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PHYLOGENETIC AFFINITIES OF THE LONG-SNOUTED DOLPHIN *EURHINODELPHIS* (CETACEA, ODONTOCETI) FROM THE MIOCENE OF ANTWERP, BELGIUM

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Abstract: A new skull belonging to the species *Eurhinodelphis cocheteuxi* (Cetacea, Odontoceti, Eurhinodelphinidae), found in the upper Lower–Middle Miocene of Antwerp (Belgium, southern margin of the North Sea Basin) associated with its ear bones (periotic, tympanic bullae, malleus and incus), is the basis of a redescription and systematic revision of the species. This species is then used as an isolated taxon in a phylogenetic study of extinct and extant odontocetes. The main results of the cladistic analyses are: a sister-group relationship between *E. cocheteuxi* and the extant family Ziphiidae (beaked whales), and a more basal position of the superfamily Physeteroidea (sperm whales) in the tree. The possible paraphyly of the family Eurhinodelphinidae needs further investigation. The results are compared with the most recent morphological and molecular analyses. The species *E. bossi*, described in the Miocene of Maryland (east coast of the USA, Calvert Formation) is recognized in the Miocene of Belgium for the first time.

Key words: *Eurhinodelphis*, Eurhinodelphinidae, Cetacea, Miocene, taxonomy, phylogeny.

THE building of fortifications around the Belgian city of Antwerp during the second part of the nineteenth century yielded huge quantitites of marine mammal bones from the Neogene (e.g. Van Beneden 1861*b*; Abel 1905). In 1867, du Bus briefly described the skull of a dolphin with a very long rostrum, the anterior two-fifths occupied by the edentulous premaxillae alone. He named it *Eurhinodelphis cocheteuxi*, in honour of captain Cocheteux, assigned to the construction of the 'Fort du Vieux-Dieu'. Besides this species, he described many additional species of small dolphin-like odontocetes (du Bus 1872), but without figures and with poor diagnoses. Some skulls were figured in the Ostéographie (Van Beneden and Gervais 1880). At the beginning of the twentieth century, Abel began a revision of the odontocetes from the Neogene of Antwerp. In 1901 and 1902, he redescribed and figured three species of *Eurhinodelphis*, *E. cocheteuxi*, *E. cristatus* and *E. longirostris*, including within these taxa most of the species of du Bus (1872). Abel (1901) created the family Eurhinodelphidae (Eurhinodelphinidae following the recommendations of Rice 1998) which, at that time, included the single genus *Eurhinodelphis*. These works were only based on cranial material; in 1931, Abel studied the skeleton of the eurhinodelphids of Antwerp and tried to link the huge scattered range of postcranial bones to the skulls of the different species. The species *E. cocheteuxi* has never been found with certainty anywhere else other than in the area of Antwerp.

In 1925, Kellogg described *Eurhinodelphis bossi* from the Middle Miocene of eastern North America. The thesis of Myrick (1979) on the eurhinodelphinids from the Calvert Formation, Lower–lower Middle Miocene of the mid-Atlantic coastal plain of North America, identified there the species *E. cristatus* and *E. longirostris* (placed by him in the genus *Rhabdosteus*) and created several additional species referred to the genera *Eurhinodelphis* and *Rhabdosteus*. Because the thesis was never published, I will not take into account his systematic conclusions, except the names validated by Muizon (1988*a*). In 1985, Pilleri described two new species of *Eurhinodelphis* from the Miocene sandstones of Belluno, north-east Italy, *E. sigmoideus* and *E. bellunensis*. In his revision of the Acrodelphinidae, Muizon (1988*a*) suggested placing *E. longirostris* in *Schizodelphis*, and regarded *Rhabdosteus* as *incertae sedis*.

The family Eurhinodelphinidae currently contains the following genera for which enough information is available for diagnosis: *Argyrocetus* Lydekker, 1893, *Eurhinodelphis* du Bus, 1867, *Macrodelphinus* Wilson, 1935, *Schizodelphis* Gervais, 1861, and *Ziphiodelphis* Dal Piaz, 1908 (Muizon 1990). All of these are from Miocene strata. The stratigraphic range of Eurhinodelphinidae might be extended by the existence, in the upper Oligocene of the Caucasus, of *Iniopsis* Lydekker, 1892, a probable eurhinodelphinid, but which is too poorly known to establish its affinities securely (Muizon 1990). Very little information is also available for *Allodelphis* Wilson, 1935 and *Protodelphinus* Dal Piaz, 1916. Fordyce (1983) provided some indications about fragmentary specimens that were provisionally identified as eurhinodelphinids.

The only figured and published periotics of well-identified eurhinodelphinids are those of *Ziphiodelphis abeli* in Dal Piaz (1977), and of *Schizodelphis barnesi* and *S. longirostris* in Muizon (1988*a*), where mallei of *S. sulcatus* and *Eurhinodelphis bossi* are also figured. The present paper focuses on the redescription of a new skull of *E. cocheteuxi*, associated with tympanic bullae, one periotic, one malleus and one incus. These elements together with the good state of preservation of the palate of this skull allow use of *E. cocheteuxi* as an isolated taxon in a phylogenetic study of the odontocetes, the position of the eurhinodelphinids being yet unresolved (Fordyce 1994). The species *E. bossi*, previously only known from the Calvert Formation, upper Lower–Middle Miocene of the east coast of the USA, is identified in Belgium (Antwerp Sands).

MATERIAL AND METHODS

Terminology and measurements. Terminology for cranial, postcranial and ear bone anatomy is mainly taken from Fordyce (1994), Heyning (1989), Kasuya (1973), Kellogg (1927) and Muizon (1984, 1987, 1988*a*–*c*). The orientations of the tympanic bulla and the periotic are simplified in the following descriptions, compared to the actual anatomical position in the skull. The long axis of the tympanic is considered as anteroposteriorly orientated, with the ventral surfaces of the lateral and medial lobe indicating the horizontal plane. The anterior direction of the periotic is given by the longitudinal axis of the anterior process, the horizontal ventral plane by the surface contacting the more ventral points of the pars cochlearis and anterior process. For explanation of the measurements, see Text-figure 1 and Table 1.

Abbreviations. AMNH, American Museum of Natural History, New York, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; M, fossil mammal collection of types and figured specimens at the IRSNB; MGPD, Museum of Geology and Palaeontology of Padova, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA; ZMA, Zoological Museum of Amsterdam, The Netherlands.

SYSTEMATIC PALEONTOLOGY

Order CETACEA Brisson, 1762
Suborder ODONTOCETI Flower, 1864
Superfamily EURHINODELPHINOIDEA Muizon, 1988*a*
Family EURHINODELPHINIDAE Abel, 1901

Type genus. Eurhinodelphis du Bus, 1967.

Included genera. Argyrocetus Lydekker, 1894, *Eurhinodelphis*, *Macrodelphinus* Wilson, 1935, *Schizodelphis* Gervais, 1861, and *Ziphiodelphis* Dal Piaz, 1908.

Remarks. The main derived character defining the family, the extreme elongation of the edentulous premaxillary part of the rostrum, is only clearly observed in *Eurhinodelphis*, *Schizodelphis* and *Ziphiodelphis*, and suggested in *Argyrocetus* and *Macrodelphinus*. Pending additional observations on the genera *Allodelphis* Wilson, 1935, *Iniopsis* Lydekker, 1892 and *Protodelphinus* Dal Piaz, 1916 (usually or sometimes considered as eurhinodelphinids; see Muizon 1990), or the discovery of new characters for the family Eurhinodelphinidae, those genera cannot certainly be included in the family.

Genus EURHINODELPHIS du Bus, 1867

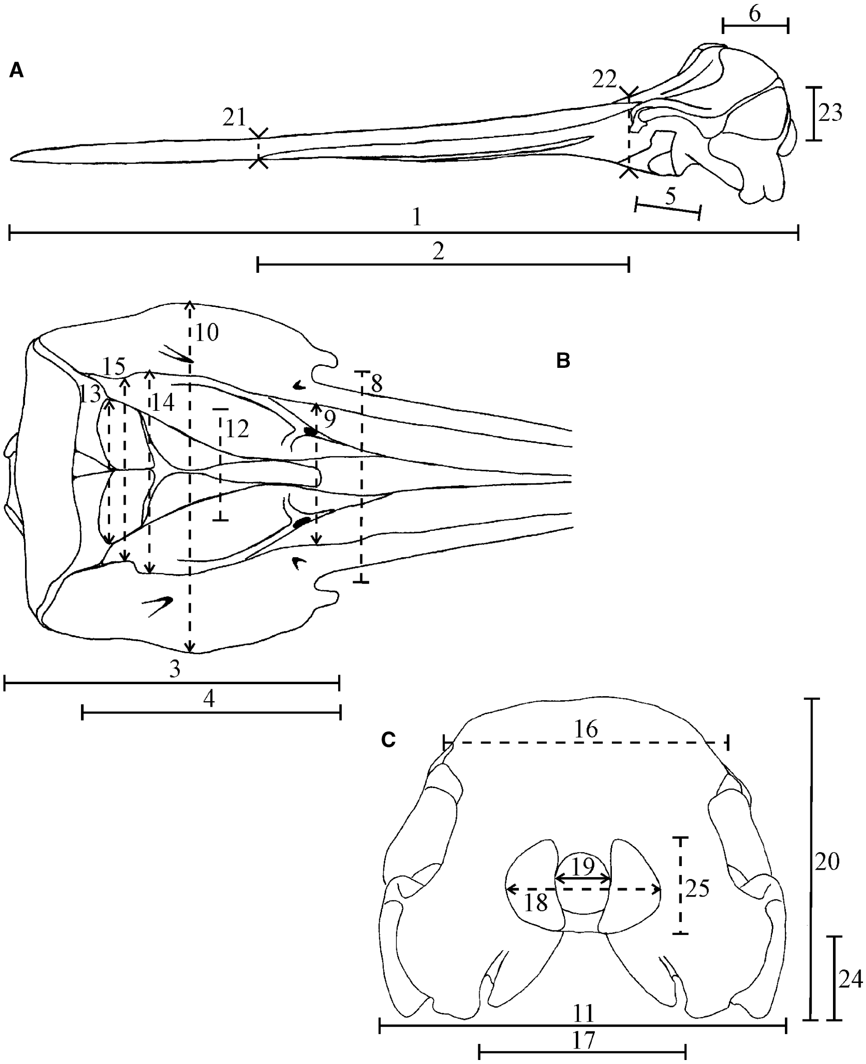
Type species. Eurhinodelphis cocheteuxi du Bus, 1867.

Included species. Eurhinodelphis bellunensis Pilleri, 1985, *E. bossi* Kellogg, 1925, *E. cocheteuxi*, *E. cristatus* (du Bus, 1872), and *E. sigmoideus* Pilleri, 1985.

Remarks. The genus *Eurhinodelphis* clearly needs revision. This taxon seems to be mainly defined by its larger size relative to *Schizodelphis*. As a result of the redescription of the type species *Eurhinodelphis cocheteuxi* here, it appears that *E. cristatus* and *E. bossi* might be more closely related to species of *Schizodelphis* than to *Eurhinodelphis cocheteuxi*, with similarities at the level of the vertex and basicranium. The Italian species *E. sigmoideus* and *E. bellunensis* also have to be revised. For example, the lateral view of *E. sigmoideus* is strikingly close to *Ziphiodelphis abeli*. This problem will be discussed further in a forthcoming paper.

Eurhinodelphis cocheteuxi du Bus, 1867
Text-figures 2–10, 12–13

Holotype. IRSNB 3252-M.294, found September 13, 1861, individual I of Abel (1901) (pls 6–8; pl. 9, fig. 1; pl. 10, figs 1, 3–4), a skull lacking the teeth, the ear bones and some pieces of basicranium.



TEXT-FIG. 1. Description of the measurements on the skull of *Eurhinodelphis*, outlines of the holotype of *E. cocheteuxi* IRSNB 3252-M.294. A, left lateral view. B, dorsal view. C, posterior view.

Type locality. Fort no. 4, Vieux-Dieu, Antwerp (Abel 1901), 51°10′11″N, 4°27′25″E. All of the specimens cited above were found in the same place, between September 1861 and September 1863, except IRSNB M.1856.

Horizon. Antwerp Sands, late early Miocene–middle Miocene, possibly latest Burdigalian to middle Serravalian (see discussion in Louwye *et al.* 2000). Radiometric analyses on the glauconite of the Antwerp Sands provided an age of 21·5–18·5 Ma with Rb–Sr and 25–20 Ma with K–Ar (Odin *et al.* 1974; Odin and Kreuzer 1988).

Referred specimens. IRSNB M.1856, discovered by R. Marquet in 1976 during the excavations of a metro station at Pelikaanstraat, Antwerp, in the inferior part of the Antwerp Sands, below the first *Glycymeris* bed (R. Marquet, pers. comm. 2001), a skull associated with both tympanic bullae, the right periotic and corresponding malleus and incus, lacking the distal part of the rostrum, some fragments of basicranium and all the teeth; partial skull IRSNB 3232-M.295 (individual IV of Abel 1902), associated with a fragment of ramus of the mandible, the right humerus (Abel 1931, pl. 28, figs 3, 8), a fragment of cervical vertebra, two thoracic vertebrae, six lumbars, one caudal, a vertebral epiphysis and 13 ribs (some of the vertebrae and ribs figured by Abel 1931, who also figured an atlas, pl. 19, fig. 4, which was not found in the collection); skull IRSNB 3253-M.296 (individual III of Abel 1902), with a complete and ventrally bent rostrum (section of the rostrum and palate figured in Abel 1901, text-fig. 15, pl. 10, fig. 2); partial cranium IRSNB 3256-M.1857 (individual II of Abel 1902); basicranium IRSNB 3255-M.297 (individual VI of Abel 1902), posterior part of braincase and inner occipital crest (figured in Abel 1901, text-figs 16–17, pl. 9, fig. 2); left part of basicranium IRSNB 3403-M.299 (individual VII of Abel 1902), associated with a right humerus (figured by Abel 1931, pl. 28, figs 9, 12); IRSNB 3254, partial rostrum, right squamosal and fragment of the roof of orbit (individual V of Abel 1902).

TABLE 1. Measurements on the skulls of *Eurhinodelphis cocheteuxi*. Measurements are in millimetres: e, indicates estimate; +, nearly complete; –, no data.

