of the orbit and the forwards indentation of the supraoccipital and frontal on the posterior edge of the maxilla laterally to the vertex, both characters defining the species *'E.' cristatus*. This skull shows actually more similarities with *'E.' bossi* and its measurements fit well with the variability observed among the individuals of that species. However, *'E.' bossi* is quite difficult to diagnose relatively to *'E.' cristatus*, as no clearly derived characters are isolated for the first species. Furthermore the skull from Pietra leccese is not well preserved and no information is available on the details of the basicranium. The strong flattening of the face might also hide characteristics of *'E.' cristatus*. Therefore, the Pietra leccese specimen is referred to *'E.'* aff. *bossi*.

The partial odontocete skull from the late Miocene of Portugal reported by DA MATA (1963) as *Eurhinodelphis* cf. *cristatus sensu* ABEL, 1902 lacks all the diagnostic characteristics of the species, contradicting MYRICK (1979, p. 13). Even its attribution to the family Eurhinodelphinidae is denied here. The morphology of the vertex, with a strong transversal pinching of the frontals behind wider nasals and the loss of contact between the posterior apex of the premaxillae and the frontals might indicate affinities with some kentriodontids, e.g. *Liolithax pappus* (see KELLOGG, 1955; BARNES, 1978).

As suggested by FORDYCE (1983), the periotic from the Miocene 'faluns' of Touraine and Anjou (France) identified by GINSBURG & JANVIER (1971) as *Eurhinodelphis* sp. lacks several features present in the family Eurhinodelphinidae, for example the well excavated anterior bullar facet. It was actually compared by GINSBURG & JANVIER (1971) to the physeterid periotic from Antwerp erroneously reported by ABEL (1902, pl. 17, figs. 11-12) to *Eurhinodelphis longirostris*. The periotic of the 'faluns' shows similarities with kentriodontids such as *Liolithax pappus* (KELLOGG, 1955) (see BARNES, 1978, figs. 1j-2j).

The holotype of *Eurhinodelphis minoensis sensu* OKAZAKI, 1976 from the early to middle Miocene of Japan is a partial mandible associated to vertebrae, ribs and detached teeth. Those fragments are not diagnostic at a generic level and no character allows a strict attribution to the family Eurhinodelphinidae. *Eurhinodelphis minoensis sensu* OKAZAKI, 1976 should therefore be considered as Odontoceti *incertae sedis*.

From the same formation, OKAZAKI (1976) described a partial skull with a periotic and placed it as *Eurhinodelphis* sp. [erroneously discussed by FORDYCE (1983) as a specimen of *Eurhinodelphis minoensis*]. The periotic was compared by FORDYCE (1983) to kentriodontids. The skull is very incomplete and the reconstruction of the vertex by OKAZAKI (1976, fig. 4) is doubtful. From plate 2, figure 3, there are no contradictions to the kentriodontid affinities of the periotic, excluding the specimen from the family Eurhinodelphinidae. An additional isolated periotic identified as *Eurhinodelphis* sp. by OKAZAKI (1976, pl. 2, fig. 1) might also belong to a kentriodontid. It is referred here, as the first one, to the superfamily Delphinoidea *sensu* MUIZON (1988b).

The cervical vertebra from the early Miocene of Catalonia, Spain, identified by PILLERI (1988) as *Eurhinodelphis* sp. (cf. *E. sigmoideus*) is probably not diagnostic at the generic level, as already suggested by BIANUCCI & LANDINI (2002) who considered it as Eurhinodelphinidae indet. From the systematic revision of the genus *Eurhinodelphis*, I only recognize the species *E. cocheteuxi* and *E. longirostris*, for which no associated cervical vertebra are known.

Systematic discussion

MUIZON (1988a, p. 40-41) differentiated the Belgian specimens from the American specimens of *Schizodelphis longirostris*, contradicting MYRICK (1979), by a list of cranial characters: shape and position of the nasals, height of the mesethmoid, excavation of the premaxillary sac fossae and their elevation towards the vertex, morphology of the base of the rostrum. From the observation of the Belgian specimens, most of those differences are present in the holotype of *Eurhinodelphis longirostris* IRSNB 3249-M.342 (see description above), but they are absent in the second most complete specimen of *E. longirostris sensu* ABEL, 1902, IRSNB 3235-M.343:

- While the nasals of the holotype of *E. longirostris* are in contact with the supraoccipital, 15 mm separate those bones from the supraoccipital on IRSNB 3235-M.343.
- The mesethmoid of IRSNB 3235-M.343 reaches the antero-dorsal margin of the nasals, but this character is also observed in some American specimens.
- The elevation of the premaxillae towards the vertex of IRSNB 3235-M.343 begins more posteriorly and is more abrupt than in the holotype of *E. longirostris*, as is the case in the American specimens.
- The premaxillary sac fossae of IRSNB 3235-M.343 are distinctly more concave than in the holotype of *E. longirostris*, as is the case in the American specimens.
- The left side of the rostrum of IRSNB 3235-M.343 is interrupted 140 mm anteriorly to its base, and its slightly medially compressed right side shows a slight transverse swelling, probably homologous to the swelling described by MUIZON (1988a) for the American specimens.

In fact, it seems that, in his comparison of the Belgian and American specimens, MYRICK (1979) referred more to the skull IRSNB 3235-M.343, well figured in dorsal and ventral view by ABEL (1902, pl. 14, figs. 1-2), than to the holotype of *E. longirostris* IRSNB 3249-M.342.

IRSNB 3235-M.343 should be excluded from *E. longirostris*, and referred to the same genus as the American specimens, *Schizodelphis*. This skull IRSNB 3235-M.343 was first described by DU BUS (1872) as the only specimen of the species *Priscodelphinus morckhoviensis* (and thus the holotype). It was not figured by DU BUS (1872), but the fact that it is identifiable from his description, and that it is well preserved and associated with a periotic and a fragment of tympanic bulla, leads to recognize IRSNB 3235-M.343 as the holotype of *Schizodelphis morckhoviensis* (see below).

Schizodelphis GERVAIS, 1861

Type species. Schizodelphis sulcatus (GERVAIS, 1853)

Included species. *S. sulcatus*, ? *S. barnesi* MUIZON, 1988a, and *S. morckhoviensis* (DU BUS, 1872)

Diagnosis. This genus differs from:

- *Eurhinodelphis* in: maxillary part of the rostrum relatively shorter; vertical medial plate of the maxilla along the vertex less antero-dorsally developed; concave supraoccipital shield; less elevated and wider paroccipital process of the exoccipital, with lower occipital condyles (ventral margin of the condyles much lower than the level of the floor of the temporal fossa); more excavated premaxillary sac fossa; zygomatic process of the squamosal lower in lateral view and wider in ventral view; presence of a small fossa for the postorbital lobe of the pterygoid sinus on the ventral surface of the supraorbital process.

- *Ziphiodelphis* in: narrower and thicker triangular surface of the premaxilla medially to the premaxillary foramen lacking the more regular flatness and lateral slope seen in *Ziphiodelphis*; vertical medial plate of the maxilla along the vertex less postero-dorsally extended, giving the postero-dorsal outline of the skull a more rounded aspect in lateral view; narrower vertex with narrower nasals lacking the antero-dorsal projection characterizing *Ziphiodelphis*.
- *Argyrocetus* and *Macrodelphinus* in: more elevated and more transversely compressed vertex with narrower nasals; more erected supraoccipital shield close to the vertical.
- *Mycteriacetus* n. gen. by: relatively wider and shorter face; more elevated vertex with frontals shorter than the nasals; more vertical supraoccipital shield.

Schizodelphis morckhoviensis (DU BUS, 1872)

* 1872 *Priscodelphinus morckhoviensis* DU BUS, p. 495.
v. 1872 *Priscodelphinus pulvinatus* DU BUS, p. 496.
v. 1880 *Priscodelphinus morckhoviensis* VAN BENEDEN & GERVAIS, p. 495.
v. 1902 *Eurhinodelphis longirostris* ABEL, pl. 14, figs. 1-2, pl. 17, fig. 5, pl. 18, fig. 2.
v. 1979 *Rhabdosteus longirostris* MYRICK, pl. 19, figs. b-d, pl. 20, figs. a, c and d, pl. 21, fig. b, pl. 22, fig. b and fig. 10 (unpublished).
v. 1988a *Schizodelphis longirostris* MUIZON, p. 45, figs. 7a and 8a.

Diagnosis. Schizodelphis morckhoviensis differs from the type-species *S. sulcatus* in its rostrum being higher at the level of its base. Apart from that feature, no clear diagnostic character could be isolated, mainly because of the incompleteness of the holotype of *S. sulcatus* (see comparison below).

S. morckhoviensis differs from the possibly valid species *S. barnesi* in: a less transversely compressed vertex with relatively wider frontals; nasals wider than long; the median margin of the maxilla along the vertex distinctly more lateral than the lateral margin of the bony nare (those two margins are roughly at the same level in *S. barnesi*).