Measurements on the skulls of *Eurhinodelphis cocheteuxi*	Holotype IRSNB 3252-M.294	IRSNB M.1856	IRSNB 3232-M.295	IRSNB 3256-M.1857	IRSNB 3253-M.296
1. total length skull	+1074	–	–	–	–
2. length base rostrum-anterior maxilla	516	–	–	–	–
3. length anterior orbit-posterior skull	255	e255	–	–	e275
4. length anterior supraoccipital-anterior orbit	172	157	162	180	153
5. length orbit	121	84	94	92	95
6. length temporal fossa	110	–	–	–	–
7. width rostrum anterior maxillae	29	–	26	–	–
8. width base rostrum	e158	144	–	134	160
9. width premaxillae base rostrum	104	102	–	103	117
10. width skull postorbital processes	276	+251	–	247	286
11. width skull zygomatic processes	274	–	–	–	320
12. width bony nares	68	68	55	–	–
13. width nasals	90	92	e66	–	–
14. maximal posterior premaxillary width	140	126	122	126	139
15. minimal posterior distance between maxillae	114	120	90	96	e112
16. width skull junction supraocc.-frontal-parietal	186	165	–	–	–
17. width medio-ventral margins exoccipitals	136	e132	–	–	143
18. width lateral margins occipital condyles	99	102	–	96	102
19. width inner margins occipital condyles	34	e38	–	37	35
20. height cranium	219	e209	–	–	–
21. height rostrum at anterior maxillae	29	–	26	–	–
22. height base rostrum	89	79	–	87	91
23. height temporal fossa	65	–	–	–	–
24. height ventral margin occipital condyles	63	48	–	–	65
25. height occipital condyles	60	63	–	–	–

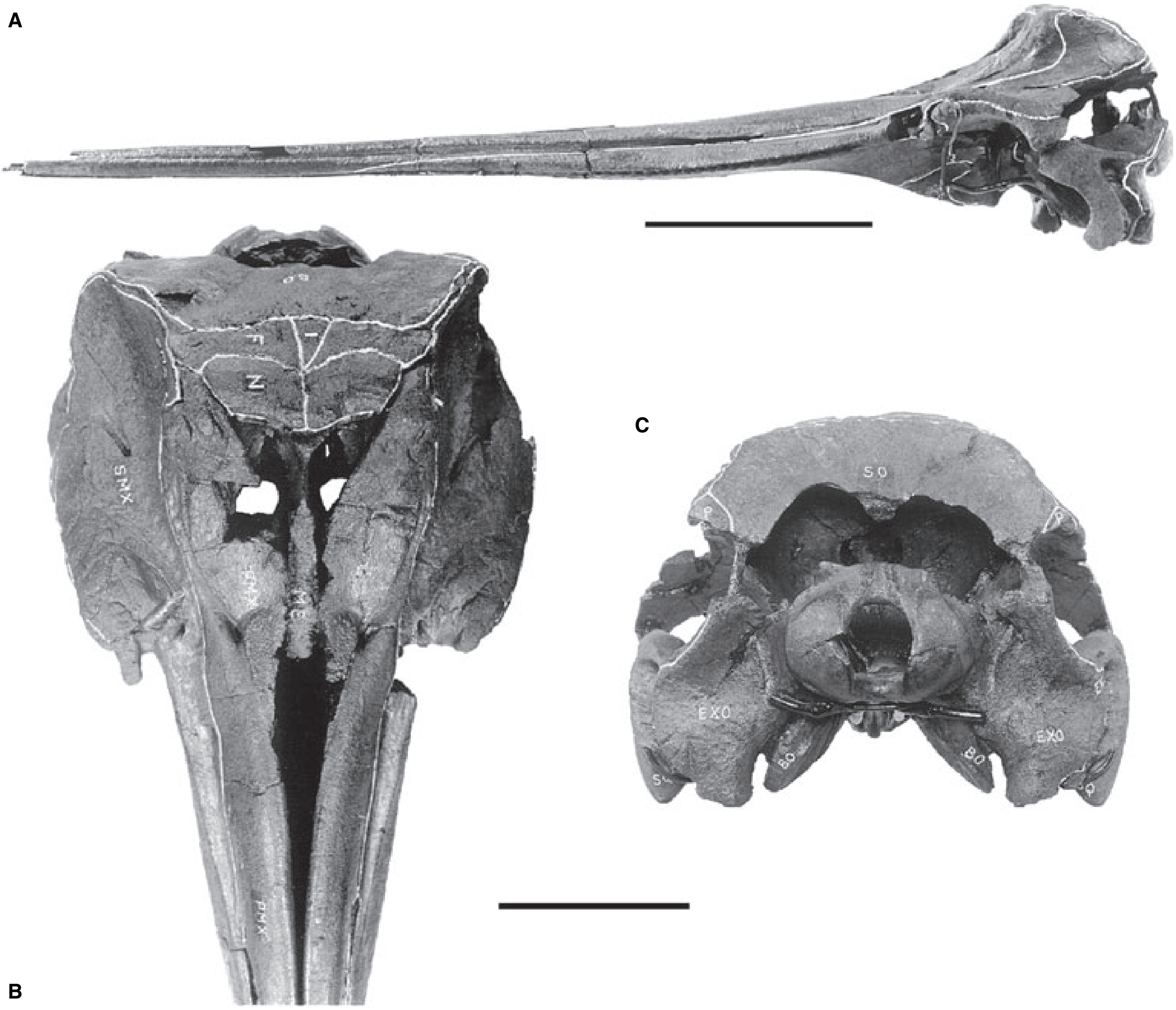
Emended diagnosis. This large species, with a skull close in size to *Ziphiodelphis abeli*, is characterized by the following unique combination of characters: wide rectangular vertex formed by the prominent nasals, wider than long, the frontals and the wide posterior projection of the premaxillae contacting the frontals and forming distinct transverse premaxillary crests; vertex laterally limited by vertical concave plates of maxillae dorsoanteriorly extended along the wide apices of the premaxillae; posterior margins of the maxillae extending posteriorly beyond the posterior limit of the vertex; vertical transverse plate of the mesethmoid almost reaching the highest point of the vertex; great reduction of the lateral lamina of pterygoid, probably not contacting the anterolaterally deflected falciform process of the squamosal. A complete lateral lamina of the pterygoid in contact with an anteromedially directed falciform process of the squamosal is observed in *Eurhinodelphis cristatus* and *E. bossi*. The lateral lamina is lost in *E. sigmoideus* but the falciform process is also anteromedially directed.

This species is larger, with a relatively wider vertex and wider nasals, than *Eurhinodelphis bellunensis*, *E. bossi*, *E. cristatus* and *E. sigmoideus*. The dorsomedian portion of the occipital shield is flat or slightly convex, posteriorly sloping, contrary to the concave and often roughly vertical upper part of the shield in *E. bossi* and *E. cristatus*.

Description of the holotype

General aspect. This well-preserved skull shows a very elongated rostrum forming more than 75 per cent of the total length of the skull (Table 1). The base of the rostrum is robust, and the cranium is wide, with a distinctly elevated and wide rectangular vertex (Text-figs 2–3).

Dorsal view. The rostrum is nearly complete. Its tip is made of the premaxillae alone for a length of more than 325 mm. The posterior separation of the premaxillae begins 200 mm anterior to the base of the rostrum, where the premaxillae also become flatter, forming two dorsolaterally orientated plates, separated by 27 mm at the level of the antorbital notches. At this level, a wide infraorbital foramen is present on the premaxilla, at the junction of slight anteromedian, posterolateral and posteromedian sulci, isolating a median, triangular and very roughened surface (probably part of the area of insertion of nasal plug muscles; Mead 1975). The posterolateral sulcus limits laterally a wide, smooth

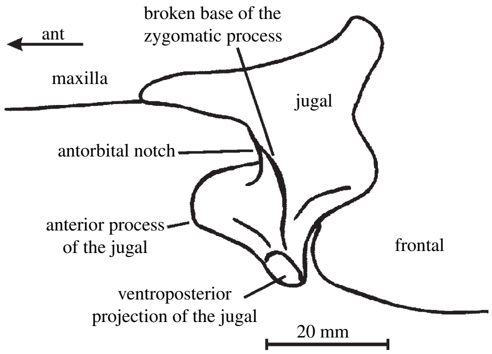


TEXT-FIG. 2. Skull of the holotype of *Eurhinodelphis cocheteuxi* IRSNB 3252-M.294, from the Miocene of Antwerp. A, left lateral view. B, dorsal view of the face. C, posterior view. The labels were drawn on the skull at the time of Abel. bo, basioccipital; exo, exoccipital; i, interparietal; me, mesethmoid; n, nasal; p, parietal; pmx, premaxilla; smx, maxilla (old French name = susmaxillaire); so, supraoccipital; sq, squamosal. Scale bar for A represents 200 mm, for B and C, 100 mm.

and weakly concave premaxillary sac fossa, dorsally recurving towards the vertex. The sulcus disappears at some distance from the vertex. The closest distance between the median margins of the two premaxillary sac fossae is 15 mm, keeping the mesethmoid uncovered. The posterior extremity of the premaxilla is a wide ascending process that reaches the frontal, wedging between the medial vertical plate of the maxilla and the nasal.

The dorsal exposure of the maxilla widens posteriorly; it is still narrower than the premaxilla until the base of the rostrum. The antorbital notch is deep, isolating a lateral, anteriorly projecting finger-like antorbital process of the maxilla (length 15 mm). This process widens posteriorly, forming a slightly elevated dome on the anterior part of the roof of the orbit. This elevation, however, is lower than the median margin of the premaxillary sac fossa. Two dorsal infraorbital foramina pierce the right maxilla at the level of and 50 mm anterior to the antorbital notch. A larger foramen is present at the centre of the supraorbital process of each maxilla. The maxilla totally covers the frontal above the orbit and nearly closes the roof of the temporal fossa. The maxilla is posteriorly very long, extending back beyond the anterior level of the supraoccipital. Medially, the maxilla becomes concave, steepens and adopts a vertical position against the lateral margin of the vertex, extending dorsoanteriorly and slightly laterally along the extremity of the premaxilla. This condition is more pronounced than in *Waipatia* from the Upper Oligocene of New Zealand, and shows interesting similarities with *Notocetus marplesi*, also from the uppermost Oligocene of New Zealand (see Fordyce 1994, fig. 16e); it is tentatively regarded as homologous to the higher lateral margins of the synvertex (Heyning 1989) of ziphiids.

The nodular large nasal is roughly parallelogram-shaped, wider than long, with a convex and roughly horizontal dorsal surface constituting the highest point on the vertex. Its anteromedian angle projects forward, and a short anterior process of



TEXT-FIG. 3. Line drawing of the detail of the right antorbital notch of the holotype of *Eurhinodelphis cocheteuxi* IRSNB 3252-M.294, from the Miocene of Antwerp, in ventral view, showing the long ventroposterior projection of the jugal.

the frontals wedges between the posteromedian angles of the two nasals. The nearly complete, strongly keeled, vertical plate of the mesethmoid is appressed against the anterior border of the nasals, nearly until their top.

The frontal is shorter, wider and slightly lower than the nasal on the vertex. Its dorsal surface is more irregular. The two frontals are medially separated by a triangular bone, probably the interparietal (R. E. Fordyce, pers. comm. 2003), which is also observed on the vertex of some delphinids and ziphiids (Geisler *et al.* 2000), but with strong individual variation. The frontal has a wide contact with the premaxilla anterolaterally, and is only visible on a narrow and prominent crest between the maxilla and supraoccipital in a posterolateral direction. This narrow strip forms a distinct obtuse angle with the rectilinear posterior margin of the vertex. The skull is slightly asymmetrical; the premaxillary sac fossae are the same width but the right nasal is 3 mm wider than the left, and the suture between the nasals is slightly deviated to the left relative to the internal occipital crest.

The flat supraoccipital shield is hollowed by two circular depressions on its dorsolateral corners, possible areas of origin for the m. semispinalis or longissimus capitis (see Pabst 1990, on *Tursiops*). The supraoccipital is at an angle of *c.* 45 degrees with a vertical plane. In a dorsal view, the parietal appears as a posteriorly orientated small triangle occupying the dorsoposterior margin of the temporal fossa. The occipital condyles do not strongly protrude posteriorly and their condylar pedicle is poorly pronounced.

Lateral view. A deep longitudinal groove hollows the lateral face of the rostrum from 155 mm anteriorly to the antorbital notch, where it appears to be the anterior extension of a foramen which progressively opens laterally. The height of the groove increases forwards as its depth progressively reduces. It totally disappears within a few centimetres of the preserved tip of the rostrum. The lateral suture between the maxilla and premaxilla leaves the groove, runs ventrally and passes to the ventral face of the rostrum 520 mm anterior to the antorbital notch. On the roof of the orbit, the maxilla and frontal are the same thickness except for a thicker anterior lobe and massive postorbital process of the frontal. The orbit is long and little arched, lower than the roof of the temporal fossa.

The lacrymal-jugal complex extends in a thin posterior projection between maxilla and frontal. The jugal ventrally duplicates the finger-like anterior projection of the maxilla, lateral to the antorbital notch. Additionally, the jugal sends a short and robust ventroposteriorly directed projection, lateral to the base of the zygomatic process (Text-fig. 3).

The postglenoid process of the squamosal is slightly less robust than the zygomatic process. The latter is high and wide, and its dorsal edge extends posteriorly in a sharp crest at the lateral margin of the widely excavated bottom of the temporal fossa. Posterior to the zygomatic process, two deep fossae incise the lateral face of the squamosal along the suture with the paroccipital process of the exoccipital (insertion of sternomastoideus and/or other facial muscles; see review in Fordyce 1994). The postglenoid process is distinctly rounded with an expanded apex. The wide external auditory meatus separates this process from a reduced posterior part of the squamosal (post-tympanic process), partially covered by the curved paroccipital process of the exoccipital, which is anterolaterally recurved under the temporal fossa.

Ventral view. The tip of the rostrum is made of the joined premaxillae only, for more than 320 mm. The ventral face of the premaxilla is hollowed by a deep longitudinal groove which lacks alveoli. Ninety millimetres anterior to the antorbital notches, the maxillae are separated by an anteriorly widening fenestra showing the robust ventral keel of the vomer, with a maximum width of 21 mm. More anteriorly, the vomer is wedged between the premaxillae for approximately 80 mm. The alveoli for the maxillary teeth are distinct, slightly eroded, with a diameter of 8–10 mm and septa 4–5 mm thick. There are more than 32 alveoli on the right and more than 31 on the left side. The most posterior ones are poorly preserved and the first anterior ones are less pronounced. The lateral edge of the tooth row is thin, sharp and rectilinear, upturning towards the antorbital notch posteriorly.

The palate is transversely compressed, forming a wide and robust keel. The palatines are short and do not extend anteriorly more than 30 mm beyond the antorbital notches. They are separated anteriorly by a short posterior projection of the maxillae and posteriorly by the vomer for a length of 45 mm. Their lateral margins strongly diverge posteriorly up to a triple point considered by Abel (1901, pl. 7) as the junction of palatine, maxilla and pterygoid. This part is better preserved on the paratype and is described below. The palatine is excavated by a short and deep fossa for the pterygoid sinus, just anterior to the choana, nearly reaching the orbit ventrally, but several centimetres posterior to the level of the antorbital notch. Right and left fossae are separated by 16 mm of palatine and vomer. The part of the pterygoid anterior to the choana is missing. No lateral lamina of the pterygoid or palatine is preserved and the falciform process of the squamosal is broken. The choanae are wide, with a vertical and slightly diverging ventral part, and a dorsal part more clearly posteriorly directed, converging towards the external nares.

In ventral view, the jugal is U-shaped, its ventral crest surrounding the antorbital notch. No trace of the lacrymal is visible. It is either missing or fused to the frontal. The large infraorbital foramen between the palatine and frontal extends anterolaterally and posteromedially in a wide sulcus. The ventral face of the roof of the orbit is smooth like the roof of the temporal fossa; those two surfaces are separated by an unexcavated postorbital ridge (the ridge is, for example, deeply excavated by a fossa for the postorbital lobe of the pterygoid sinus in *Eurhinodelphis cristatus*). The orbitosphenoid presents a narrow groove directed towards the cranial cavity that might be the dorsal part of the orbital foramen. The alisphenoid is poorly preserved but a smooth concave medioanteroventrally facing surface is present on both alisphenoids. This is interpreted as a wide pterygoid sinus fossa located close to the roof of the orbit, but probably not contacting it. The glenoid fossa of the squamosal is wide and long. It is medially limited by a shallow and narrow tympanosquamosal recess (Fraser and Purves 1960) for the middle pterygoid sinus, which tapers and ends 40 mm before the tip of the zygomatic process, and is only present on the inner side of the postglenoid process for a short distance. No basicranium foramina are preserved on this skull. The thick basioccipital crest extends the median lamina of the pterygoid and diverges posteriorly, thus widening the basioccipital basin. The ventral margin of the exoccipital is strong and prominent between the basioccipital crest and the squamosal, rolled up like a vertical cylinder.

Description of the referred specimen IRSNB M.1856

This skull provides additional information on the tympanic bulla, periotic and malleus, and on the morphology of the palate. The main anterior part of the rostrum, a fragment of the left premaxillary sac fossa, and fragments of the basicranium are missing, but the preserved surfaces are less eroded than on the holotype.

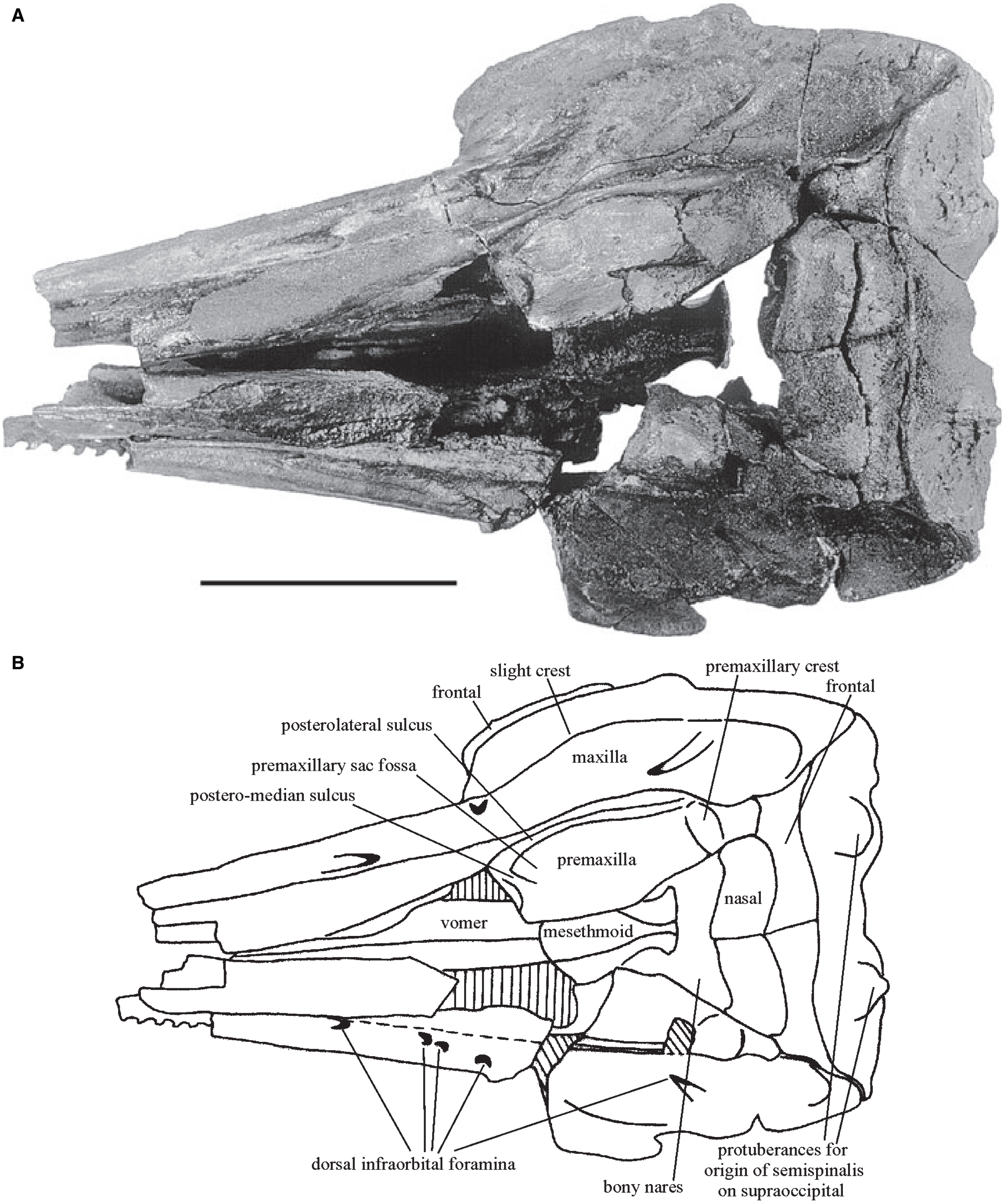
Dorsal view (Text-fig. 4). The premaxilla is poorly preserved but the premaxillary sac fossa is long and wide. The ascending process of the premaxilla is stongly steepened and presents a wide apex wedged between maxilla and nasal, contacting the frontal as on the holotype. The posterolateral sulcus, which borders the premaxillary sac fossa laterally, nearly reaches the vertex. As a result, the transverse thickening of the premaxilla just before the posterior projection is better defined. This transverse crest gives a T shape to the posterior process of the premaxilla and can be compared to the more pronounced premaxillary crest of the ziphiids [e.g. *Mesoplodon* or the fossil *Ziphirostrum* (= *Mioziphius* Abel 1905)], but also of the strange ziphiid-like delphinid *Australodelphis*, from the Pliocene of East Antarctica (Fordyce *et al.* 2002).

There are at least three dorsal infraorbital foramina piercing the maxilla anterior to and at the level of the antorbital notch on the right side of the skull, and four on the left. A slight crest extends from the lateral margin of the rostrum onto the supraorbital process. It curves slightly lateroposteriorly and runs posteriorly 30 mm medially to the lateral edge of the supraorbital process. This crest probably corresponds to the lateral edge of the surface of insertion of the pars anterointernus facial muscle (Heyning 1989). A crest stronger, but similar in its position, is present in *Pontoporia*, and more laterally in *Inia*. The supraorbital process of the maxilla is also long and relatively narrow, extending more than 20 mm beyond the anterior margin of the supraoccipital, with the same median vertical plate against the ascending process of the premaxilla and the frontal, as in the holotype.

The nasals are wide and short. They protrude anteromedially and bear a small anterolateral triangular projection. The frontals are slightly shorter, lower and much wider than the nasals on the vertex. On this skull, the subcircular shallow depression in the dorsolateral angle of the supraoccipital is ventrally limited by a strong protuberance.

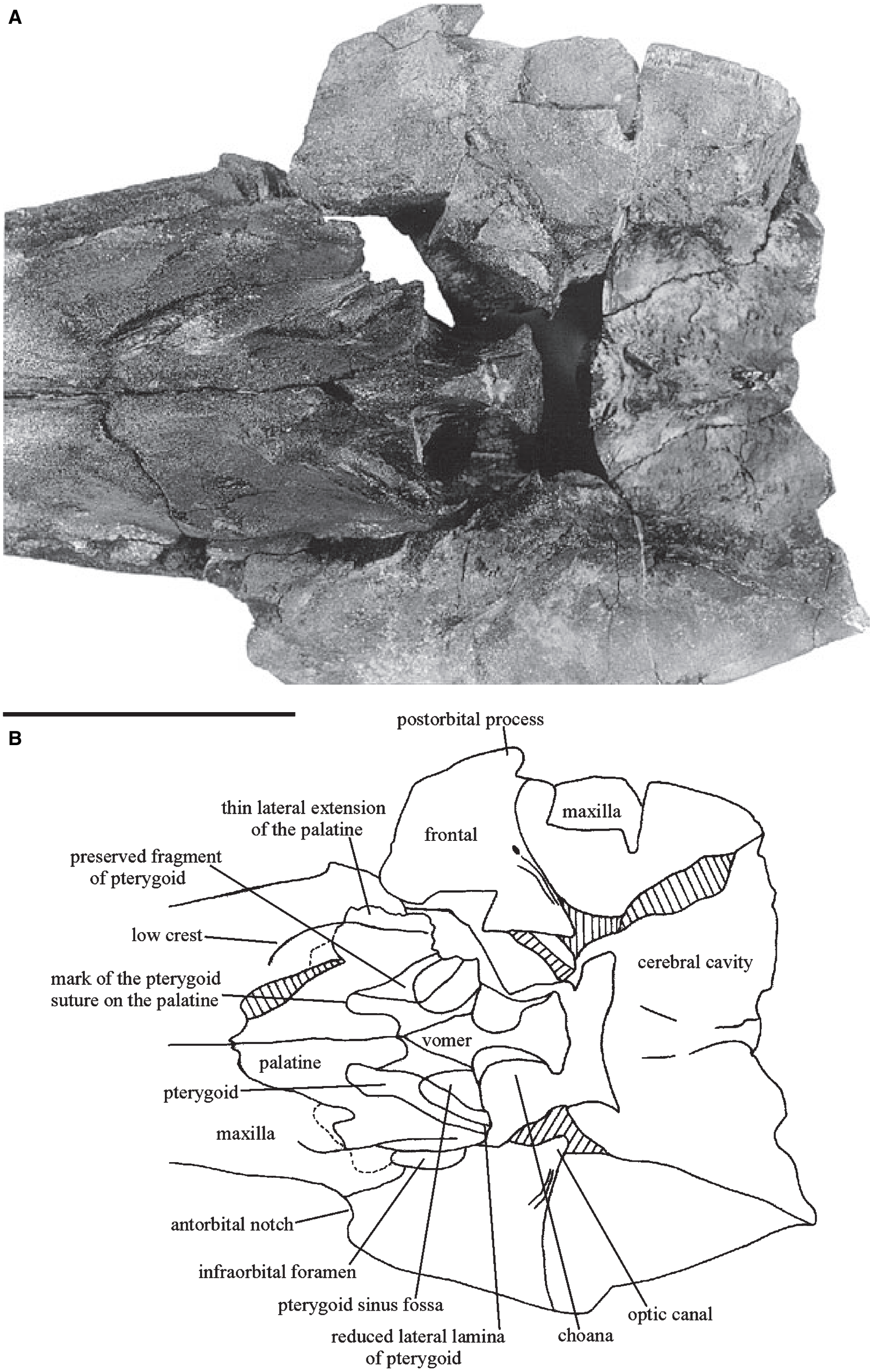
Lateral view. The zygomatic process of the squamosal is very high, dorsoanteriorly orientated, and more robust in lateral view than the distally rounded postglenoid process. The two posterolateral fossae are deep and smooth compared to the rest of the lateral face of the squamosal. The external auditory meatus distinctly separates a short post-tympanic process of the squamosal from the postglenoid process. The anterolaterally bent paroccipital process of the exoccipital contributes for more than 40 mm to the ventral margin of the temporal fossa. The bottom of this fossa is strongly excavated and wide.

Ventral view (Text-figs 5–6). The alveoli for the maxillary teeth are distinct but poorly preserved. Both jugals are lost, with a small trace of the suture with the frontal distinct on the right side but no evidence for the presence of the lacrymal was found. The most interesting part of this view is the palate. The palatines are nearly complete anterior to the choanae and fragments of the pterygoid are preserved on the medioanterior part. The palatine shows the same anterior morphology as on the holotype, except a very thin, pointed, anterior projection. The two palatines are closely joined for most of their length, and are only separated by the vomer for 20 mm immediately anterior to the choanae. The lateral margin diverges posteriorly; after 35 mm, this margin takes a clear lateral direction with a strong widening of the bone as a consequence. This part of the palatine is a thin plate appressed against the maxilla, and is marked by a shallow longitudinal crest which disappears on the maxilla anteriorly (see Text-fig. 6). This laterodorsal extension of the palatine, reaching the median margin of the large ventral infraorbital foramen, was interpreted by Abel (1901) as a fragment of pterygoid. The pterygoid is in fact more ventromedian; its anterior and anterolateral part are preserved around the pterygoid sinus fossa anterior to the choana. This fossa is less excavated than on the holotype, and its dorsal surface is still partially formed by the pterygoid, the palatine appearing only medially. This kind of fenestra on the pterygoid is also present in *Schizodelphis barnesi*, following Muizon (1990), and has been interpreted by him as an intermediate condition before the formation of the lateral lamina of the palatine as in the Delphinida. However, the excavation of the pterygoid sinus fossa also deforms the palatine on the ziphiids for which the fossa is dorsally covered by a very thin plate of pterygoid anterior to the choanae; in *Ziphius cavirostris* and *Berardius arnuxii*, small



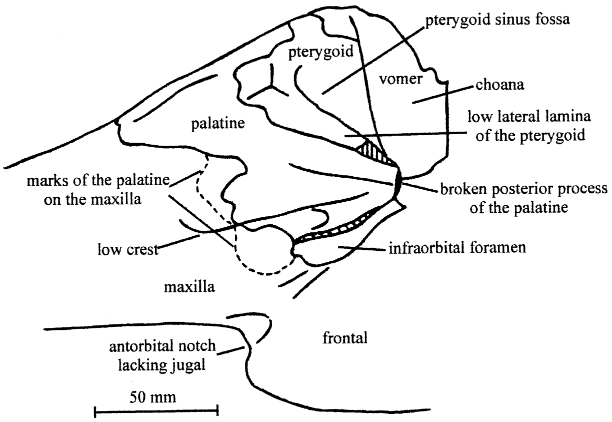
TEXT-FIG. 4. Skull of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp. A, dorsal view. B, corresponding line drawing. Scale bar represents 100 mm.

fenestrations appear on this plate, exposing the overlying palatine. The lateral lamina of the pterygoid presents a complete ventral margin 25 mm anterior to the choana on the right and 15 mm on the left, with respective heights of 15 and 6 mm. This strongly suggests a very reduced lateral lamina of the pterygoid, posteriorly narrowing. This low lateral lamina, with a thick dorsal base and a sharp ventral margin, resembles the condition of ziphiids like *Ziphius* or *Mesoplodon*. This anterior part of the lateral lamina is not reduced in *Delphinus* or *Tursiops* (lateral lamina of the hamular fossa) but fenestrations are present in *Lipotes* and a reduction is also visible in *Inia*. Among the identified eurhinodelphinids, *Schizodelphis barnesi* (see Muizon 1988*a*) and *Eurhinodelphis bossi* (see Kellogg 1925) still have a complete lateral lamina of the pterygoid. The state of preservation of Ital-



TEXT-FIG. 5. Skull of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp. A, ventral view without the basicranium. B, corresponding line drawing. Scale bar represents 100 mm.

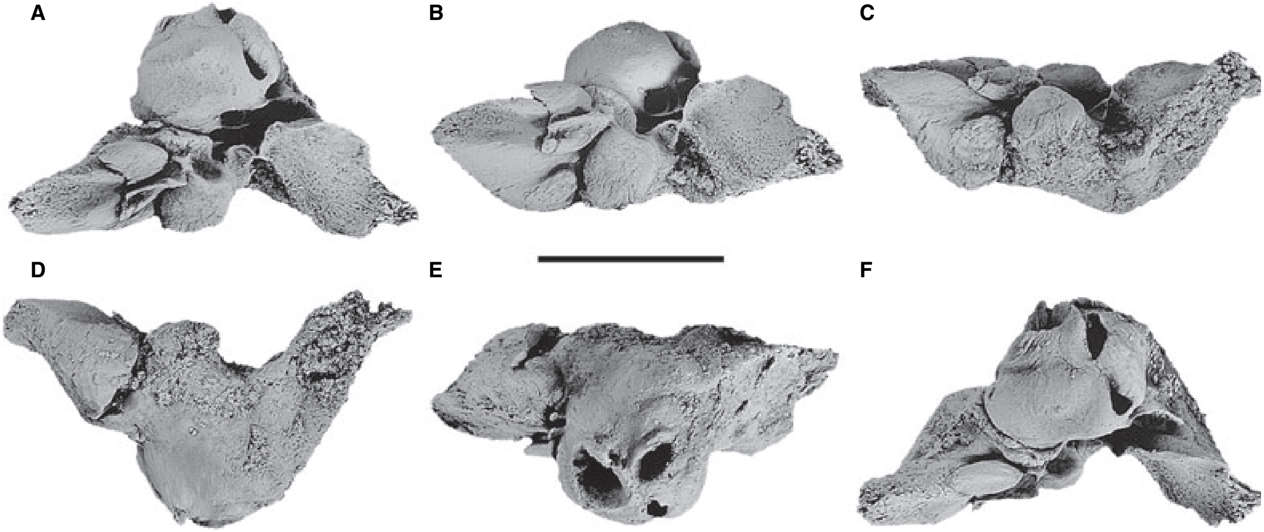
ian eurhinodelphinids (*Eurhinodelphis bellunensis*, *E. sigmoideus* and *Ziphiodelphis abeli*), *Macrodelphinus* and species of *Argyrocetus* does not allow the identification of such a structure. The palatine is broken at the level of the choana and its thick rectangular section suggests a more or less long missing posterior portion, ventral to the optic foramen. The base of the rostrum is wide and the palate is transversely compressed without a sharp ventral keel.