Holotype. IRSNB 3235-M.343, a well preserved skull, associated with the left periotic (figured by MUIZON, 1988a, p. 45, figs 7-8) and a fragment of left tympanic, lacking the anterior part of the rostrum, the teeth and fragments of the basicranium (found June the 4th 1861, holotype of *Priscodelphinus morckhoviensis sensu* DU BUS, 1872, individual 4 of *Eurhinodelphis longirostris* in ABEL, 1902, figured in pl. 14, figs 1-2 and 17, fig. 1).

Referred specimens. IRSNB 3239-M.345, a partial skull (holotype of *Priscodelphinus pulvinatus sensu* DU BUS, 1872 and individual 6 of *Eurhinodelphis longirostris sensu* ABEL, 1902); IRSNB M.1859, a left tympanic bulla associated with a malleus {found by R. Marquet in June 1996, in Antwerp, on the excavations for a car park near the Keyzerlei (under the Rex cinema)}; and at least the individuals USNM 21291, USNM 187306, USNM 167676, from the east coast of the USA, identified by MYRICK (1979) as *Rhabdosteus longirostris*.

Discussion. The partial skull IRSNB 8343Z-M.1860 (Pl. 5, Figs a-b, found in Kessel, 18 km south-east of Antwerp, January the 30st 1913, lacking the apical portion of the rostrum and the squamosals) shares characters with members of the genus *Schizodelphis*: very low occipital condyles and probably concave dorso-median surface of the supraoccipital. However, it seems to lack a fossa for the postorbital lobe of the pterygoid sinus, and the postero-median plate of the maxilla might be less concave than in that genus. Nevertheless, the preservation state – numerous small plates of bone separated by intervals filled with sediment, very different from the previously described specimens from Antwerp, precludes good estimations of the three dimensional morphology. It seems therefore more conservative to place IRSNB 8343Z-M.1860 in Eurhinodelphinidae aff. *Schizodelphis*.

Locus typicus. The holotype was found on June 4th 1861, in Antwerp, and the locality cited by ABEL (1902) is '*3e Section*'. This section is situated north-east to the 4e section where the holotype of *Eurhinodelphis longirostris* was found, also along the present motorway around the city.

Stratum typicum. No data are avalaible for the holotype. The tympanic bulla IRSNB M.1859 was found in the Antwerp Sands, late early to middle Miocene (LOUWYE *et al.* 2000). The specimens USNM 21291, USNM 187306 and USNM 167676 all come from the Calvert Formation, and more precisely from the beds 3, 11 and 12 respectively, as defined by SHATTUCK (1904) (see MYRICK, 1979). Those beds are late early to middle Miocene of age (VERTEUIL & NORRIS, 1996, fig. 4).

Redescription of the holotype of S. morckhoviensis *IRSNB 3235-M.343*

Skull (Pl. 2, Figs 2a-b ; Pl. 3; Figs. 6-9)

The following parts of the skull are missing: apical part of the rostrum, right preorbital process, fragments of the maxillae on the face, fragments of the supraoccipital and of the parietals, the right zygomatic process, and a major part of the pterygoids. The teeth are lost, as on most of the eurhinodelphinids from Antwerp. The right periotic and the fragmentary right tympanic were detached from the skull after the description of ABEL (1902). The main measurements are given hereafter (Table 2). This skull is slightly smaller than the holotype of *Eurhinodelphis longirostris*.

Dorsal view. The rostrum is preserved for only 200 mm. The flattening of the premaxilla towards the base of the rostrum is located on the lateral part of that bone, which has a dorsal level roughly the same as the bordering maxilla at the level of the antorbital notch. Medially, the elongated and raised rugous triangular plate of the premaxilla, limited by the antero-median sulcus, reaches the dorsal level of the preorbital surfaces of the maxillae. The premaxillary foramen, slightly more posterior than the antorbital notch, is followed by a marked postero-lateral sulcus and a shallow postero-median sul-

Table 2 – Measurements on skulls of *Schizodelphis morckhoviensis* and ? *S. barnesi*. Measurements are in millimetres. (e) indicates estimate, '+' nearly complete, and '–' no data. The four first specimens are placed in *Schizodelphis morckhoviensis*, and the three last (USNM 244403, 187312 and 187317) in the possibly valid *S. barnesi*.

Measurements on the skulls of *Schizodelphis morckhoviensis* and ?*S. barnesi*	IRSNB 3235-M.343	USNM 21291	USNM 187306	USNM 167676	?*S. barnesi* USNM 244403	?*S. barnesi* USNM 187312	?*S. barnesi* USNM 187317
3. length anterior orbit-posterior skull	170	172	175	165	177	160	152
4. length anterior supraoccipital-anterior orbit	120	120	107	102	125	117	120
5. length orbit	67	61	–	–	61	e56	e53
8. width base rostrum	93	88	91	–	106	87	89
9. width premaxillae base rostrum	56	61	59	–	53	46	44
10. width skull postorbital processes	185	e202	–	e186	214	178	176
11. width skull zygomatic processes	187	–	185	e177	201	184	177
12. width bony nares	32	26	28	20	24	e23	22
13. width nasals	52	43	36	34	26	26	23
14. maximal posterior premaxillary width	73	80	76	68	72	72	69
15. minimal posterior distance between maxillae	60	68	57	43	34	28	24
16. width medio-ventral margins exoccipitals	102	–	98	89	95	91	88
17. width lateral margins occipital condyles	80	74	80	83	73	78	74
18. width inner margins occipital condyles	34	35	36	37	30	–	33
19. height cranium	150	–	–	–	–	–	–
21. height base rostrum	60	53	e63	–	55	–	e50
22. height temporal fossa	58	–	39	–	–	–	–
23. height ventral margin occipital condyles	22	–	32	26	e20	–	22
24. height occipital condyles	42	–	38	39	36	–	37

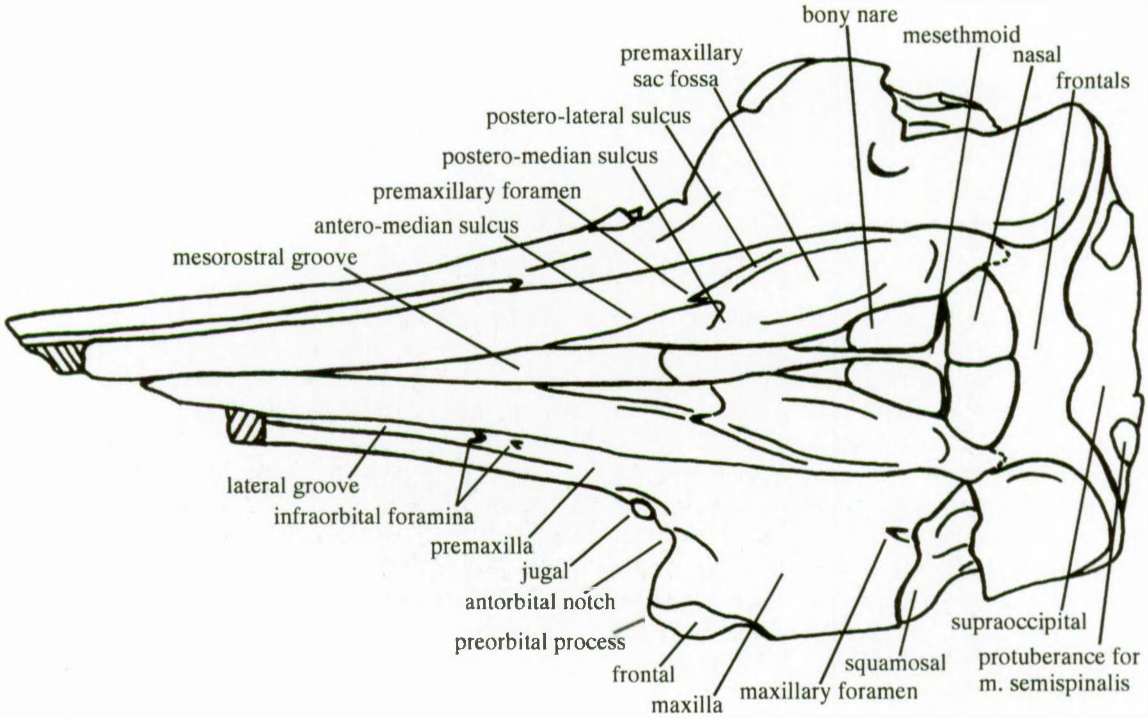

Fig. 6 – Schematic drawing of the dorsal view of the skull of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype) from Antwerp, ? Antwerp Sands, late early to middle Miocene.

cus. The premaxillary sac fossa is relatively short, concave, with a laterally sloping median portion partially covering the mesethmoid in front of the bony nares. The elevation of the premaxilla towards the vertex is accentuated on the last centimetres. The posterior apex of the premaxilla extends at least farther than mid-length of the nasal, and exhibits a wide contact with the frontal. The shape of the suture between premaxilla and frontal is probably less clearly defined than suggested by the figure of ABEL (1902, pl. 14, fig. 1).