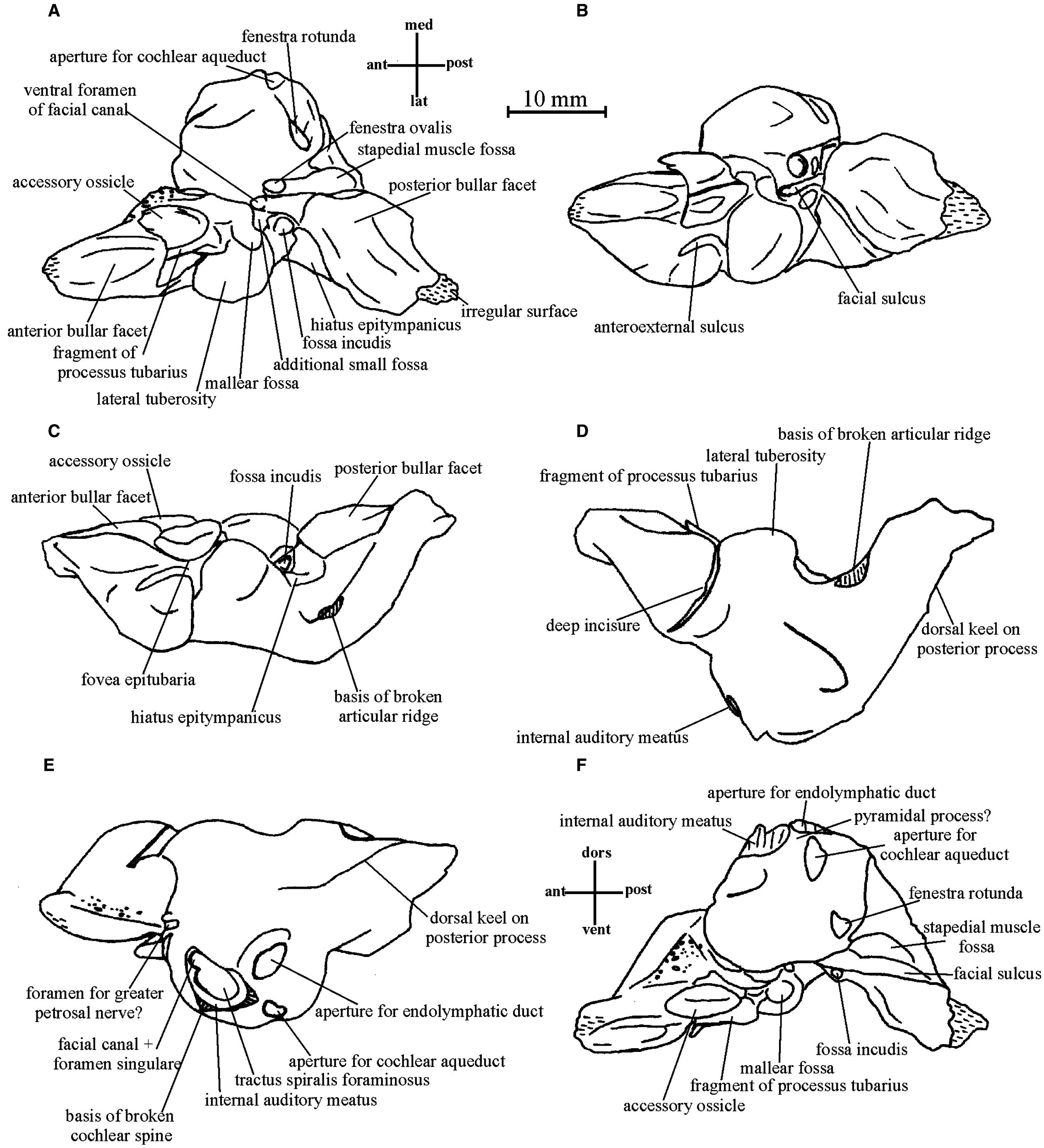
TEXT-FIG. 6. Detail of the right part of the palate of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp, in ventrolateral view, showing the reduced lateral lamina of the pterygoid and the wide lateral extension of the palatine.

There is no trace of pre- or postorbital lobes of the pterygoid sinus, the ventral face of the roof of the orbit being smooth. The poorly preserved small triangular orbitosphenoid does not show any particular structure. A fragment of the left alisphenoid is preserved and the only identifiable surface is also a smooth circular, ventrally facing depression, which corresponds to the pterygoid sinus fossa. The foramen ovale and the other basicranium foramina are not preserved. The squamosal has a wide and strongly curved glenoid fossa, medially bordered by a triangular tympanosquamosal recess. The tympanosquamosal recess is anteriorly short, not extended along the median surface of the zygomatic process, and has a very irregular surface marked by thin ridges near its posterior margin along the anterior meatal crest.

Ear bones. The right periotic is well preserved, with a total length of 43 mm (Text-figs 7–8). The anterior process is very long, more than 85 per cent of the length of the pars cochlearis. In ventral view, this process is narrow and excavated by a long, distinct longitudinal groove, the anterior bullar facet, slightly widening and shallowing anteriorly. Posteromedial to this groove, the anterior process bears an elongated small accessory ossicle embedded in a deep fovea epitubaria (seen in medial view) and linked to a lateral crest-like fragment of processus tubarius curving dorsolaterally in the posterior continuation of the longitudinal ridge. The shape and size of the fused accessory ossicle are similar to that of *Ninoziphius* and *Mesoplodon*, but are smaller and more elongated than in *Physeter* and *Kogia*. In lateral view (Text-fig. 7C), the prominent lateral tuberosity is clearly separated from the anterior process by a deep narrow transverse incisure that turns anteroventrally to become a wide and shallow longitudinal anteroexternal sulcus. In dorsal view (Text-fig. 7D), the incisure interrupts after a small anterior curvature. In medial view (Text-fig. 7F), the contact between anterior process and pars cochlearis shows a small transverse fold that splits into two dorsally, displaying the compression of the pars cochlearis against the anterior process. Just posterodorsal to the fold is a small elongated foramen, connected to the ventral foramen of the facial canal. It could be the hiatus fallopii which is the anterior exit of the greater superficial petrosal nerve, a branch of the facial nerve (Luo and Gingerich 1999). A similar foramen was observed by Fordyce (1994) in *Waipatia*, but closer to the internal auditory meatus. In medial view, the ventral margin of the anterior process is straight. Dorsal to the accessory ossicle is a slight smooth depression limited more dorsally by a longitudinal protuberance pierced by several tiny foramina. The large lateral tuberosity, rounded in ventral view, bears a wide mallear fossa. This fossa is separated from the ventral foramen of the facial canal by a small fossa, anterior to the fossa incudis. This fossa is observed and discussed by Muizon (1984) in the ziphiids *Ziphius* and *Hyperoodon* and in the physeterids *Aulophyseter* and *Orycterocetus*. The ventral foramen of the facial

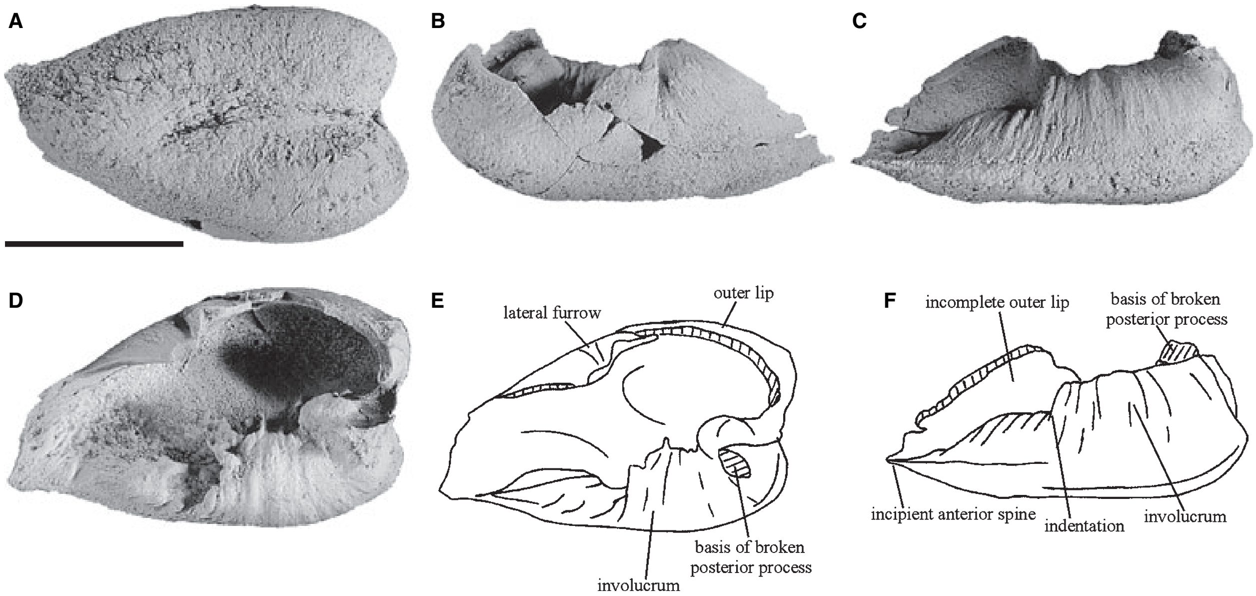


TEXT-FIG. 7. Right periotic of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp. A, ventral, B, ventrolateral, C, lateral, D, dorsal, E, dorsomedial, F, medial views. Scale bar represents 20 mm.



TEXT-FIG. 8. Line drawings of the right periotic of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp, in A, ventral, B, ventrolateral, C, lateral, D, dorsal, E, dorsomedial, and F, medial views.

canal extends posteriorly in a deep facial sulcus parallel to the medial, wide, stapedial muscle fossa. The sulcus turns on the dorsal face of the medioanteriorly expanded posterior bullar facet where it becomes less pronounced. A deep triangular hiatus epitympanicus separates the lateral tuberosity from the posterior bullar facet. The apex of the hiatus is occupied by a wide fossa incudis. The posteroventrally orientated posterior process is long, concave on its ventral bullar facet, with a triangular apical section due to the presence of a distinct dorsal keel. The dorsolateral surface of the posterior process is rough, irregular and might indicate a contact with the basicranium. The broken base of a longitudinal ridge on the dorsolateral edge of the base of the posterior process indicates an incipient articular process as in *Waipatia*, *Notocetus* or *Prosqualodon* (Fordyce 1994).

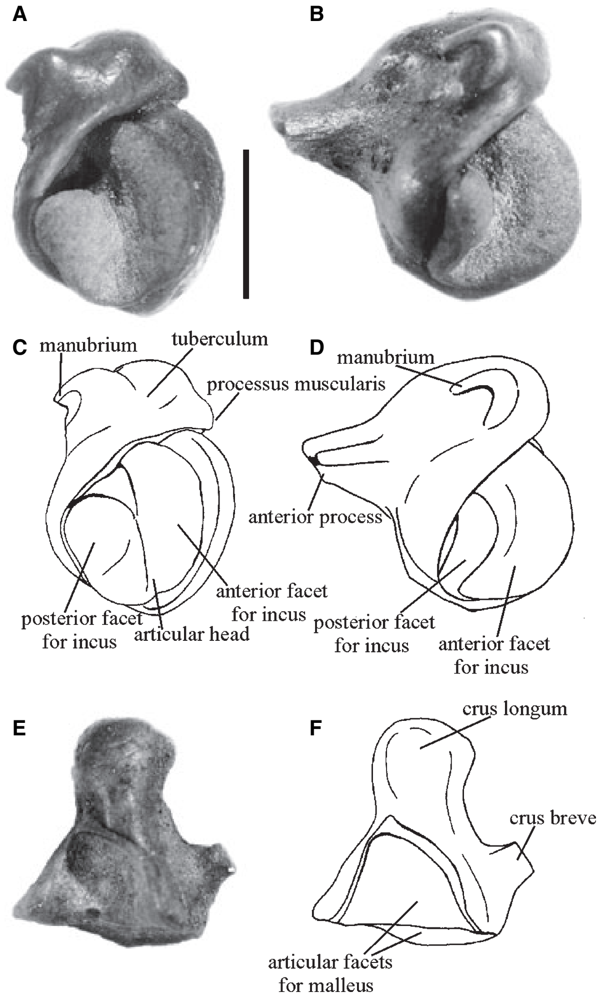


TEXT-FIG. 9. Incomplete right tympanic of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp, lacking the posterior process and a part of the outer lip. A, ventral, B, lateral, C, medial, and D, dorsal views. E–F, line drawings of E, dorsal, and F, medial views. Scale bar for A–D represents 20 mm.

A rounded and smooth protuberance is present on the same position for *Mesoplodon*. The pars cochlearis is moderately high, with a rounded ventral profile distorted by the presence of incipient cochlear spines around the internal auditory meatus (the ventral spine is not fully preserved). Such spines are more developed on *Ninoziphius* or *Berardius* (Muizon 1984), and are sometimes present in mature delphinids (e.g. *Globicephala*, R. E. Fordyce, pers. comm. 2003). The fenestra ovalis is more posterior than the ventral foramen of the facial canal, and separated from the stapedial muscle fossa by a small transverse groove. The fenestra rotunda is reniform, elongated and prolonged by a shallow groove towards the aperture for cochlear aqueduct. The latter is situated medioposteriorly, on the top of the pars cochlearis, with its opening dorsally orientated, equidistant from the internal auditory meatus and the aperture for the endolymphatic duct. The small surface between these three apertures shows breaks indicating a prominent broken structure close in position to the pyramidal process identified by Luo and Marsh (1996) on a squalodontid-like petrosal. The position of this process is not homologous to that of *Physeter* and *Kogia*, outside the triangular surface between the three foramina and considered as derived (also Luo and Marsh 1996). The condition of the periotic of *Eurhinodelphis cocheteuxi* could therefore be primitive as in archeocetes, mysticetes, *Xenorophus* and the squalodontids. The pyramidal process is present between the apertures for the endolymphatic duct and the cochlear aqueduct in *Mesoplodon*. The internal auditory meatus is only slightly elongated, nearly circular, far from the base of the anterior process and without an anterior fissure. The transverse septum separating the tractus spiralis foraminosus from the tiny foramen singulare and the facial canal is reduced.

The two tympanic bullae are preserved but both lack the sigmoid and posterior processes and a part of the processus tubarius (Text-fig. 9). The anterior apex is incomplete on both, but the extremity is thin, so the total length must be close to the 45 and 46 mm, respectively, measured for the right and left tympanics. This also suggests the absence of an individualized thick anterior spine. The maximum width of the tympanics is 28 mm. In ventral view, the outer posterior prominence is slightly more developed than the inner posterior prominence. They are separated by a wide interprominental notch which is followed by a median groove shallowing and widening anteriorly, with a slight lateral deviation on its extremity that reaches a level just beyond the level of the lateral furrow. The lateral margin is regularly convex and the median margin shows a short concave area just before the medially directed apex. This condition is close to what is observed in *Ninoziphius*. In lateral view, the right lateral furrow is visible, incising less than half the height of the lateral face of the bone, in a median position. The involucrum is high with dorsal and ventral margins parallel for half its length in medial view. The dorsal margin is then cut by a deep indentation, which reduces the height of the involucrum of one third, with a new short horizontal level followed anteriorly by the apical descent. A similar succession of indentation, horizontal portion and apical lowering is present in *Ninoziphius* and also, but less distinctly, in *Ziphius*, *Mesoplodon* and *Berardius*. The indentation is also marked in dorsal view, with a very thick posterior part of the involucrum and a narrow anterior part. A wide posterior cleft extends dorsally from the deep interprominental notch.

The right malleus and the corresponding incus are well preserved (Text-fig. 10). In a posteromedial view, with the long axis positioned vertically, the articular head down and the anterior process hidden, the malleus has a length of 6 mm and a width of 4 mm. The facets for the incus occupy more than two-thirds of the length of the bone, with a very short tuberculum. The tuberculum represents more than half the length of the bone in



TEXT-FIG. 10. A–D, right malleus of *Eurhinodelphis cocheteuxi* IRSNB M.1856, Antwerp Sands, Antwerp, in A, posteromedial, and B, posteroventral views. C–D, corresponding line drawings. E, right incus of *Eurhinodelphis cocheteuxi* IRSNB M.1856 in posterolateral to lateral view. F, corresponding line drawing. Scale bar for A, B and E represents 3 mm.

mysticetes, the platanistoids *Pomatodelphis*, *Notocetus* and the Delphinida (*sensu* Muizon 1988*b*). In ziphiids and physeterids, it is very reduced (see Muizon 1985; Text-fig. 11 herein), with the articular head occupying nearly all the posteromedian surface. The proportions of the malleus of *Eurhinodelphis cocheteuxi*, and also *E.* '*vaughni*' and *Schizodelphis sulcatus* (see Muizon 1985), can be seen as intermediate between these two groups. The Australian malleus identified by Fordyce (1983) as belonging to a rhabdosteid (= eurhinodelphinid *sensu* Muizon 1988*a*) has a relatively long tuberculum, more than half the length of the bone.

The larger anterior facet for the incus of the specimen described here is perpendicular to and twice the size of the posterior one. A deep groove separates them from the tuberculum. This groove reaches the small protuberance of the processus muscularis (insertion of the tensor tympani) in an anterior direction. Again with the same orientation, the hook-like small manubrium (insertion of the tympanic ligament) is slightly higher than the processus muscularis, a character considered as primitive by Muizon (1985); the derived higher processus muscularis is present in Inioidea and Delphinoidea (*sensu* Muizon 1988*b*).

The corresponding incus is 4 mm long. The crus breve is broken at its base, with a small section. The crus longum has a distal rounded hook that is dorsally directed, with a distinct dorsal articular facet for the stapes (see Kellogg 1927 for *Kentriodon pernix*).

Discussion on additional material attributed to Eurhinodelphis cocheteuxi

A redescription of all the specimens of *Eurhinodelphis cocheteuxi* is not the goal of this paper but several additional partial skulls allow the description of some details not preserved on the holotype and referred specimen IRSNB M.1856.

IRSNB 3232-M.295. This skull is preserved in many fragments and some of them are so glued that several structures are hidden. The vertex is well preserved but lacking the nasals. The frontals are wide, and shorter than on the type and specimen IRSNB M.1856, thus providing an indication of the variation of longitudinal compression of the face. The same T-shaped posterior extremity of the premaxilla is present, with the vertical and concave dorsoanteriorly directed medial plate of the maxilla along the posterior projection of the premaxilla. The squamosal is small in lateral view, with a slender postglenoid process.

IRSNB 3256-M.1857 (Text-fig. 12). This partial skull has suffered some degradation since it was first described by Abel (1901). The rostrum is very fragmented and the skull is composed of six major fragments. The vertex, lacking the nasals, shows wide and shorter frontals, as on IRSNB 3232-M.295. The ventral view of the squamosal allows the observation of a fragment of falciform process, which is distinctly anterolaterally orientated; its posterior part is in a medial position because of the development of a medial corner of the tympanosquamosal recess, and its anterior part is laterally displaced by the deep circular fossa of the alisphenoid, as described on the holotype and on IRSNB M.1856. This deviation is evident when compared to the anteriorly and slightly medially directed falciform process of the squamosal in *Squalodon bariensis*. The lateral deviation of the falciform process in *Eurhinodelphis cocheteuxi* might be a good indication of the lateral progression of the pterygoid sinus just anterior to the ear bones, towards the temporal fossa.

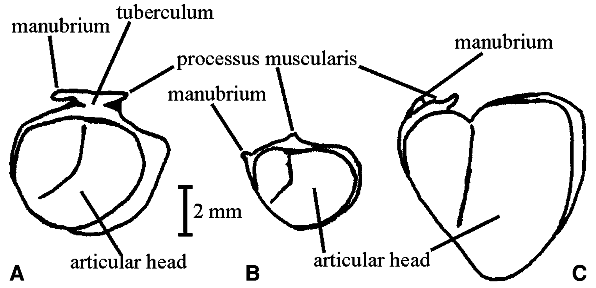
IRSNB 3253-M.296 (Text-fig. 13). This robust skull (see Table 1) lacks the nasals, fragments of the right posterior part of maxilla and frontal, and portions of the basicranium. It shows the main characteristics of the wide vertex of *Eurhinodelphis cocheteuxi*. The complete rostrum (with a total length of 920 mm) differs from the straight rostrum of the holotype in being distinctly curved anteroventrally (though this curvature must be slightly exaggerated by transverse breakages). The falciform process of the squamosal shows the same anterolateral deviation as on the skull IRSNB 3256-M.1857, with an anteromedially facing alisphenoid fossa. At the anterior base of the incomplete right falciform process, between this plate and the fossa, is an anterolaterally directed groove, the path for the mandibular nerve V3 (Fordyce 1994), opening in the temporal fossa. This opening probably corresponds to the foramen pseudo-ovale, usually piercing the lateral lamina of the pterygoid. This ventrally open groove indicates that there was probably no contact between the falciform process of the squamosal and the lateral lamina of the pterygoid in *Eurhinodelphis cocheteuxi*. This corroborates the condition on the specimen IRSNB M.1856, which lacks the anterior part of the lateral lamina of pterygoid. The complete anterior surface of the ventral part of the exoccipital does not show any excavation related to a posterior sinus (*sensu* Fraser and Purves 1960).

Systematic revision of specimens previously attributed by Abel (1901) to Eurhinodelphis cocheteuxi

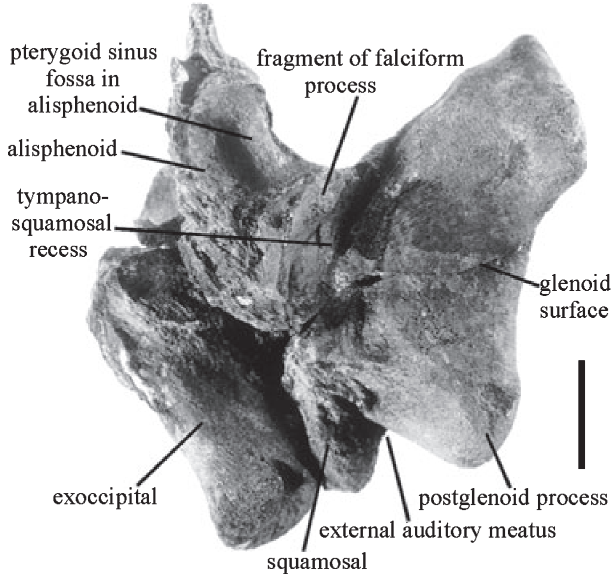
IRSNB 3451-M.300. This large squamosal, first identified by du Bus (1872) as *Priscodelphinus validus* and later revised by Abel (1901; individual IX, figured pl. 5, fig. 5) as *Eurhinodelphis cocheteuxi*, shows strong differences from this species: a pointed postglenoid process, a wide basin for the bottom of the temporal fossa, a high zygomatic process and a well-developed small fossa dorsal to the spiny process. This fragment is attributed to the genus *Squalodon* from which only teeth, mandible and rostrum fragments were previously described from the Antwerp Sands (*Squalodon antwerpiensis* Van Beneden, 1861*a*).

IRSNB 3257-M.298. This vertex, referred by Abel to *Eurhinodelphis cocheteuxi* (1901, individual VII, figured pl. 10, figs 5–6), has a minimal posterior distance between the two maxillae of 75 mm. This is shorter than in *E. cocheteuxi* (see measurements; not less than 90 mm). Furthermore, the nasals are more prominent here and anteriorly rounded; the mesethmoid is lower; the overhanging of the median plate of the maxilla is more developed. This specimen shares some similarities with the kentriodontid *Macrokentriodon* Dawson, 1996, from the Miocene of Maryland, but a contact is retained between the premaxillae and the frontals on the vertex. This probable plesiomorphic feature, added to the enlarged nasals and elevated vertex, might also bring IRSNB 3257-M.298 closer to the ziphiids. It is, however, too fragmentary to allow a more precise attribution than Odontoceti *incertae sedis*.

IRSNB 3552. This fragment of left premaxilla, identified by du Bus as *Priscodelphinus crassus* (1872) and revised by Abel as *Eurhinodelphis cocheteuxi* (1901, individual X) is not diagnostic and its shape does not clearly match *E. cocheteuxi*. It is also considered as Odontoceti *incertae sedis*. The same conclusion is reached for the fragments of right premaxilla IRSNB 3411 and IRSNB 3412 referred to *Priscodelphinus teres* by du Bus (1872) and placed in *Eurhinodelphis cocheteuxi* by Abel (1901, individuals XI, XII).



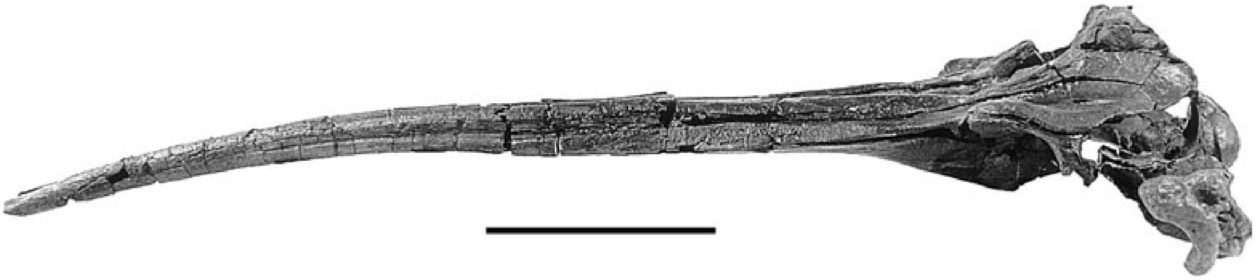
TEXT-FIG. 11. Line drawings of extant odontocete right mallei in posteromedial view, showing the relative sizes of the tuberculum and the articular head, bearing the articular facets with the incus. A, *Ziphius cavirostris* USNM 504347. B, *Kogia breviceps* USNM 22016. C, *Physeter catodon* USNM 49488.



TEXT-FIG. 12. Left part of the basicranium of *Eurhinodelphis cocheteuxi* IRSNB 3256-M.1857, from the Miocene of Antwerp. Anteromedial and slightly ventral view. Scale bar represents 30 mm.

IRSNB 3380 and IRSNB 3400. These are two fragments of ramus of the mandible placed by Abel (1901) in *Eurhinodelphis cocheteuxi* (respectively individuals XIV and XV). The only skull of *E. cocheteuxi* associated with a fragment of the mandible is IRSNB 3232-M.295. This fragment of ramus does not closely fit the pieces cited above. Those should, therefore, be considered as Odontoceti *incertae sedis*, even if the size of the alveoli roughly matches what is observed on the rostra of *E. cocheteuxi*.

IRSNB 3449. The associated fragments of the base of the rostrum IRSNB 3449 were referred to *Eurhinodelphis cocheteuxi* by Abel (1901, individual XIII). Because of its very narrow mesorostral groove, the posterior fragment could not belong to *Eurhinodelphis*. The anterior fragment might be related to *E. bossi*, but this is by no means certain. Hence, authors should be careful with associations of fragments from ancient collections when



TEXT-FIG. 13. Skull of *Eurhinodelphis cocheteuxi* IRSNB 3253-M.296, from the Miocene of Antwerp, in left lateral view. The basicranium is not in connection with the anterior part of the skull and their relative position is not exact, because of former reconstruction mistakes. Scale bar represents 200 mm.

there is no contact between the pieces, especially those from the Neogene of Antwerp.

Many isolated postcranial bones were placed by Abel (1905, 1931) in *E. cocheteuxi*, essentially on the basis of the size. Because of the presence in the same beds of several taxa of eurhinodelphinids, with sizes consistently variable for any one species, those attributions must be treated carefully; for now, no clear discriminant characters were found using postcranial bones.

Eurhinodelphis bossi Kellogg, 1925

Text-figure 14

Remarks. This species was described by Kellogg (1925) from the Calvert Formation, early–early middle Miocene (Gottfried *et al.* 1994), of the eastern coast of North America, on the basis of four individuals. The holotype (USNM 8842) includes a well-preserved skull (only lacking the ear bones), the mandible and teeth, 16 vertebrae, ten ribs, a scapula, a humerus and part of the sternum. The three other individuals are isolated partial skulls (USNM 10714, 10464 and 10711). A redescription of the four skulls by Myrick (1979) did not bring additional information to the complete study of Kellogg (1925), except for emphasizing a strong intraspecific morphological variation. Kellogg (1925, p. 6) wrote: 'After a careful detailed study of the skulls of *Eurhinodelphis* in the National Museum, I am unable to satisfy myself that any one of them [referring to the four individuals of *Eurhinodelphis bossi*] is identical specifically with any of the European species [the three species of the genus *Eurhinodelphis sensu* Abel 1905], though it is not unlikely that such identity may be established later.'

The partial skull IRSNB 3243-M.367 (Text-fig. 14), from the Antwerp Sands, lacking the apical part of the rostrum, nasals and ear bones, was first identified by du Bus (1872) as the type and only specimen of *Priscodelphinus productus*, with some words of description and no figure. Abel (1902) referred this specimen to *Eurhinodelphis cristatus*, because of the stronger compression of the top of the skull and the shape of the palatines. He provided a schematic drawing of the palate region (Abel 1902, pl. 18, fig. 3). This specimen was the only one in the species *E. cristatus* (*sensu* Abel 1902) to show a partially preserved rostral suture between the maxilla and premaxilla, anteriorly descending as in *E. cocheteuxi* or *Schizodelphis longirostris*. This skull differs from *Eurhinodelphis cristatus* (*sensu* Abel 1902) in the following characters: narrower and more convex premaxillae just anterior to the antorbital notch; wider and longer facial part of the maxillae; less acute posterior margin of the frontal on the vertex (less pronounced longitudinal compression of the facial skull); maxillae thinner on the roof of the orbit; zygomatic process of the squamosal longer, more flattened and more anteriorly directed with a stronger curvature than the erected process of *E. cristatus*; shallower tympanosquamosal recess. Its identity as *Eurhinodelphis bossi* is supported by: maxilla as wide as the premaxilla at the level of the antorbital notch; thin maxilla on the roof of the orbit, with a small uncovered anterolateral portion of the frontal; short and wide sulcus prolonging posterolaterally the large dorsal infraorbital foramen located at the level of the antorbital notch; similar trapezoidal joined frontals on the vertex; similar long and low zygomatic process of the squamosal. Some measurements taken by Myrick (1979, table 7) on individuals of *Eurhinodelphis bossi* are compared here with the skull IRSNB 3243-M.367 (Table 2). The measurements on the latter are in each case close to the four individuals of Kellogg (1925), especially to the skull USNM 10714 (except the larger orbit of the Belgian specimen). The descending rostral suture between maxilla and premaxilla seen on this skull was not reported on the specimens of *Eurhinodelphis bossi* from the Calvert Formation by Kellogg (1925). This author simply described a shallow, poorly defined groove in a similar position. We prefer to keep the name *Eurhinodelphis bossi* instead of replacing it by *E. productus*, because of the better quality of the American type, and the long period of time that the name *E. bossi* has been used.