The antorbital notch is short and wide. The narrow concave medial plate of the maxilla along the lateral edge of the vertex is abrupt. The posterior margin of the bone is also elevated against the supraoccipital shield, forming a thick postero-laterally directed crest. This crest extends posteriorly farther than the anterior margin of the supraoccipital.

The nasals are wider than long, higher than the frontals, with a smoother dorsal surface, slightly sloping anteriorly. They are anteriorly margined by the posterior plate of the mesethmoid, only partially preserved. However, fragments applied on the anterior face of the nasals show that the plate was reaching the level of the antero-dorsal edge of the nasals. Without those small and thin fragments, not connected to the more ventral part of the plate, it would have been concluded that the mesethmoid is lower than the nasals. On the postero-lateral corner of the bony nare, at the junction between mesethmoid and maxilla under the level of the premaxilla, is a thin lamina of the maxilla medially limiting a small rounded fossa (Pl. 2, Fig. 2a ; Fig. 7). This fossa is antero-ventrally followed by a short sulcus along the mesethmoid. This hollowed space of the maxilla inside the bony nare is too lateral relatively to the terminal nerve foramina observed in for instance *Tursiops* (ROMMEL, 1990, fig. 2) to be directly correlated to an olfactory function. Its position seems to be homologous to that of a small foramen observed in several odontocetes, ventrally exiting on the orbit roof, in the posterior portion of the large infraorbital foramen (observed in *Mesoplodon*), or just posterior to that foramen (in *Tursiops* or *Delphinus*). It would then correspond to the additional dorsal exit from the infraorbital complex described by ROMMEL (1990, p. 36) on the lateral aspect of the internal bony nares of *Tursiops*, and considered as an arterial foramen, probably joined to a branch of the infraorbital nerve. A small foramen is indeed localised on the ventral surface of the orbit roof of IRSNB 3235-M.343, 5 mm posteriorly to the large infraorbital foramen.

The dorso-medial part of the supraoccipital shield is strongly concave with a vertical wall against the frontals for more or less 10 mm. The ventral two thirds of the shield are globally convex towards the occipital condyles, with a sagittal groove. Well developed circular protuberances are present on the dorsolateral areas of the supraoccipital shield for the insertion of the muscle semispinalis.

Lateral view. The suture between maxilla and premaxilla on the rostrum is hollowed by a deep longitudinal groove anteriorly following a dorsal infraorbital foramen piercing the maxilla 50-60 mm anteriorly to the antorbital notches. The rostrum is too incompletely preserved to estimate the apical shape of the suture – and therefore the relative length of the maxillae and premaxillae. The frontal part of the preorbital process is moderately thickened, while the maxilla is very thin in that region. The roof of the temporal fossa is slightly higher than the roof of the orbit.

The zygomatic process of the squamosal is thick in lateral view, stronger than the narrow lobe of the post-

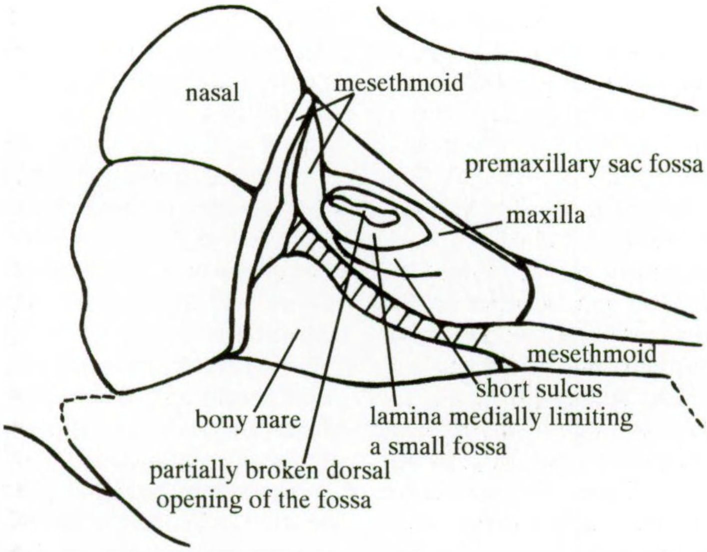

Fig. 7 – Schematic drawing of the bony nares of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene, in right dorso-lateral view, with the detail of a small fossa on the left side.

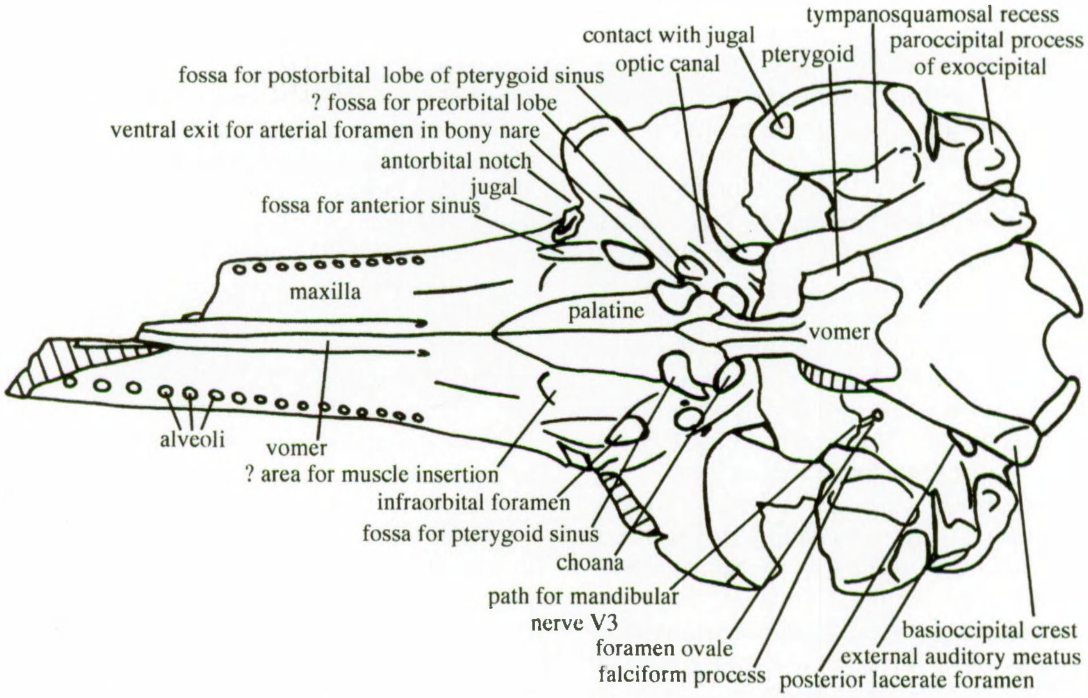

Fig. 8 – Schematic drawing of the ventral view of the skull of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene.

glenoid process. The occipital condyles are strongly protuberant, with a long distinct condylar pedicle.

Posterior view. The dorsal margin of the supraoccipital shield is regularly rounded. The paroccipital process of the exoccipital is relatively low and wide (when compared for example with *Eurhinodelphis longirostris*), slightly shorter ventrally than the thick basioccipital crests. The occipital condyles are very low, with a ventral margin much lower (ca. 30 mm) than the floor of the temporal fossa.

Ventral view. The first small alveolus appears at 75 mm of the antorbital notch. It has a diameter of 3 mm and is separated from the next one by a septum of 3 mm. On the right side, 16 alveoli are present on a length of 118 mm. The last one has a diameter of 5 mm, and is separated from the previous one by a septum of 4.5 mm. The vomer is ventrally visible through a fenestra between the maxillae, with a maximal width of 7 mm.

The palatines are long and narrow on the base of the rostrum, with a pointed apex 55 mm anterior to the antorbital notches. The median additional curve drawn on the palate of the specimen to limit a smooth and slightly excavated surface (see ABEL, 1902, pl. 14, fig. 2) probably corresponds to an area of insertion of muscles (and not to the insertion of a sinus, as proposed by ABEL, 1902, pl. 18, fig. 2). The finger-like lateral curve corresponds to the limits of a fossa for the anterior sinus. This well defined narrow fossa medially borders the base of the jugal, with the apex 30 mm anterior to the antorbital notches. This fossa has a shape and position similar to the anterior sinus of delphinids such as *Tursiops* or *Delphinus* (FRASER & PURVES, 1960, fig. 25 and plates 44-46), but with a more limited extension. It should be noticed that the anterior sinuses of *Tursiops* and *Delphinus* are not always positioned in well defined and deep fossae as those described on the specimen IRSNB 3235-M.343. The fossa for the pterygoid sinus on the palatine reaches anteriorly the level of the antorbital notches. The pterygoids are lost in that region of the skull.

The base of the jugal is antero-medial to the antorbital notch. The lacrymal is partially lacking and the lacrymal-maxilla suture is not visible.

The optic canal is posteriorly bordered for its most medial part by a deep fossa, at the junction between the lateral wall of the cranial cavity and the roof of the orbit. This fossa, laterally limited by a crest, is homologous to the fossa for the postorbital lobe of the pterygoid sinus observed in *'Eurhinodelphis' cristatus*. Its shorter lateral development on the specimen IRSNB 3235-M.343 is considered as primitive relatively to *'E.' cristatus*, but more derived than in *Eurhinodelphis* (as defined here). A slightly concave and smooth surface, anterior to the optic canal and at the same transverse level than that fossa, might be a shallow fossa for the preorbital lobe of the pterygoid sinus.