The partial vertex IRSNB 3497 (individual VII from the species *Eurhinodelphis cristatus sensu* Abel 1902),

TEXT-FIG. 14. Skull of *Eurhinodelphis bossi* IRSNB 3243-M.367, from the Miocene of Antwerp. Dorsal view of the face. The rostrum is incomplete and the nasals are lost. Scale bar represents 100 mm.

including the posterior part of the maxillae, frontals and premaxillae, shows a morphology similar to the skull IRSNB 3243-M.367, and is also referred to *Eurhinodelphis bossi*. Actually, Abel (1902) indicated that the size of this specimen perfectly matches the skull IRSNB 3243-M.367. The left side of a face IRSNB 3495 (*Eurhinodelphis ambiguus sensu* du Bus 1872 and individual XV of the species *E. longirostris sensu* Abel 1902) is probably a part of a young *E. bossi*. It has a shallow fossa for the postorbital lobe of the pterygoid sinus on the ventral face of the roof of the orbit, and the shape of the supraorbital process of the maxilla is similar to IRSNB 3243-M.367.

PHYLOGENETIC ANALYSIS

Eurhinodelphinidae were previously placed in phylogenetic trees as the sister-group of the Squalodontidae + Squalodelphinidae (Barnes 1990), and as the sister-group of the Eoplatanistidae in a superfamily Eurhinodelphinoidea, in turn the sister-group of the Delphinida (Muizon 1990). The only phylogenetic study of odontocetes using parsimony software and including eurhinodelphinids is that by Fordyce (1994) on *Waipatia maerewhenua*. In this analysis Fordyce considered the family Eurhinodelphinidae as a whole, with taxa and/or characters reviewed by Muizon (1988*a*, *b*, 1990), and suggested that the affinities of this group with the Delphinida need more study. With such a poorly diagnosed family, which could well be non-monophyletic, I suggest using isolated species or genera in cladistic analyses. The species *Eurhinodelphis cocheteuxi*, which is the type species of the type genus of the family, seems to be a good place to start for a revision of the phylogenetic position of the eurhinodelphinids. Moreover, this is one of the best known species of the group, with several skulls and ear bones. The species *Eurhinodelphis bossi* is not used in the cladistic analysis because of the

TABLE 2. Measurements on skulls of *Eurhinodelphis bossi* from the IRSNB and the USNM (taken from Myrick 1979). Measurements are in millimetres: e, indicates estimate; –, no data.

Measurements on the skulls of *E. bossi*	IRSNB 3243-M.367	Holotype USNM 8842	USNM 10714	USNM 10464	USNM 10711
3. length anterior orbit-posterior skull	e217	–	215	190	220
5. length orbit	86	–	60	55	70
8. width base rostrum	128	108	129	117	125
10. width skull postorbital processes	221	233	225	220	240
12. width bony nares	35	31	29	33	50
13. width nasals	e45	44	49	42	58
14. maximal posterior premaxillary width	98	89	107	94	114
15. minimal posterior distance between maxillae	53	70	65	52	58
18. width lateral margins occipital condyles	86	80	89	–	90
25. height occipital condyles	48	50	50	71	53

fragmentary material preserved in the IRSNB and the need for a systematic revision of the eurhinodelphinids from the east coast of the USA preserved at the USNM. Two additional eurhinodelphinid taxa are included in the analysis: *Schizodelphis*, including French and American specimens of *S. sulcatus*, *S. longirostris* and *S. barnesi sensu* Muizon (1988*a*) and *Ziphiodelphis abeli* from the Italian Miocene. The Belgian specimens of *S. longirostris* need systematic revision, and *Argyrocetus*, *Iniopsis* and *Macrodelphinus* are currently too poorly known.

A cladistic analysis was carried out with the program PAUP, version 4.0 beta 10 (Swofford 1998), with a matrix of 73 characters (excluding uninformative characters, and all treated as unweighted and unordered) for 17 taxa (see Appendix for the description of the characters and the data-matrix). Two outgroups were chosen *a priori*: the archaeocete *Zygorhiza kochii* and the primitive odontocete *Archaeodelphis patrius*.

The cladistic analysis included the following taxa (numbered specimens were directly studied, information on the others comes from literature): *Zygorhiza* (USNM 11962, 16638; Kellogg 1936), *Archaeodelphis* (Allen 1921), *Orycterocetus* (USNM 14730, 22926; Kellogg 1965), *Physeter* (skeleton IRSNB 21229, ear bones USNM 49488; Flower 1869; Van Beneden and Gervais 1880), *Kogia* (numerous skulls from the ZMA, particularly *K. breviceps* ZMA 16030, 16035, *K. simus* ZMA 14765, 13180, ear bones of *K. breviceps* USNM 22016), *Squalodon* (cast of *Squalodon bariensis* MHNL Dr15; Muizon 1990; *S. calvertensis* USNM 10484; Kellogg 1923*b*), *Waipatia* (Fordyce 1994; cast of the holotype skull at the USNM), *Notocetus* (Lydekker 1893), *Platanista* (skulls of *P. gangetica* IRSNB 5592-1507, ZMA 10465), *Eurhinodelphis cocheteuxi* (see the referred specimens above), *Ninoziphius* (skull MNHN SAS 941; Muizon 1984), *Mesoplodon* (skulls of *M. bidens* IRSNB 19.822, 9942-1505b, 9942-892), *Ziphius* (skull IRSNB 24939-4027, ear bones USNM 504347), *Schizodelphis* (Muizon 1988*a*, skull of *S. sulcatus* MNHN RL 12, skull of *S. barnesi* MNHN AMN 19), *Ziphiodelphis abeli* (skulls MGPD 26187–26194, 26390, 26391), *Pontoporia* (skulls of *P. blainvillei* IRSNB 6804-1506, ZMA 15518, ear bones USNM 501127, 482772), *Lipotes* (USNM 218293, photographs from skeleton AMNH 5333, casts of ear bones AMNH 5333), *Atocetus* (Muizon 1988*c*), *Delphinus* (numerous skulls and skeletons, particularly the skull of *Delphinus delphis* IRSNB 3750-1520).

Squaloziphius emlongi Muizon, 1990 was not used in the analyses because the skull is incomplete and lacks ear bones. However, its apparent affinities with the ziphiids (Muizon 1990 built a subfamily Squaloziphiinae for *Squaloziphius* among the Ziphiidae) and the fact that Fordyce and Barnes (1994) found on this skull some reminiscence of eurhinodelphinids indicate that the status of *Squaloziphius* should be further investigated.

Results

The result of the heuristic search that was performed is a unique minimal cladogram of 162 steps with a CI of 0·53 and an RI of 0·73 (Text-fig. 15). Five cladograms with 163 steps and 12 with 164 steps were also obtained.

The first point of the analysis discussed here is the position of *Eurhinodelphis cocheteuxi*. Authors such as Abel (1901, 1902), Dal Piaz (1977) and Pilleri (1985) have already noted similarities between eurhinodelphinids and the ziphiids. Muizon (1984) indicated resemblances between ear bones of the two groups, although the sister-group relationship of the ziphiids and physeterids prevents closer relationships (Muizon 1990). The most parsimonious tree obtained here shows a sister-group relationship between *Eurhinodelphis cocheteuxi* and the four ziphiids used in the analysis. The ziphiids have more distant relationships with *Ziphiodelphis abeli*, *Schizodelphis* and *Waipatia*. Another clade recognized here is the Platanistoidea (*sensu* Muizon 1987) + Delphinida (*sensu* Muizon 1988*b*) group. The Physeteroidea (Physeteridae + Kogiidae) are more basal.

Discussion

The position of *Eurhinodelphis cocheteuxi* at the base of the ziphiids is also found in the 17 cladograms of 163 and 164 steps. The main characters supporting this relationship are the curvature and extension in antero-dorsal direction of the postero-medial plate of the maxilla along the elevated vertex (character 12, also present but variable in *Notocetus*) and the loss of contact of the lateral lamina of the pterygoid with the falciform process of the squamosal (character 33). The last character is present in the physeterids and the group *Lipotes*–*Atocetus*–*Delphinus*. The program considers also the very large posterior process of the tympanic as a synapomorphy of the clade *Eurhinodelphis cocheteuxi* + ziphiids (character 57). The posterior process of the tympanic was not observed in *E. cocheteuxi* but the morphology of the ventral margin of the exoccipital and of the squamosal seems to indicate the absence of a large posterior process, as is the case in *E. bossi*. In the same way, the sigmoid process of the tympanic is not preserved in *E. cocheteuxi* (character 67).

This close relationship of *Eurhinodelphis cocheteuxi* with the ziphiids questions the monophyletic status of the family Eurhinodelphinidae, as *Ziphiodelphis abeli* and *Schizodelphis* are more primitive. This problem needs more attention, however, and the revision of the different genera of Eurhinodelphinidae and Eoplatanistidae (e.g. one tree of 164 steps groups *Schizodelphis* and *Ziphiodelphis abeli*). With *Ziphiodelphis abeli*, the clade *E. cocheteuxi* + ziphiids shares the following main characters: presence of transverse premaxillary crests on the vertex (character 6, also present on the delphinid *Australodelphis*) and posterior margin of the maxilla beyond the dorsomedian margin of the supraoccipital (character 14). The common characters with *Schizodelphis* are: apex of the rostrum constituted by the only premaxillae on more than 10 per cent of its total length, portion lacking teeth alveoli (character 1); posterior process of the periotic projecting ventrolaterally (character 54); dorsal margin of the involucrum of tympanic cut by a median indentation in medial view (character 58); and abrupt anterior narrowing of the involucrum at more or less mid length in dorsal view (character 59). This clade is also characterized by a relative shortening of the tuberculum of the malleus (character 69, unknown on *Ziphiodelphis abeli*), but because of the lack of information on several taxa, this character is interpreted in the most parsimonious tree as present in all odontocetes, undergoing a reversion on the clade Platanistoidea + Delphinida (*sensu* Muizon 1990).

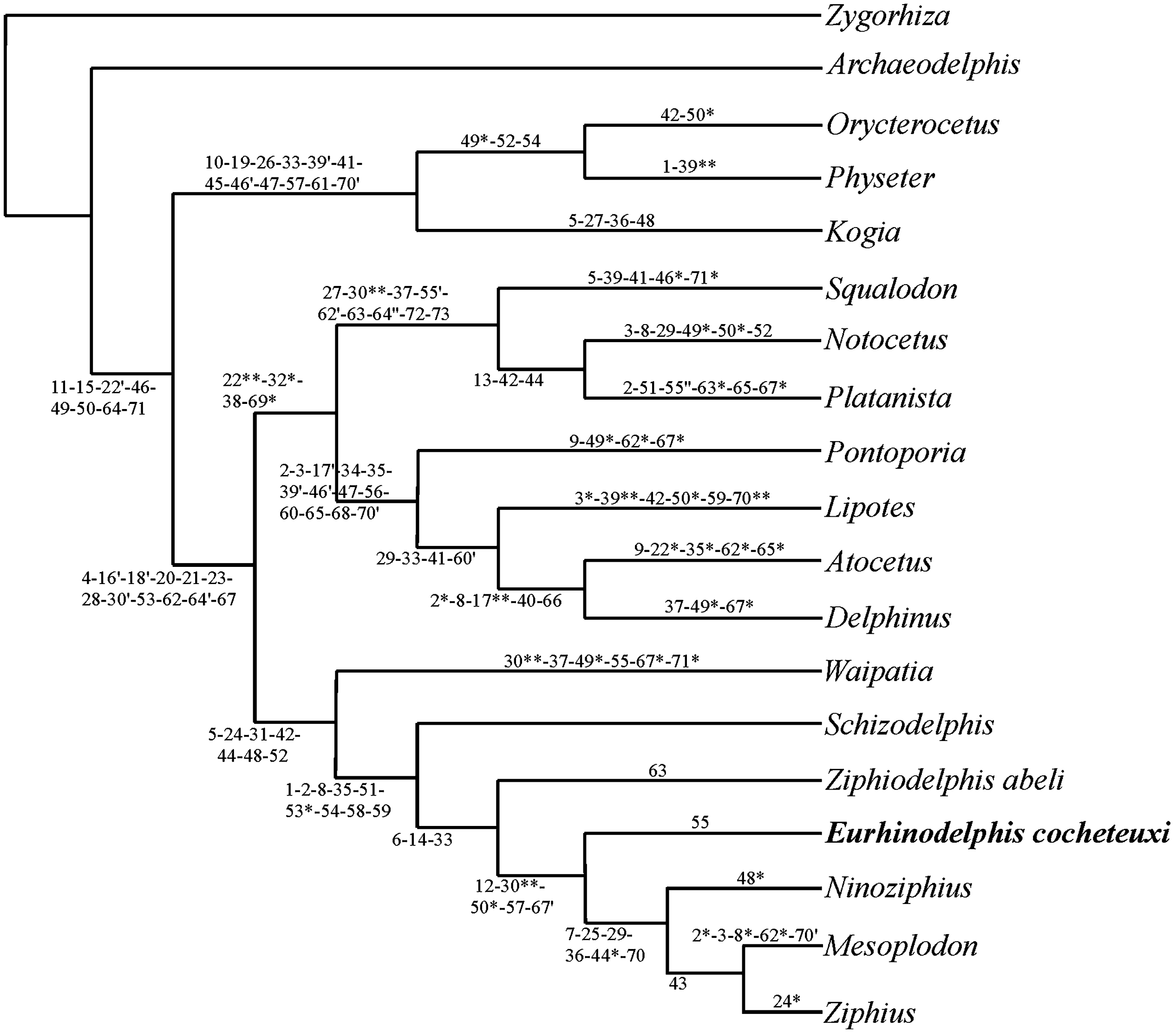
Waipatia has here a completely different position than in the analysis of Fordyce (1994), where it was nested among the Platanistoidea *sensu* Muizon 1987. This genus is obviously primitive and its position varies in longer trees. The addition of close parents of the waipatiids in a cladistic analysis could lead to a better resolution.

The relationships between the members of the Platanistoidea are the same on the shortest tree as in Muizon (1987, 1990) but some variation appears in trees of 163 and 164 steps, with two trees positioning *Platanista* as sister-taxon of a clade *Squalodon* + *Notocetus* and two others suggesting a monophyletic group *Platanista* + *Squalodon*.

The situation in the Delphinida clade is intriguing as *Pontoporia* is more basal than *Lipotes*, a solution never found in other analyses (morphological as well as molecular; see Muizon 1988*b*; Messenger and McGuire 1998; Cassens *et al.* 2000; Hamilton *et al.* 2001). Having regard to this result, the presence of a complete lateral lamina of the pterygoid in *Pontoporia* might be interpreted as primitive, contrary to the common hypothesis of reversion. The addition of *Inia* to the analysis could, however, lead to other results. The grouping of *Delphinus* and the kentriodontid *Atocetus* is congruent with the Delphinoidea definition of Muizon (1988*b*). Here again, relative positions of the different Delphinida are variable on trees with one or two additional steps and more typical characters of this clade should be used to resolve its internal relationships, probably then losing resolution on other parts of the tree.

The general topology of the cladogram is similar to the morphological studies on extant odontocetes of Heyning (1989) and Messenger and McGuire (1998, analyses with complete and reduced morphological data), with *Platanista* as sister-group of the Delphinida, and the ziphiids more derived than the physeterids. This differs from the results of Muizon (1990) and Fordyce (1994), who suggested a sister-group relationship between ziphiids and physeterids (= Physeterida of Muizon 1990). The characters supporting this last hypothesis are discussed. In the tree presented here, the enlarged posterior process of the tympanic common to ziphiids and physeterids is considered as a convergence. The posterior process of *Kogia*, wide and short, is, for example, very different from the much longer one in *Berardius* or *Mesoplodon*. The reduction of the tuberculum of malleus also seems to occur in a different way in *Kogia* and *Physeter* relative to *Mesoplodon* or *Eurhinodelphis cocheteuxi*, with a different relative position of the two facets (see discussion of character 69). The loss of the posterior part of the lateral lamina of the pterygoid also occurs in Delphinida. The increase in size of the pterygoid sinus occurs as an excavation of the dorsal lamina of the pterygoid in ziphiids but no fossa is visible in physeterids. Tentative quantification of the character ‘increase in size of the basioccipital basin’ (Muizon 1990) did not give conclusive results. The ratio used gives nearly the same value for *Mesoplodon* and *Delphinus*, for example, and this character could also be linked to the absolute size of the taxon, the basin being relatively larger in *Ziphius* than in the smaller *Mesoplodon* (and larger in *Tursiops* than in *Delphinus*). It could, therefore, be considered as a convergence between large ziphiids and large physeterids. Fordyce (1994) also used the enlarged accessory ossicle of the periotic, subspherical and fused tightly to the periotic, to characterize the clade *Physeter* + *Kogia* + *Mesoplodon* + *Tasmacetus*. The fusion of the accessory ossicle to the periotic is variable (seen, for example, on undescribed physeterids from Antwerp) and the ossicle of *Mesoplodon* or *Ziphius* is smaller, narrower and more medially inserted on the anterior process of the periotic than for *Orycterocetus*, *Physeter* or *Kogia*, in a way similar to *Eurhinodelphis cocheteuxi*.