The ventral surface of the zygomatic process is wide and flat, with the exception of a protuberance indicating the contact with the jugal. The glenoid surface is wide, pointed towards the apex of the postglenoid process. The tympanosquamosal recess is well excavated and ante-

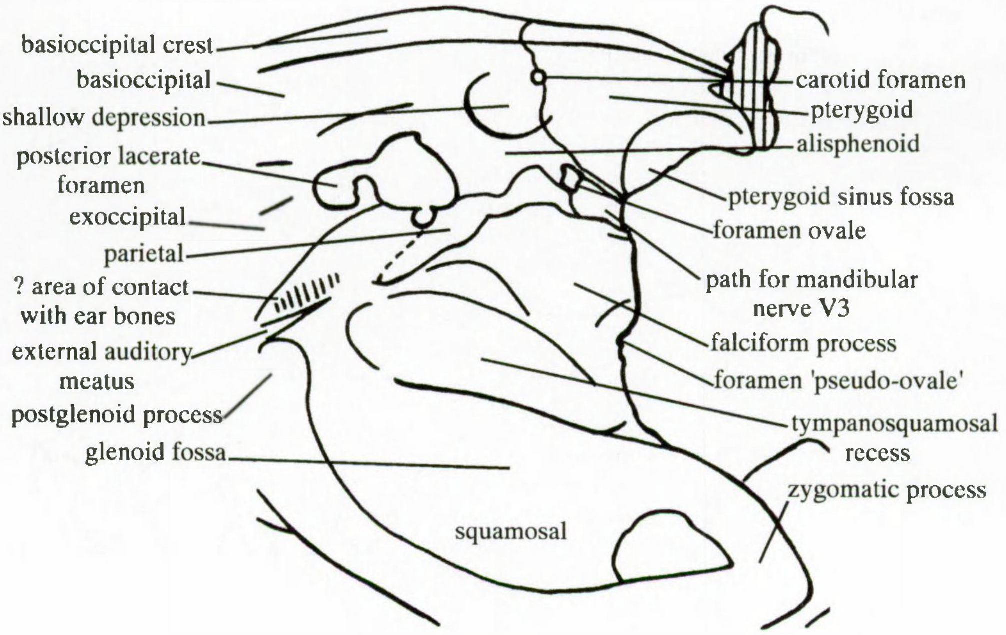

Fig. 9 – Detail of the left side of basicranium of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene in ventro-lateral view.

riorly limited to the anterior margin of the roof of the temporal fossa. The falciform process of the squamosal is high and antero-medially developed. By comparison with better preserved specimens of *Schizodelphis* from the Calvert Formation (e.g. USNM 187211), this morphology clearly indicates a contact with a complete lateral lamina of the pterygoid.

On the alisphenoid, the small foramen ovale (diameter of 4-5 mm) is followed latero-anteriorly by a sulcus (path for mandibular nerve V3 *sensu* Fordyce, 1994) that pierces the dorsal surface of the alisphenoid after 8-9 mm. It emerges in a small cavity dorso-median to the falciform process of the squamosal, pierces the lateral wall of that cavity, and reaches the roof of the temporal fossa dorsally to the falciform process (= foramen 'pseudo-ovale'). The cavity is probably a dorso-posterior extension of the pterygoid sinus fossa in the alisphenoid, which is not preserved here. The carotid foramen, located on the lateral face of the basioccipital crest at the longitudinal level of the foramen ovale, is surrounded by a slightly depressed and smooth area. The posterior lacerate foramen might be more or less completely divided in a smaller posterior and a larger anterior portion by a transverse septum.

Before removal by Muizon (pers. comm.), the left periotic and tympanic were firmly fixed to the basicranium (see Abel, 1902, plate 14, fig. 2). However, the position of the ear bones at that time was already the fact of a replacement, as a number written by Abel or an older author appears on the dorsal face of the periotic. Nevertheless, the breaks on the basicranium and ear bones suggest that the attachment was made by the posterior processes of the periotic and tympanic at the level of the posterior meatal crest and post-tympanic process of the squamosal. No depression excavates the squamosal dorsally to the spiny process or the anterior surface of the paroccipital process of the exoccipital.

Ear bones (Pl. 4; Figs. 10-11)

Periotic. The complete left periotic of IRSNB 3235-M.343, figured by Muizon (1988a, figs. 7a-8a), has a total length of 35 mm. The slender and long anterior process is hollowed in ventral face by a very long and deep anterior bullar facet. This groove is occupied on more than the two thirds of its length by a fragment of the processus tubarius of the tympanic, indicating a firm contact of the two bones at that level. The elongated accessory ossicle is also preserved, medially to the facet. In lateral view, the anterior process is pointed, with a base slightly widened by a small tubercle that follows posteriorly the low dorsal crest. The moderate sized lateral tuberosity has an angulated lateral margin, and is as separated from the anterior process as for example in *Eurhinodelphis cocheteuxi*. The mallear fossa is well individualized. The hiatus epitympanicus is wide and shallow, nearly continuous with the posterior bullar facet surface. That ventral surface of the posterior process is wide, medio-ventrally and postero-latero-ventrally curved, elongated in a ventrally to ventro-lateral direction. It is separated from the pars cochlearis by a wide space including the facial sulcus and the stapedial muscle

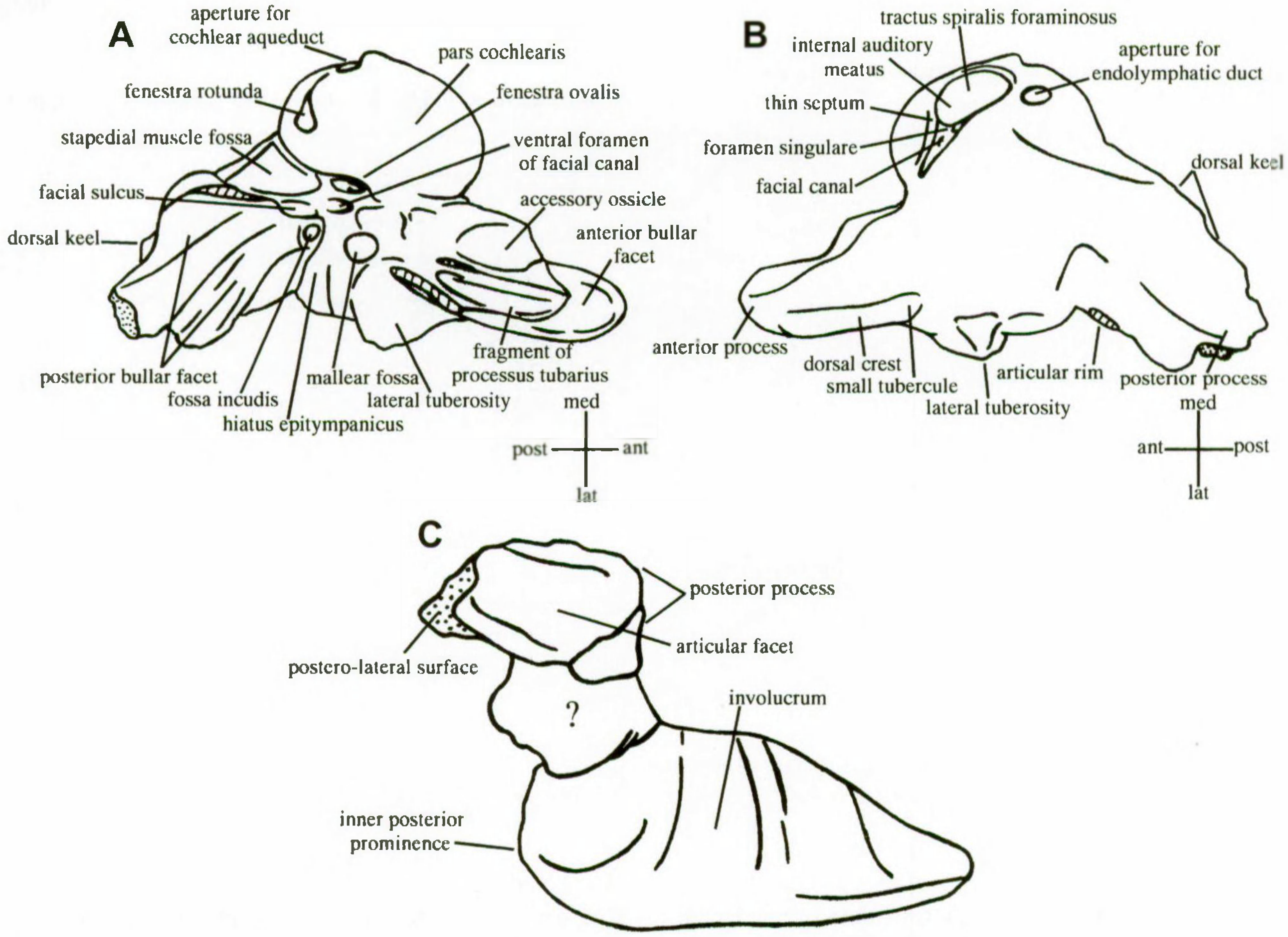

Fig. 10 – Schematic drawings of the left periotic and tympanic of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene. A-B. left periotic. A. ventral view. B. dorsal view. C. left tympanic in median view.

fossa. The small fossa incudis, located on the anterior apex of the posterior bullar fossa, is antero-ventrally oriented. The dorsal face of the posterior process bears an acute keel, progressively lowering and widening towards the internal auditory meatus. The keel delimits, with the median margin of the posterior bullar facet, a wide and concave median surface of the process. A low ridge on the ventro-lateral edge of the posterior process, just posterior to the hiatus epitympanicus, probably corresponds to the articular rim discussed by MUIZON (1987) on platanistids and squalodelphinids, and by FORDYCE (1994) on *Waipatia*.

The pars cochlearis is relatively small, regularly rounded and medio-laterally flattened in ventral view. The fenestra rotunda is roughly circular, with a slight medial elongation and a very shallow groove towards the aperture of the cochlear aqueduct. The latter is large, located on the medio-posterior area of the pars cochlearis, with an opening dorsally oriented. The aperture for the endolymphatic aqueduct is small and circular, medial to the anterior extremity of the dorsal keel of the posterior process, at the transverse level of the tractus spiralis foraminosus. The latter is included in the antero-laterally elongated internal auditory meatus. The meatus nearly reaches the pars cochlearis-anterior process contact. In the meatus, the small foramen singulare and the more anterior facial canal are clearly separated from the tractus spiralis foraminosus by a thin longitudinal septum.

Tympanic bulla. The only preserved parts of the left tympanic bulla of IRSNB 3235-M.343 are the median half of the bone and the posterior process. At least two levels of break between the involucrum and the posterior process were previously approximately repaired; the relative orientations of those two parts could therefore not be described. The total length of the bone (without the posterior process) is more than 33 mm, with a maximal height of the involucrum of 14 mm. The inner posterior prominence is narrow in ventral view, laterally margined by a well marked groove, probably ending at 22 mm from the posterior limit of the bone. The dorsal margin of the involucrum is high and parallel to the ventral margin for 13 mm. More anteriorly, the involucrum strongly narrows transversely and the dorsal margin descends progressively ventrally, without indentation. The posterior process is rectangular and convex in postero-medial view. Irregular surfaces on the postero-lateral and anterolateral surfaces and a relatively long process indicate a more or less strong attachment to the basicranium.

A second left tympanic IRSNB M.1859 (Pl. 4, Figs. 2a-d), found in situ in the Antwerp Sands, is associated with the corresponding malleus (Pl. 4, Figs. 2e-f; Fig. 11). The involucrum of this tympanic is roughly identical to that of the holotype of *Schizodelphis morckhoviensis*. The tympanic, only lacking the posterior process, has a total length of 38 mm and a width of 22.5 mm. The median groove is deep and antero-laterally deflected. The inner posterior prominence is distinctly shorter and narrower than the outer one. There is no anterior spine and antero-lateral concavity. The dorsal margin of the involucrum is flat for 16 mm, then it descends progressively anteriorly, without indentation, until a 4-5 mm long thin lamina. The sigmoid process is regularly transversely oriented, with a rounded postero-ventral margin. The lateral furrow is long, narrow and deep. The similarities with *S. morckhoviensis* IRSNB 3235-M.343 at the level of the involucrum and inner posterior prominence are also present on the isolated tympanic of *S.* cf. *sulcatus* figured by MUIZON (1988a, fig. 6c-d). No tympanic or periotic is known for *Eurhinodelphis longirostris*, precluding a comparison with this roughly similarly sized species.

The associated malleus has a robust processus gracilis, with a long contact to the base of the sigmoid process of the tympanic. The malleus has a total length of 5.3 mm in postero-medial view, including 3.7 mm for the articular facets. The tuberculum is then relatively short, and more pointed than in *Eurhinodelphis cocheteuxi*, *'E.' cristatus* and *'E.' bossi*. The manubrium is slightly higher than the processus muscularis. This malleus is close to the ones referred by MUIZON (1988a, figs. 5a-b) to *Schizodelphis sulcatus* (MNHN RL11) and *S.* cf. *sulcatus* (none of them is articulated to a skull).

Comparison with the holotype of Schizodelphis sulcatus

As suggested by MUIZON (1988a), the holotype of *Schizodelphis sulcatus* MNHN RL 12 has a relatively flattened rostrum base, with a height of 46 mm at the level of the antorbital notches. This is less than the 60 mm measured on the skull IRSNB 3235-M.343, with a similar general size. This character is very variable among the American specimens of *Schizodelphis*. For example, in the group F of the species *Rhabdosteus* (= *Schizodelphis*) *hruschkai sensu* MYRICK (1979), one skull has a height of the rostrum at the level of the antorbital notches of 47 mm, and the other one of 63 mm, for a general size of the skull differing very little.

The second difference between *S. sulcatus* and the American and Belgian *Schizodelphis sensu* MUIZON (1988a) is, according to MUIZON (1988a), the more slender and less thick zygomatic process of the squamosal. This difference is clearly present between *S. sulcatus* and the Belgian *Eurhinodelphis longirostris* as revised here. However, the squamosal of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 has a zygomatic process very similar to that of *S. sulcatus*, flattened in lateral view and wide in ventral view.

Additional measurements taken on both the holotype of *S. sulcatus* and IRSNB 3235-M.343 give very similar size and proportions. Actually, the size differences for the face and basicranium between those two specimens almost never exceed 6-7 mm, with the exception of the height of the base of the rostrum. Among other differences, the fossa for the postorbital lobe of the pterygoid sinus is deeper in IRSNB 3235-M.343, and the depression for the preorbital lobe is less individualized. The absence of informations about the vertex and the dorsal part of the

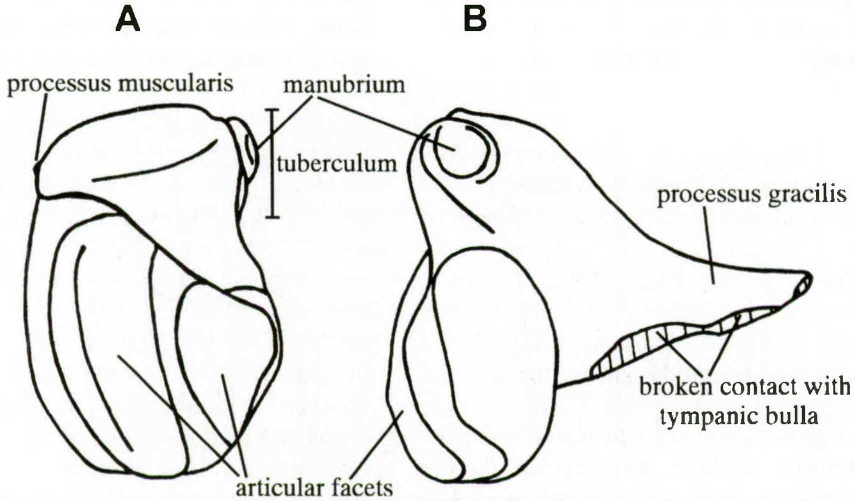

Fig. 11 – Schematic drawings of the detached left malleus of *Schizodelphis morckhoviensis* IRSNB M.1859, from Antwerp, Antwerp Sands, late early to middle Miocene. A. postero-median view. B. postero-ventral view.

supraoccipital shield of *S. sulcatus* precludes deeper comparison. I assume those two specimens to be similar enough to be placed in the same species, but the fragmentary state of the holotype of *S. sulcatus* and its lower rostrum base lead us to retain IRSNB 3235-M.343 in a distinct species of the same genus, *S. morckhoviensis*.

Comparison with the American Schizodelphis

Considering the transfer of some Belgian specimens to the genus *Eurhinodelphis*, the restricted species *Schizodelphis morckhoviensis* is compared to the skulls from the Calvert Formation placed in *Rhabdosteus* (= *Schizodelphis sensu* MUIZON, 1988a) *longirostris* by MYRICK (1979).

The holotype of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 has skull measurements very close to those of the American specimens USNM 21291, USNM 187306 and USNM 167676, all of them identified as *Rhabdosteus* (= *Schizodelphis*) *longirostris* by MYRICK (1979) (Table 2). The general morphology of the skull is similar, with a concave and short premaxillary sac fossa, a thin maxilla on the preorbital process, a vertical and concave medial plate of the maxilla along the vertex, depressed frontals with an irregular surface on the vertex, a dorso-ventrally flattened zygomatic process of the squamosal, a short fossa for the postorbital lobe of the pterygoid sinus on the ventral surface of the roof of the orbit, and a low and wide paroccipital process of the exoccipital with low occipital condyles. The only main difference is the size of the nasals; they are wider in IRSNB 3235-M.343 than in any of the three USNM specimens. The very thin dorsal part of the posterior plate of the mesethmoid is not well enough preserved in those specimens to predict the height it reaches in front of the nasals. Nevertheless, skulls like CMM-V-886, from the Calvert Formation, clearly congeneric with the USNM specimens, have a mesethmoid plate nearly as high as the nasals.