The remark of Fordyce (2002) about the similarities of the archaic Oligocene odontocete *Simocetus* with the eurhinodelphinids (toothless premaxilla, elongate conical pterygoid hamulus, thick postglenoid process and recurved anteroexternal sulcus on the periotic) is interesting for two reasons. First, the toothless premaxilla and the thick postglenoid process are characters that group eurhinodelphinids and ziphiids. Second, the elongate conical pterygoid hamulus and the thick postglenoid process are also present in the Oligocene *Squaloziphius*, in a way very close to eurhinodelphinids and *Simocetus*. The description of well-preserved older eurhinodelphinids (eurhinodelphi-



TEXT-FIG. 15. Most parsimonious tree showing the relationships of *Eurhinodelphis cocheteuxi*. Numbers at each node refer to characters discussed in the text and listed in the Appendix. Change from state 0 or 1 to state 2 ('); change from state 0, 1 or 2 to state 3 ("); reversal from state 1 to state 0 (*); reversal from state 2 to state 1 (**).

nids have already been recorded from the Upper Oligocene of Australia but with fragmentary specimens) could help to resolve the problematic phylogenetic affinities of the monogeneric families Squaloziphiidae and Simocetidae. In particular, information about the shape of the vertex and the first steps towards the longer edentulous premaxillae of archaic eurhinodelphinids would be informative.

The most recent molecular analyses seem to reach a consensus for the relationships of extant odontocetes. Cassens *et al.* (2000) and Hamilton *et al.* (2001) on nuclear and mitochondrial DNA sequences, and Nikaido *et al.* (2001) using the SINE method, all obtained the same general topology with the following succession: *Platanista*, Ziphiidae, Delphinida (*sensu* Muizon 1988*b*). This pattern is different from that of the most parsimonious tree obtained here. However, Cassens *et al.* (2000) commented that their results are not highly significant for the position of *Platanista*, partly because of a probable very rapid succession of splitting events producing *Platanista*, physeterids, ziphiids and mysticetes lineages. The same remark can be made about the results presented here; the clade Delphinida + Platanistoidea (*sensu* Muizon 1990) only shares one derived character, with three reversions. This relationship must, therefore, be considered as weak, contrary to the clade Delphinida for example, supported by 14 derived characters.

In this study, one less parsimonious tree of 163 steps and two of 164 steps give a sister-group relationship between the Platanistoidea and the *Schizodelphis* + *Eurhinodelphis cocheteuxi* + Ziphiidae clades (with a variable position of

Waipatia), more distantly related to the Delphinida. This is consistent with the tree of Cassens *et al.* (2000) obtained under Goloboff fit criterion with $k = 2$.

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APPENDIX

List of characters used in the cladistic analysis

1. Apex of the rostrum constituted by the only premaxillae on more than 10 per cent of its total length and lacking alveoli: absent (0), present (1). The primitive condition is relatively long premaxillae bearing teeth as in ancestral terrestrial mammals, seen in archaeocetes and primitive forms like *Squalodon* and *Waipatia*. Among physeterids, *Orycterocetus* retains premaxillary teeth but not *Physeter*, as for *Kogia* which has an apex made of the maxillae, premaxillae and vomer. *Eurhinodelphis cocheteuxi* has very elongated edentulous premaxillae, a condition incipient in *Messapicetus* (ziphiid from upper Miocene of Italy, Bianucci *et al.* 1992) and *Tasmacetus*. In *Mesoplodon* and *Ziphius*, the premaxillae are relatively shorter than in the latter genera, but always clearly longer than the maxillae and do not bear alveoli. In the Delphinida, the premaxillae are sometimes slightly longer than the maxillae but then bear alveoli (except *Grampus* without premaxillary teeth, but with premaxillae not significantly longer than the maxillae). Interestingly, the archaic Oligocene odontocete *Simocetus* lacks premaxillary teeth (Fordyce 2002).
2. Rostral suture between premaxilla and maxilla deeply grooved (Fordyce 1994): absent (0), present (1).
3. Mesorostral canal: premaxillae separated anterior to the bony nares, exhibiting the mesethmoid (0), joined premaxillae closing the mesorostral canal (at least on its posterior part) (1).
4. Premaxillary sac fossae differentiated from the rest of the premaxillae lateral to the bony nares: no (0), yes (1). These plates form a shelf for the premaxillary sacs of all extant odontocetes except the physeterids. For this taxon, the development of the supracranial basin could have eliminated the premaxillary sacs. Premaxillary sac fossae are present on *Agorophius*. The premaxillae of *Xenorophus sloanii* (Kellogg 1923*a*) are narrow and crest-like laterally to the bony nares but a more anterior widening might represent incipient premaxillary sac fossae. The premaxillae of the holotype of *Archaeodelphis* are too poorly preserved to comment on the condition of this genus.
5. Premaxillae reaching dorsally the same level as the frontals: absent (0), present (1). The condition of Delphinida (progressive shortening of the premaxillae) is regarded as a reversion at least partially related to the increase in size of the braincase.
6. Transverse premaxillary crest: absent (0), present (1). This crest is a transverse thickening of the premaxilla before the short posterior process of premaxilla wedged between nasal and maxilla. It gives this part of the premaxilla a T shape, present in *Eurhinodelphis cocheteuxi*, an undescribed primitive ziphiid from Antwerp, *Messapicetus*, *Mesoplodon*, *Berardius* and *Tasmacetus*. In *Ziphirostrum*, *Choneziphius* and *Ziphius*, the crest is more obliquely oriented.
7. Development of an elevated synvertex (*sensu* Moore 1968) (modified from Muizon 1990): absent (0), present (1). This synvertex, characteristic of the ziphiids, is mainly formed by the vertical posterior part of the premaxillae joined to medial plates of maxillae and the nasals, immediately posterior to the bony nares (Heyning 1989). The synvertex is also better defined by the overhanging of the premaxillae over the maxillae.
8. Dorsal elevation of the nasals on the vertex: lower or at the same level as the frontals (0), higher (1).
9. Internasal fossa (Muizon 1988*b*): absent (0), present (1). This fossa was regarded by Muizon (1988*b*) to characterize the kentriodontids, with possible reversion in *Delphinodon*, *Kentriodon* and '*Lophocetus*' *repenningi*. It is also present in *Pontoporia*.
10. Supracranial basin (Heyning 1989): absent (0), present (1). This character, only seen in physeterids, is related to the development of spermaceti organ and the loss of one nasal, regarded as different characters by Fordyce (1994).
11. Maxilla present in anterior wall or floor of orbit (Fordyce 1994): yes (0), no (1). The loss of this morphology, primitively present on archaeocetes and mysticetes, characterizes all the odontocetes except *Archaeodelphis*.
12. Curvature and lengthening in an antero-dorsal direction of the postero-medial edge of the maxilla along the elevated vertex: absent (0), present (1). This character, pronounced in ziphiids, is distinct in *Eurhinodelphis cocheteuxi*, more than in *Waipatia*, with a higher vertical plate of the maxilla.
13. Posterior maxillary (infraorbital) foramen placed posteromedially, near the bifurcation in the posterior of the premaxilla

(Fordyce 1994): no (0), yes (1). This character is present in *Notocetus*, *Zarhachis* and *Platanista*.

14. Posterior margin of the maxilla goes far posteriorly beyond the dorsomedian margin of the supraoccipital: absent (0), present (1).
15. Complete transverse strip of the parietals exposed on the vertex: yes (0), no (1). Parietals are present on the vertex of archaeocetes, primitive mysticetes and the primitive odontocetes *Archaeodelphis* and *Agorophius*. Abel (1912) also identified a strip of parietals in *Prosqualodon australis*.
16. Nasal passages (modified from Heyning 1989; Fordyce 1994): separated (0), single blowhole with nasal passages still separated distal to bony nares (1), fusion of nasal passages on their whole length (2). The separated passages of extant mysticetes are regarded as primitive. The condition of *Physeter* with two distal apertures in a common furrow is considered by Heyning (1989) as secondarily derived, compared to the passages confluent at a deeper level on *Kogia*, but might also be more primitive in the progressive way of fusion of the two passages.
17. Vestibular sac: absent (0), present (1), hypertrophied (2). The vestibular sac is present on extant Delphinida (*sensu* Muizon 1988*b*) and hypertrophied on *Inia*, *Pontoporia* and *Lipotes* (Heyning 1989).
18. Proximal sac: absent (0), single frontal sac (1), sac complex with nasofrontal sacs and vestibule (2). There are some difficulties in finding the homologies for the facial sacs of physeterids and other extant odontocetes. The presence of a proximal sac is regarded as a synapomorphy of all odontocetes, this sac evolving into a frontal sac in the physeterids and a sac complex in the rest of odontocetes. Neither of those two states could be considered as more derived than the other.
19. Distal sac: absent (0), present (1). This feature is present in extant physeterids (Heyning 1989).
20. Blowhole ligament: absent (0), present (1). This soft anatomic structure is present in all recent odontocetes except physeterids (Heyning 1989).
21. Jugal (Barnes 1990): robust (0), slender (1). The strong posterior projection of the jugal in archaeocetes and physeterids contrasts with the much thinner jugal of more crownward odontocetes. The jugal of *Kogia* is considered by Heyning (1989) to be lost.
22. Size of temporal fossa: fossa constituting more than 60 per cent of the height of skull (0), between 60 and 40 per cent (1), less than 40 per cent (2).
23. Position and orientation of origin for temporal muscle on supraorbital process of frontal (Fordyce 1994): origin lies on the posterior face of the supraorbital process and is directed roughly posteriorly (0), origin lies on posteroventral face of supraorbital process and is directed roughly ventrally (1). This character reflects the orientation of the posterior surface of the supraorbital process: posterior to posterodorsal for archaeocetes, *Agorophius*, *Archaeodelphis* and physeterids and posteroventral for more derived odontocetes.
24. Shape of the apex of postglenoid process of the squamosal in lateral view: progressively narrowing in a ventral direction (0), widening to form a rounded ventral tubercule (1). A similar character was used by Muizon (1990) to characterize the Eurhinodelphinoidea. This rounded apex is present in most of the eurhinodelphinids, *Squaloziphius*, *Messapicetus*, *Ninoziphius*, *Tasamcetus* and sometimes *Mesoplodon*.
25. Relative ventral projection of postglenoid and post-tympanic processes of the squamosal: postglenoid process more ventral or at the same level as post-tympanic process (0), apex of the postglenoid process clearly higher (1). The derived condition characterizes the ziphiids, including the fossil *Ninoziphius* and an undescribed primitive ziphiid from Antwerp. The condition on *Messapicetus* is unclear and *Squaloziphius* shows a very long postglenoid process, like *Eurhinodelphis cocheteuxi*.
26. External auditory meatus visible in lateral view as a groove separating postglenoid and post-tympanic process (postmeatal process *sensu* Muizon 1987) of the squamosal: yes (0), no (1). In physeterids such as *Orycterocetus*, *Physeter* and *Kogia*, the pointed postglenoid process is closely appressed to the paroccipital process of the exoccipital. In lateral view, no differences can be distinguished between postglenoid and post-tympanic processes. On the type of *Scaldicetus mortselensis* both processes are clearly separated by a wide external auditory meatus. The groove is very narrow in delphinids like *Delphinus*, but still well marked.
27. Anterior contact between pterygoid and maxilla: absent (0), present (1). This contact is present in *Squalodon*, *Platanista* and their relatives but also in the ziphiid *Berardius* and *Kogia*. However, the condition in Platanistidae and Squalodelphinidae is linked to a lateral shift of the palatine (Muizon 1990), absent in *Berardius* and *Kogia*, and incipient in *Squalodon*.
28. Pterygoids excavated anterior to the choanae by the pterygoid sinuses, with a distinct anterior fossa clearly limited forwards by a rounded wall: absent (0), present (1). Contrary to the condition in the other odontocetes, no anterior fossa hollows the pterygoids of the physeterids. This could be a reversion by overflowing of the sinuses outside the fossae. However, the pterygoids of the Miocene physeterid *Orycterocetus* are already small and flat anteriorly.
29. Anterior level reached by the pterygoid sinus fossae: interrupted before or at the level of antorbital notches (0), going clearly beyond that level (1).
30. Depth of pterygoid sinus fossa in basicranium (modified from Fordyce 1994): shallow or little excavated (0), deep, excavated dorsal to level of foramen ovale (1), deep and extended dorsally into orbit (2). Here again, there is no trace of an excavation of the basicranium by sinuses in physeterids although these sinuses are very developed (see Fraser and Purves 1960).
31. Hamular process of pterygoid: small (0), very enlarged ventro-posteriorly, going beyond the level of the ventral margin of basicranium (1). This structure is enlarged in ziphiids, which have a very large anteroventral part of the pterygoid sinus. The hamular processes are never preserved in *Eurhinodelphis cocheteuxi*, but they are enlarged and deeply excavated in *Ziphiodelphis abeli* (specimen MGPD 26391), in

a way very similar to *Squaloziphius* or *Argyrocetus joaquinensis* (see Kellogg 1934).