The similarities are convincing enough to place the specimens USNM 21291, USNM 187306 and USNM 167676 in the species *Schizodelphis morckhoviensis*. Those newly referred specimens add information about the species at the level of the rostrum and the basicranium.

The rostrum of USNM 21291 is nearly completely preserved, with a total length of at least 659 mm. This length is slightly smaller (relatively to the width of the face) than in *'Eurhinodelphis' bossi*, *'E.' cristatus* and *E. longirostris*, but close to *E. cocheteuxi*. However, the number of specimens of the same species with a roughly complete rostrum is low, and the relative length should only be considered as indicative. The posterior part of the suture between maxilla and premaxilla on the rostrum is visible on USNM 21291. 400 mm anteriorly to the antorbital notch, the maxilla still has a height of 8 mm. The maxillary part of the rostrum is therefore relatively longer than in *Eurhinodelphis longirostris*, for which the maxilla ends at 390 mm of the antorbital notches.

The basicranium of the specimen USNM 167676 is finely preserved, with a complete lateral lamina of the pterygoid in contact with the falciform process of the squamosal. A high and antero-medially directed falciform process, as observed on *Schizodelphis morckhoviensis* IRSNB 3235-M.343, seems to be a good indicator of the presence of a lateral lamina of the pterygoid, a fragile structure never preserved in Belgian specimens.

Besides the species *Rhabdosteus latiradix* COPE, 1868 (Odontoceti incertae sedis following MUIZON, 1988a) and *R. longirostris*, MYRICK (1979) described two additional species of the genus in the Calvert Formation : *R. barnesi* and *R. hruschkai*. The diagnoses given by MYRICK (1979) provide only few differences between the species, mainly based on the size of the skull, the shape of the nasals and the proportions of the vertex. Inside the species *R. hruschkai*, he also isolated seven morphological groups (A, A1, B, C, D, E and F), mainly differentiated by the shape of the nasals (MYRICK, 1979, p. 121).

When comparing the specimens two by two, strong differences quickly appear, that could easily be interpreted as diagnostic at a specific level. However, when groups of more than three or four specimens must be isolated by a series of characters, strict limits are hardly found. For example, for the shape of the nasals, it is possible to find a series of morphological intermediates between completely different conditions. In that way, it seems difficult to give a clear definition of *R. hruschkai*

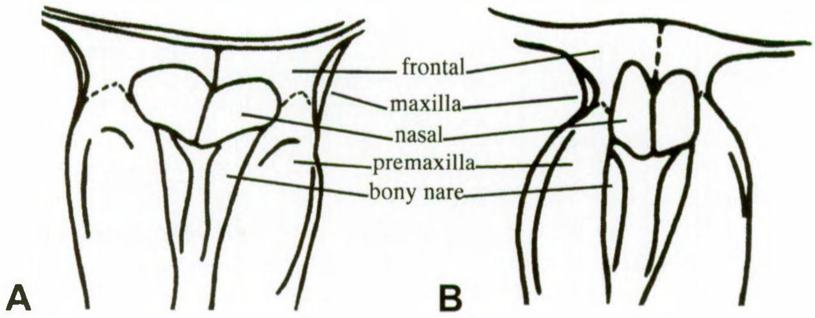

Fig. 12 – Schematic drawings of the vertex of *Schizodelphis* specimens in dorsal view, showing the difference in the degree of transverse compression between the species *S. morckhoviensis* and *S. barnesi*. A. *S. morckhoviensis* USNM 21291. B. *S. barnesi* USNM 244403. Both of them come from Maryland, USA, Calvert Formation, late early to middle Miocene.

sensu MYRICK, 1979, with a combination of characters found in all the specimens of the species.

For *R. barnesi sensu* MYRICK 1979, with a lower number of specimens, the measurements on the skulls and the morphology are more homogeneous (three skulls on Table 2). The four specimens USNM 244403, USNM 187624, USNM 187312, and USNM 187317, all of them found in the bed 12 of the Calvert Formation (*sensu* SHATTUCK, 1904), are characterized by nasals longer than wide on a vertex very transversely compressed. This character can be visualized by the median margin of the maxilla along the vertex being roughly at the same transverse level than the lateral margin of the bony nare (see Fig. 12). This seems sufficient to define an additional species of *Schizodelphis*, but only because it represents one extremity of the range of morphologies for the vertex in the American *Schizodelphis*.

To summarize, the possibility exists that, contradicting the hypothesis of MUIZON (1988a), more than one species of the genus *Schizodelphis* (*sensu* MUIZON, 1988a) is present on the Calvert Formation, but because of the high variability observed for the shape of the vertex, the definition of supplementary species does not provide much additional systematic information. The only species of *Schizodelphis* from the Calvert Formation also present in Antwerp is *S. morckhoviensis*.

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Explanation of plates

PLATE 1

Fig. 1 — Skull of *Eurhinodelphis longirostris* IRSNB 3249-M.342 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene. A. left lateral view. Scale bar = 150 mm. B. dorsal view. C. posterior view. D. ventral view. Scale bar for B -D = 50 mm. Labels on the skull were written at the time of the work of Abel (see comments on the text for some of them wrongly identified). as: alisphenoid; bo: basioccipital; bs: basisphenoid; eo: exoccipital; me: mesethmoid; pl: palatine; pmx: premaxilla; pt: pterygoid; smx: maxilla; so: supraoccipital; v: vomer.

Fig. 2 — Skull of *Eurhinodelphis* cf. *longirostris* IRSNB 3238-M.344, from Antwerp, ? Antwerp Sands, late early to middle Miocene, in dorsal view. Scale bar = 100 mm.

PLATE 2

Fig. 1 — *Eurhinodelphis longirostris* IRSNB 3250-M.1858, from Antwerp, ? Antwerp Sands, late early to middle Miocene. A. Dorsal view of the right part of the face. Scale bar = 30 mm. B. Sagittal section giving a medial view of the right half of the vertex. Scale bar = 20 mm. C. Ventral view of the palate showing the right alveolar row. Scale bar = 30 mm.

Fig. 2 — Skull of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene. A. bony nares in right dorso-lateral view with the detail of a small fossa on the left side. Scale bar = 20 mm. B. posterior view. Scale bar = 50 mm. Labels on that skull were written at the time of the work of Abel. eo: exoccipital; me: mesethmoid; n: nasal; pmx: premaxilla; so: supraoccipital.

PLATE 3

Skull of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene. A. dorsal view. B. left lateral view. C. ventral view. Scale bar for A-C = 50 mm. D. detail of the left side of basicranium in ventro-lateral view. Scale bar = 20 mm. Labels on the skull were written at the time of the work of Abel. as: alisphenoid; bo: basioccipital; bs: basisphenoid; f: frontal; me: mesethmoid; n: nasal; pl: palatine; pmx: premaxilla; pt: pterygoid; smx: maxilla; so: supraoccipital; v: vomer.

PLATE 4

Fig. 1 — Ear bones of *Schizodelphis morckhoviensis* IRSNB 3235-M.343 (holotype), from Antwerp, ? Antwerp Sands, late early to middle Miocene. A-D. left periotic. A. ventral view. B. medial view. C. dorsal view. D. lateral view. Scale bar for A-D = 10 mm . E. partial left tympanic in medial view. The contact between posterior process and rest of the bone is broken at several levels, precluding checking of the correct relative position of the two parts. Scale bar = 10 mm.

Fig. 2 — Ear bones of *Schizodelphis morckhoviensis* IRSNB M.1859, from Antwerp, Antwerp Sands, late early to middle Miocene. A-D. left tympanic. A. medial view. B. lateral view. C. ventral view. D. dorsal view. Same scale bar than 1E. E-F. SEM pictures of left malleus. E. postero-median view. F. postero-ventral view

PLATE 5

Eurhinodelphinidae aff. *Schizodelphis* IRSNB 8343Z-M.1860, from Kessel, Antwerp Sands, late early to middle Miocene. A. dorsal view. B. posterior view. Scale bar = 100 mm.

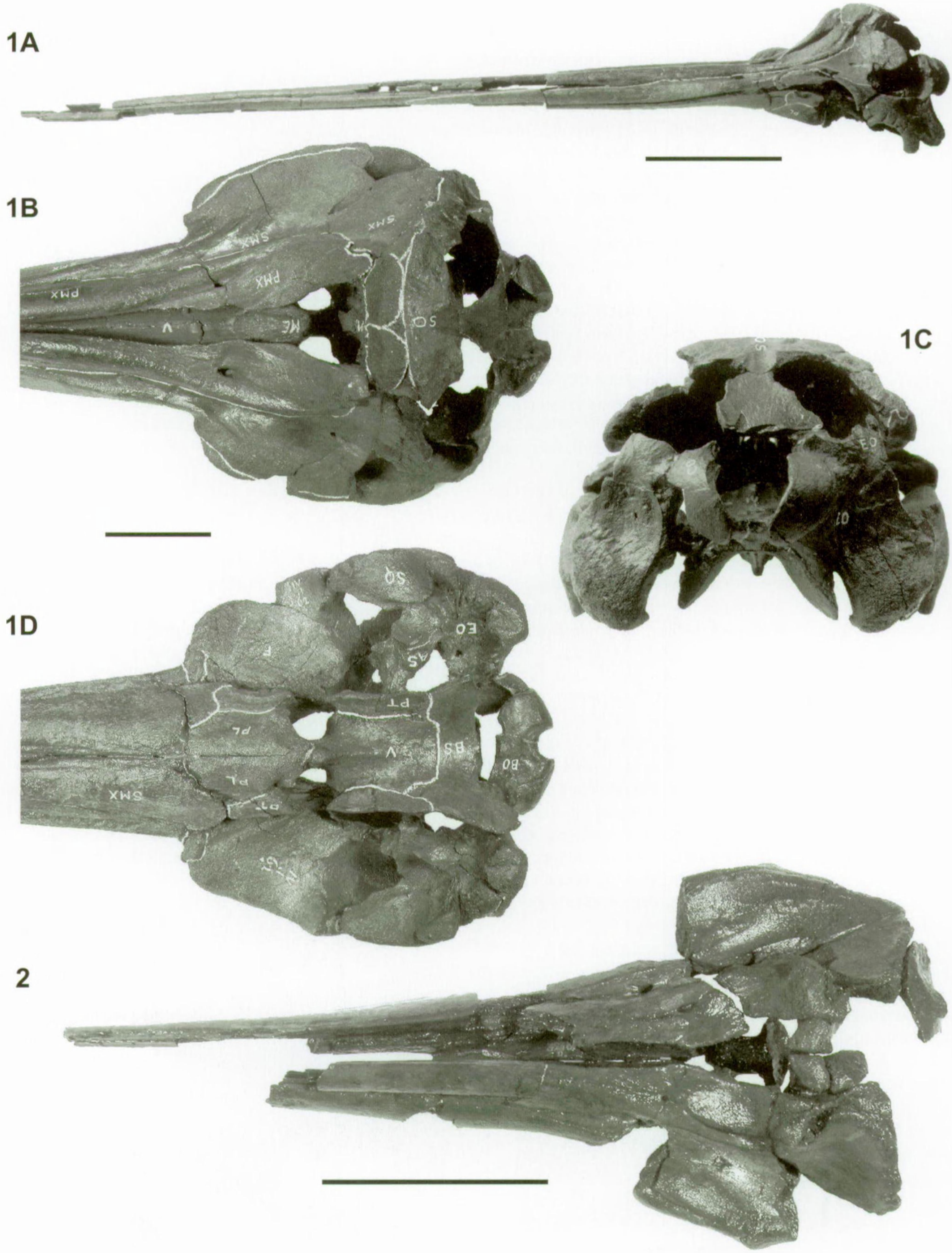
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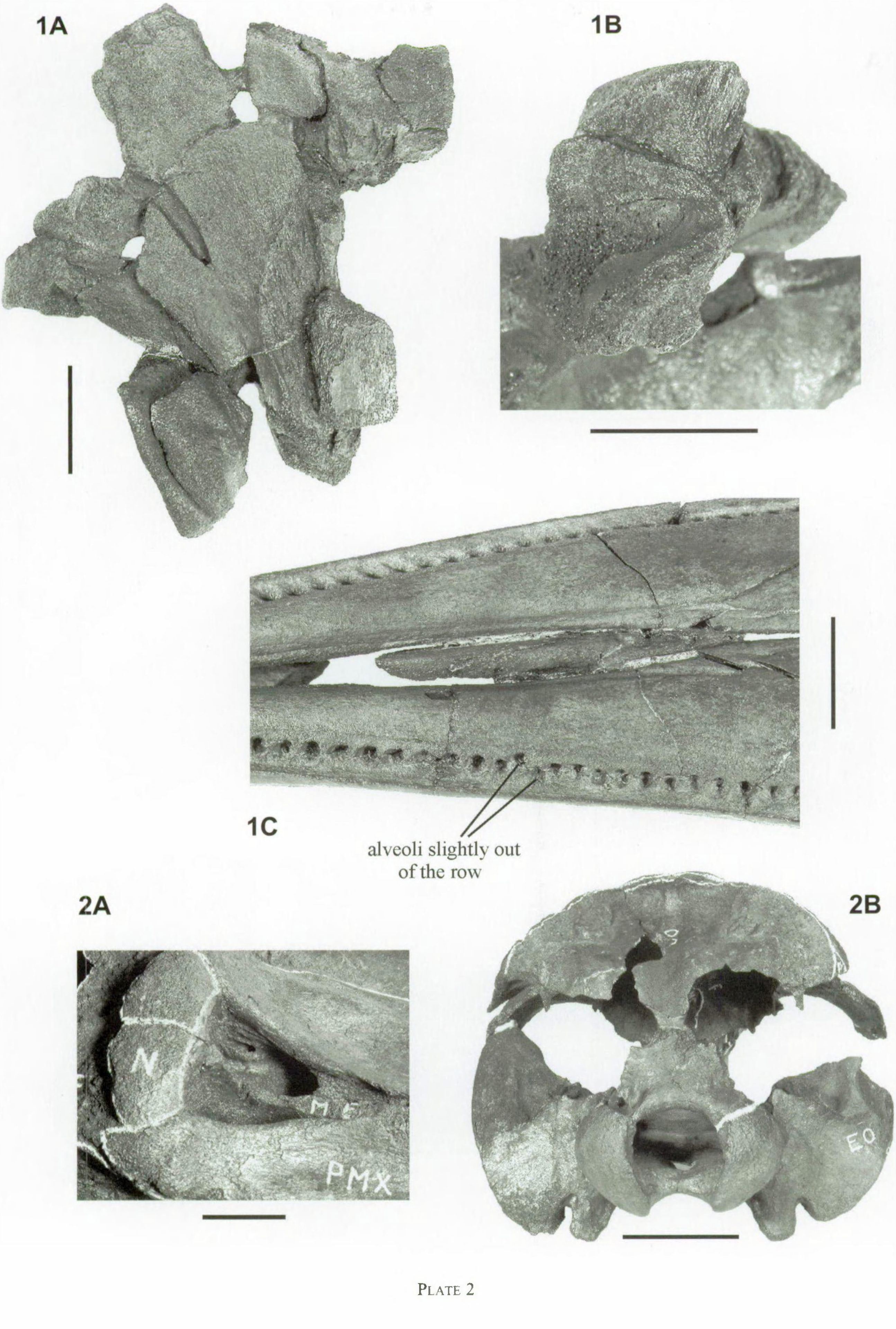
PLATE 1



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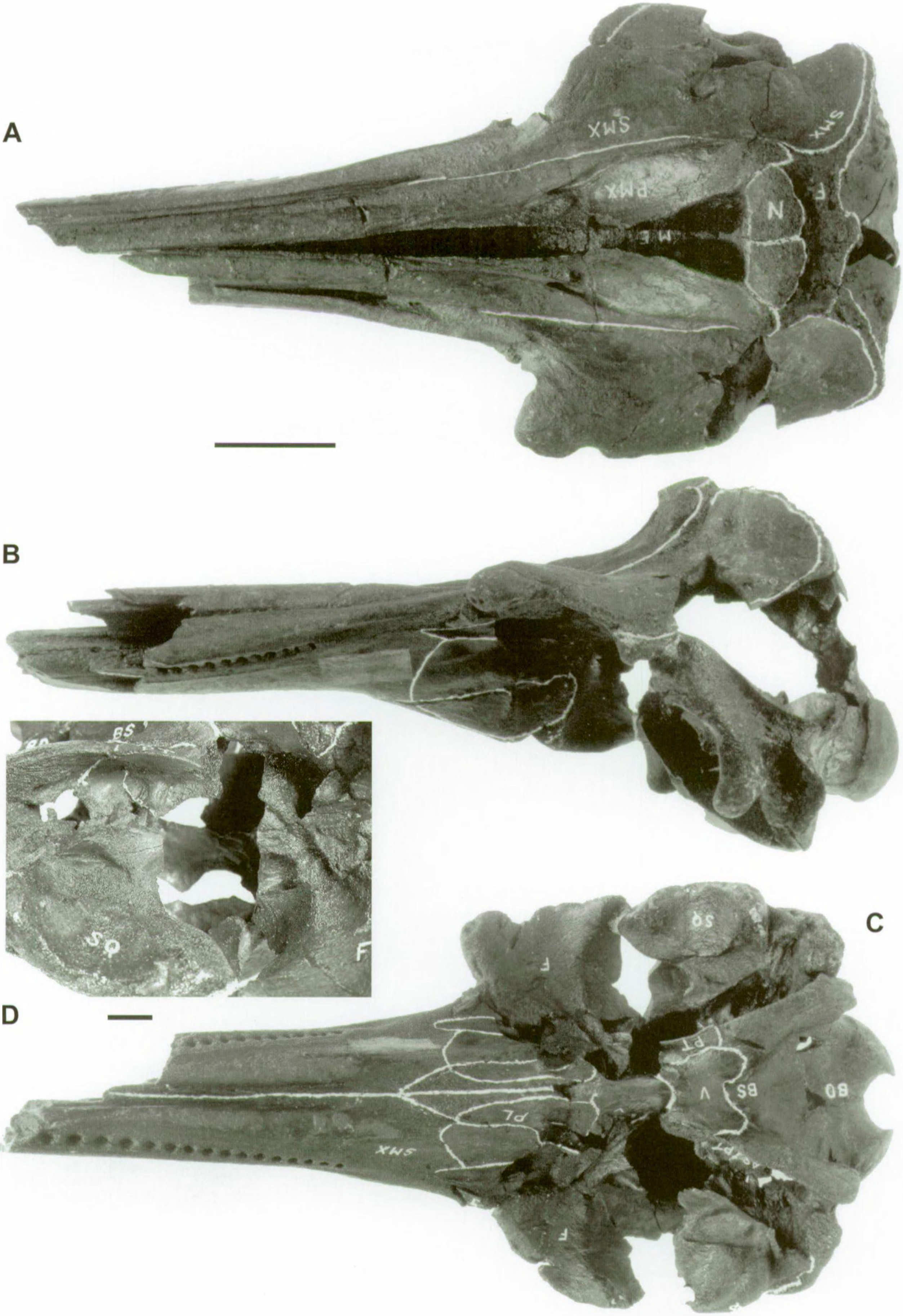