32. Lateral lamina of the hamular process of pterygoid: present (0), very reduced (1). The hamular processes are absent in archeocetes. There is no lateral lamina in physeterids and strong reduction is seen in ziphiids and *Eurhinodelphis cocheteuxi*. In *Lipotes*, there are large fenestrations on this lateral lamina. The reduction is also important in *Inia* and fossil relative *Ischyrorhynchus* (Muizon 1988*b*).
33. Lateral lamina of the pterygoid contacting the falciform process of squamosal (modified from Muizon 1988*b*): present (0), absent (1). The anterolaterally directed falciform process of *Eurhinodelphis cocheteuxi* precludes any contact with the pterygoid. The presence of a lateral lamina of the pterygoid in Pontoporiidae was considered to be a reversion by Muizon (1988*b*).
34. High lateral lamina of the palatine reaching posteriorly at least the level of the choanae (modified from Muizon 1984): absent (0), present (1). The posterior projection of the palatine is present in ziphiids (see for example *Ziphius*) and *Eurhinodelphis cocheteuxi*, but this projection is very low and there is no comparison with the high lateral plate of the Delphinida (*sensu* Muizon 1988*b*). This lateral lamina might also be present on *Prosqualodon* (Cozzuol 1989).
35. Tympanosquamosal recess on the squamosal: area medially continuous with the glenoid surface (0), recess more deeply excavated with a distinct wall separating it from the glenoid surface on most of its length (1). On *Platanista*, a deep, short fossa is present, but more posteriorly, and the anterior part of the area shows a medially continuous glenoid surface.
36. Falciform process of the squamosal: well developed (0), strongly reduced by lateroposterior opening of the pterygoid sinus anterior to the periotic-tympanic complex (1). The reduction is seen in ziphiids for which only an isolated peg of the falciform process is preserved. In *Eurhinodelphis cocheteuxi*, the present falciform process is strongly anterolaterally deflected. An anteromedially orientated falciform process is still present in physeterids such as *Scaldicetus mortsenlensis* and *Physeter*.
37. Deep subcircular fossa dorsal to the spiny process of the squamosal (Muizon 1987): absent (0), present (1). See also the description of the periotic fossa in *Waipatia* by Fordyce (1994) which provisionally considers the anterior part of this fossa as homologous to the subcircular fossa. This character, present on platanistids and squalodelphinids, is incipient in *Squalodon* (Muizon 1990 on *Squalodon bariensis* and personal observation on a *Squalodon* squamosal IRSNB 3451-M.300 from Antwerp). A fossa in a similar position is also present with high variability in delphinids (e.g. *Delphinus delphis*). The fossa could, however, be non-homologous in squalodontids and delphinids relative to the other groups; it might represent a nutrient foramen, whereas the fossa is associated with a fissure towards the foramen ovale in *Waipatia* or *Notocetus* (R. E., Fordyce, pers. comm. 2003).
38. Posterior sinus fossa (Muizon 1990): absent (0), present (1). This fossa, hollowing the anterior face of the ventral part of exoccipital, is present in *Platanista*, *Notocetus* and Delphinida, incipient in *Squalodon* and absent in physeterids, ziphiids, *Eurhinodelphis cocheteuxi* and *Waipatia*. A small posterior sinus is observed in *Caperea* and *Balaenoptera* (Fraser and Purves 1960), without excavation of the exoccipital.
39. Size of anterior process of periotic (from the apex to the anterior border of pars cochlearis) relative to pars cochlearis (modified from Luo and Marsh 1996): 60–90 per cent of the length of pars cochlearis (from the anterior border to the posterior edge of the stapedial muscle fossa) (0), 40–60 per cent (1), less than 40 per cent (2). The anterior process of the periotic of *Pontoporia* is very shortened, nearly absent.
40. Apex of anterior process of periotic (modified from Muizon 1988*b*): pointed (0), thickened by a prominent dorsal tubercule giving the apex a rectangular section (1). The great reduction of anterior process for iniids and pontoporids could hide modifications which would then be considered as peculiar to Delphinoidea (*sensu* Muizon 1988*b*).
41. Shape of the apex of the anterior process of periotic in lateral view: rectilinear (0), recurved ventrally to ventromedially (1).
42. Form of the anterior bullar facet of the periotic (modified from Fordyce 1994): facet flat or convex (0), facet depressed with distinct longitudinal groove (1). The facet is hidden and flattened by the large accessory ossicle in most of the physeterids but on some undescribed physeterid periotics from Antwerp and *Orycterocetus* a short groove is present at the apex of the anterior process in a way similar to *Lipotes*.
43. Anterior process of periotic (Fordyce 1994): not thickened transversely (0), thickened transversely by expanded internal and external faces at some point beyond the base of the process (1).
44. Thickening of the base of the anterior process of the periotic on its dorsal face, anteriorly to a depressed area of the dorsal face of the pars cochlearis: absent (0), present (1). This character is a combination of two characters of Fordyce (1994): 'lateral groove or lateral depression affects profile of periotic as viewed dorsally' (character 35) and 'anteroposterior ridge on dorsal side of anterior process and body of periotic' (part of character 55).
45. Accessory ossicle of periotic (modified from Luo and Marsh 1996): small to medium (0), enlarged and subspherical (1). Fordyce (1994) used in a same character the size of the ossicle and its fusion to the anterior process of the periotic. The fusion is present in most of the odontocetes. The accessory ossicle of physeterids is larger than in any other odontocete, including ziphiids.
46. Articulation of the anterior process of the periotic to the outer lip (= processus tubarius) of tympanic (modified from Luo and Marsh 1996): contact of the ventral surface of anterior process of periotic with the outer lip of tympanic (0), contact with the thickened rim of the outer lip of the tympanic additional to a contact with the accessory ossicle (1), contact only with the accessory ossicle (2). Luo and Marsh (1996) considered all the extant odontocetes, including *Mesoplodon*, but with the exception of *Platanista*, to share the second derived character state. However, the ziphiids show an articulation by the accessory ossicle that is limited to the fovea epitubaria, while a short but distinct contact by the outer lip of the tympanic is present on the

deep anterior bullar facet. This condition of the ziphiids is very close to the condition in *Eurhinodelphis cocheteuxi*, and different from what is observed on physeterids and delphinids, with a laterally widened accessory ossicle. The contact between the thin outer lip of the tympanic and the anterior bullar facet is preserved on a long anterior distance (nearly two-thirds of the length of the anterior process) on the eurhinodelphinid periotic IRSNB 3235-M.343, *Schizodelphis longirostris sensu* Muizon (1988*a*).

47. Lateral tuberosity of the periotic separated from the anterior process by a marked transverse groove (part of the anteroexternal sulcus) in lateral view: presence of the groove (0), absence, lateral tuberosity continuous with the anterior process (1).
48. Lateral tuberosity of the periotic: in ventral view, short, narrow and poorly individualized lateral tuberosity (0), thick tuberosity, well developed laterally with an exposed ventral surface distinctly larger than the mallear fossa (1).
49. Fenestra rotunda of the periotic reniform, with a dorsal fissure directed towards the aperture for the cochlear aqueduct (Fordyce 1994): absent (0), present (1).
50. Position of the dorsal opening of the facial canal: on the dorsal face of pars cochlearis (0), at the contact between pars cochlearis and anterior process or sending a deep groove towards this junction (1).
51. Position of the aperture for the cochlear aqueduct: dorsomedial (0), medial (1).
52. Size of the aperture for the cochlear aqueduct: small (0), enlarged (1).
53. Aperture for the endolymphatic duct: in dorsal view, at the transverse level of the tractus spiralis foraminosus (0), clearly more lateral than the tractus spiralis (1).
54. Orientation of the posterior process of the periotic (Luo and Marsh 1996): posterior process projecting posterolaterally (0), ventrolaterally (1). The ventral component of the projection is, for example, obvious in ziphiids or eurhinodelphinids, with a ventral curvature of the apex of the posterior bullar facet, while in *Squalodon*, the facet is roughly flat.
55. Articular process on the periotic (Fordyce 1994): process absent (0), incipient ridge present (1), strong ridge (2), peg (3).
56. Articulation of the tympanic with the squamosal (Muizon 1984): present (0), absent (1). The isolation of the ear bones from the basicranium is reflected in the loss of articulation between the tympanic posterior process and squamosal, a condition seen on Delphinida. The posterior process of *Schizodelphis longirostris* (*sensu* Muizon 1988*a*) IRSNB 3235-M.343 shows a very clear contact with the posterior meatal crest and post-tympanic process of the squamosal. No posterior process attributable to *Eurhinodelphis cocheteuxi* is available. In *Lipotes*, the anterolateral margin of the posterior process shows a clear break, as on *Schizodelphis* cf. *sulcatus* from the Musée d'Uzès, figured by Muizon (1988*a*, fig. 6D). Following Muizon (1984), this structure in *Lipotes* does not correspond to a true articulation with the squamosal but to a secondary development of the posterior process. On an undescribed tympanic from Antwerp very close to *Schizodelphis* cf. *sulcatus* of Muizon (1988*a*), the anterolateral margin of the posterior process is very smooth, preventing the presence of an articulation with the squamosal. The condition is for now considered as variable in *Schizodelphis*, and pending revision of the Belgian specimens, not included in this analysis.
57. Very large posterior process of the tympanic (Muizon 1990): absent (0), present (1). This large process, present in *Ninoziphius*, extant ziphiids, probably *Orycterocetus* and extant physeterids, possibly developed by assimilation of some elements of the squamosal in the region posterior to the external auditory meatus (Muizon 1990), is difficult to observe in fossils. It is easily broken and its track on the basicranium is not clearly distinct. A posterior process nearly as long as the bulla is already present in archaeocetes like *Indocetus* (see Luo and Gingerich 1999). In mysticetes, the process is sutured to the very enlarged mastoid process (posterior process) of the periotic on subadults, and fused on adults (Luo and Gingerich 1999). This might give the opposite polarity (primitive) to the large posterior process of the tympanic in ziphiids and physeterids, as suggested by the tree of Heyning (1989).
58. Dorsal margin of the involucrum of the tympanic cut by a median indentation, in medial view: absent (0), present (1).
59. Abrupt anterior narrowing of the involucrum of the tympanic at more or less mid length in dorsal view: absent (0), present (1). This character is sometimes correlated to the indentation of the involucrum in lateral view, as in *Eurhinodelphis cocheteuxi*, but is present without indentation in *Lipotes*.
60. Excavation of the dorsal margin of the involucrum of the tympanic anterior to the posterior process (modified from Muizon 1988*b*): absent (0), excavation with dorsal and ventral margins of involucrum parallel (1), stronger excavation with sigmoid-shaped dorsal margin (depression deeper posteriorly) (2). The primitive state is also found in *Dorudon* (no information on *Zygorhiza*).
61. Excavation of the dorsomedian border of the involucrum of the tympanic, separating strongly convex thickened anterior and posterior parts of the involucrum: absent, continuous border of the involucrum (0), present (1). This characterizes *Physeter*, *Kogia*, *Orycterocetus* and undescribed physeterid tympanics from Antwerp.
62. Anterior spine on the tympanic (modified from Muizon 1987, 1990): absent, with a more or less rectilinear anterior margin (0), anterior margin pointed but without marked thickening (1), individualized strong anterior spine (2).
63. Anterolateral convexity of the tympanic with anterolateral notch (Muizon 1987): absent (0), present (1). The absence of a strong anterolateral convexity on *Platanista* might be a reversal. This character is present in *Ziphiodelphis abeli*.
64. Median groove on the tympanic (modified from Muizon 1987): short extension on ventral face of the interprominental notch (0), anterolateral curvature of the median groove to connect the long lateral furrow on outer lip (1), median groove reaching an anterior level beyond the lateral furrow, and often slightly laterally recurved (2), long and deep rectilinear median groove reaching at least the base of the anterior spine (3).
65. Inner posterior prominence of the tympanic in ventral view narrowing posteriorly and strongly separated from

the rounded outer posterior prominence by a deep posterior part of the median groove: no (0), yes (1). The inner posterior prominence of *Ninoziphius* is narrow but close to the outer one, as in the other ziphiids. The wide median groove is present in *Platanista*, *Lipotes*, *Pontoporia* and *Delphinus* but not in *Atocetus*.

66. Ventral margin of the tympanic in lateral view: convex (0), concave (1).
67. Sigmoid process of the tympanic: lateral crest transversely orientated (0), rounded posterior projection of the ventral part of the lateral crest (1), strong posterior projection with a distinct posteroventral angle (2). The primitive state is present in archaeocetes, *Pontoporia* and *Delphinus* for example, the first derived state in *Squalodon*, *Notocetus* and *Lipotes*, and the second in *Ninoziphius* and *Mesoplodon*.
68. Anterior inflexion of the dorsomedial tip of the sigmoid process (modified from Muizon 1988*b*): absent (0), present (1). Not clear in *Zygorhiza*, the primitive condition is observed in *Dorudon*.
69. Relative size of the tuberculum and articular head of the malleus, in posteromedial view: tuberculum constituting more than one-third of the length of the malleus (0), less than one-third, with expanded articular head (1). The primitive state is found in mysticetes (see e.g. Muizon 1985), *Squalodon*, *Notocetus* and Delphinida. The shortened tuberculum is present in physeterids, ziphiids, *Eurhinodelphis cocheteuxi*, *E. bossi*, *Schizodelphis sulcatus* and *Eoplatanista italica*. The condition of *Kogia* and *Physeter* is, however, different from the rest of the derived taxa for this character; the posteromedial face of their malleus is mostly occupied by the two articular facets, as in *Mesoplodon* or *Ziphius*, but the remains of the tuberculum, bearing the manubrium and the processus muscularis, are laterally shifted relative to the line of junction of the two facets in *Physeter* and *Kogia* (see Text-fig. 11). This might indicate convergent evolution in the reduction of the tuberculum in this group.
70. Relative levels of the manubrium and processus muscularis of the malleus in posteromedial view and with tuberculum directed upwards (modified from Muizon 1985, 1987): processus muscularis lower than manubrium (0), same level (1), processus muscularis higher than manubrium (2).
71. Double-rooted posterior teeth (Muizon 1987): present (0), absent (1). Among odontocetes, double rooted teeth are retained in at least *Agorophius*, *Simocetus*, *Prosqualodon*, *Squalodon* and relatives, and *Waipatia*.
72. Acromion located on the anterior edge of the scapula, without supraspinous fossa (Muizon 1987): no (0), yes (1). This character and the following one have been used by Muizon (1987, 1990) as key characters of Platanistoidea including Platanistidae, Squalodelphinidae and Squalodontidae. Cozzuol and Humbert-Lan (1989) noticed the existence of a supraspinous fossa and evidence of the presence of coracoid process in *Phoberodon*, which has been referred to the squalodontids.
73. Coracoid process (Muizon 1987): present (0), absent (1).

Data matrix

Data matrix of 73 characters for two outgroups and 17 analysed taxa. All characters with multiple states are treated as unordered. Primitive state, 0; derived states, 1, 2, 3; variable between 0 and 1, a; variable between 1 and 2, b; missing character, ?; irrelevant character, -.

Taxa	Characters							
	5	10	15	20	25	30	35	40
Zygorhiza	00000	00000	00-00	?????	00000	00000	0-000	00000
Archaeodelphis	????0	00000	00-00	?????	??000	0?00?	0-?00	?????
Orycterocetus	00000	00-1	10-01	?????	?200-	10000	01100	??020
Physeter	10000	00-1	10-01	10110	0200-	10000	01100	00010
Kogia	00001	00-1	10-01	10110	-2000	11000	01100	10020
Squalodon	00011	00000	10001	?????	11100	01101	00000	08110
Waipatia	00011	00000	10001	?????	12110	00100	???00	01000
Notocetus	0011?	00100	1a101	?????	11100	01111	???00	01100
Platanista	01010	00000	10101	20201	?1100	01101	00000	01100
Eurhinodelphis cocheteuxi	11011	10100	11011	?????	12110	00101	?1101	00000
Ninoziphius	???1?	???00	1????	?????	1??11	00111	1?101	???00
Mesoplodon	10111	11000	11011	20201	12111	00111	11101	10000
Ziphius	11011	11100	11011	20201	12101	00111	11101	10000
Schizodelphis	11a11	00100	10001	?????	12110	00102	??001	00000
Ziphiodelphis abeli	11011	10100	10011	?????	12110	00102	11?01	00?00
Pontoporia	01110	00010	10001	22201	11100	00102	00011	00120
Lipotes	01010	00000	10001	22201	11100	00112	00111	00110
Atocetus	00110	00110	10001	?????	10100	00112	00110	00121
Delphinus	00110	00100	10001	21201	11100	00112	00111	01121

Taxa	Characters (continued)						
	45	50	55	60	65	70	73
Zygorhiza	00000	00000	00000	00000	00000	000??	000
Archaeodelphis	?????	?????	?????	?????	?????	?????	???
Orycterocetus	11001	21000	01010	01000	10010	000??	1??
Physeter	10001	21001	01010	01000	10010	00012	100
Kogia	10001	21111	00000	01000	10010	00012	100
Squalodon	10000	00011	00102	00000	02130	01000	011
Waipatia	01010	10101	01101	00000	01020	000??	0??
Notocetus	01010	10000	0110b	00000	02130	01000	111
Platanista	01010	10011	10103	00000	02031	00000	111
Eurhinodelphis cocheteuxi	01010	10110	11011	??110	01020	0??10	1??
Ninoziphius	01000	10010	11010	01110	01020	020??	1??
Mesoplodon	01100	10110	11010	01aa0	00020	a2012	100
Ziphius	01100	101a0	a1010	01110	01020	02011	100
Schizodelphis	01010	101a1	11010	a0a10	0102a	01010	1??
Ziphiodelphis abeli	01010	?0111	11010	?0110	01120	010??	1??
Pontoporia	00000	21001	001-0	10001	00021	00102	100
Lipotes	11000	21010	00100	?0012	01021	01101	100
Atocetus	10000	21011	00100	10002	00020	11102	100
Delphinus	10000	21001	00100	10002	01021	10102	100