PLATE 3

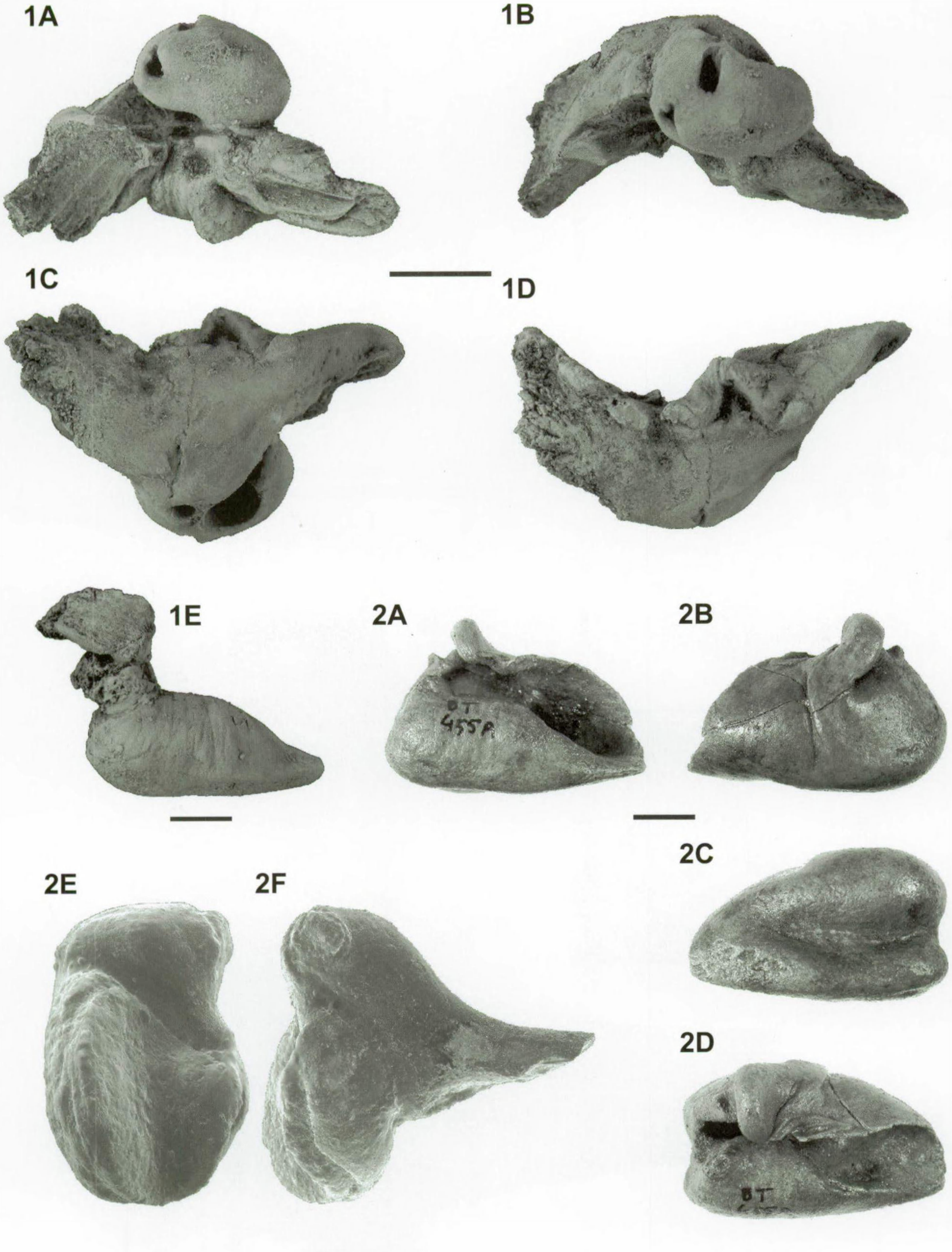

PLATE 4

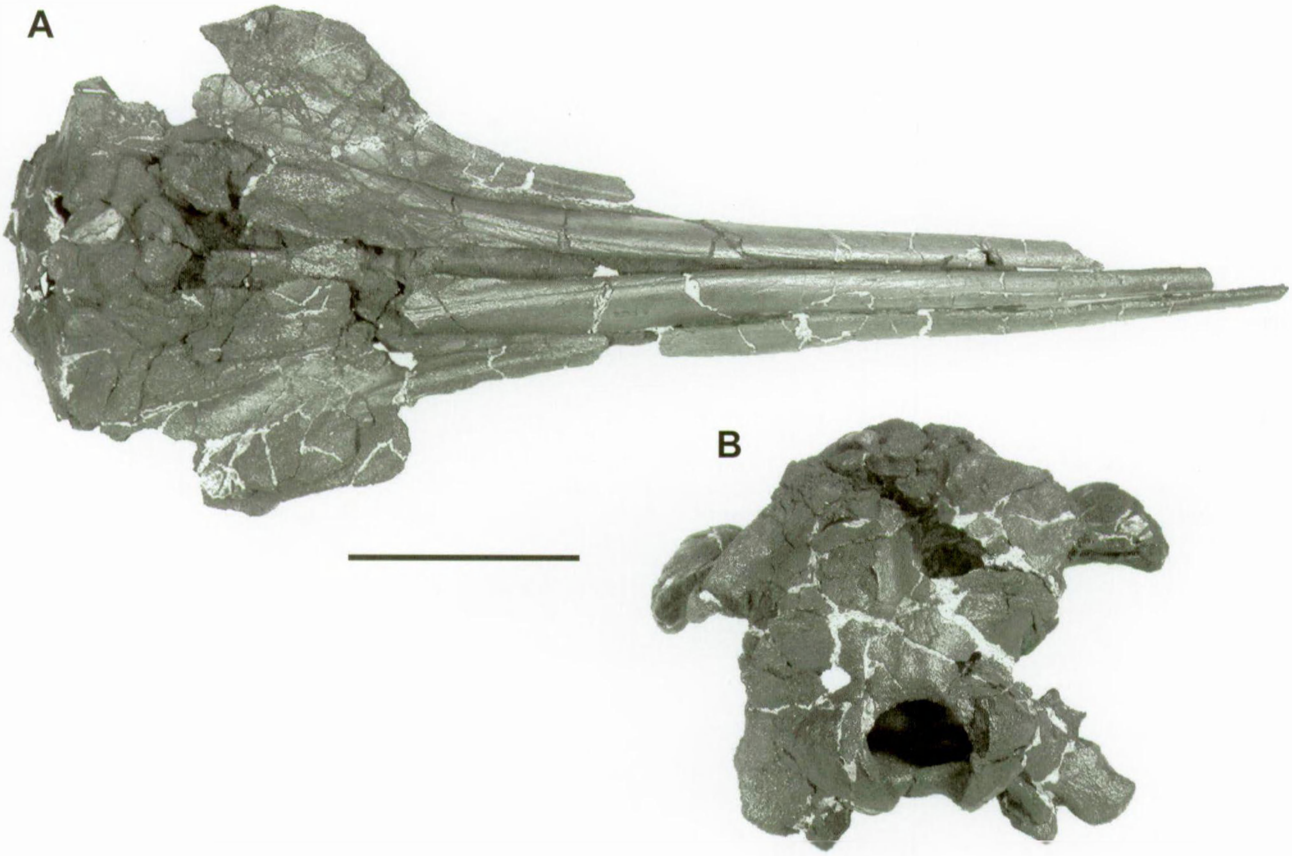

PLATE 5