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Review of the Miocene long-snouted dolphin *Priscodelphinus cristatus* du Bus, 1872 (Cetacea, Odontoceti) and phylogeny among eurhinodelphinids

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Abstract

The Miocene long-snouted dolphin species *Eurhinodelphis cristatus* (*sensu* Abel, 1902) (Cetacea, Odontoceti, Eurhinodelphinidae), recognized in the area of Antwerp (North of Belgium, southern margin of the North Sea Basin) and the east coast of the USA (Maryland and Virginia), is re-described, including several undescribed specimens associated with ear bones and teeth. The systematic affinities of this species with other members of the family Eurhinodelphinidae are investigated, leading to its inclusion in the new genus *Xiphiacetus*, together with the species *Eurhinodelphis bossi* (*sensu* Kellogg, 1925). The asymmetry of the skull is discussed, especially for a strange specimen with an asymmetrical basicranium interpreted as the consequence of pathology. Thanks to recently found specimens, the stratigraphic range of *Xiphiacetus cristatus* might be extended in the Upper Miocene, widening the Eurhinodelphinidae distribution, previously limited to an Upper Oligocene – Middle Miocene interval.

The description in *X. cristatus* of several structures related to the telescoping of the skull, hearing, and the feeding apparatus, considered as derived compared to other eurhinodelphinids, allows suggestions concerning evolutionary trends inside the family.

A cladistic analysis is undertaken in a way to examine the phylogenetic relationships between the best-known eurhinodelphinid genera. The main results of the analysis are a sister-group relationship between *Schizodelphis* + *Xiphiacetus* and *Ziphiodelphis* + (*Mycteriacetus* + *Argyrocetus*), and a more stemward *Eurhinodelphis*. This topology leads to some hypotheses concerning the evolution of the habitat of the eurhinodelphinids. An appendix contains remarks about the systematic status of several taxa usually included in, or related to, the family Eurhinodelphinidae.

Key-words: Eurhinodelphinidae, taxonomy, *Xiphiacetus cristatus*, evolutionary trends, phylogeny

Résumé

L'espèce de dauphin longirostre miocène *Eurhinodelphis cristatus* (*sensu* Abel, 1902) (Cetacea, Odontoceti, Eurhinodelphinidae), identifiée dans la région d'Anvers (nord de la Belgique, bord sud du Bassin de la Mer du Nord) et sur la côte est des Etats-Unis (Maryland et Virginie), est re-décrite, en incluant plusieurs spécimens non encore décrits, comprenant des os de l'oreille et des dents. Les affinités systématiques de cette espèce avec les autres membres de la famille Eurhinodelphinidae sont investiguées, menant à son inclusion dans le nouveau genre *Xiphiacetus*, auquel est également rapportée l'espèce *Eurhinodelphis bossi* (*sensu* Kellogg, 1925). L'asymétrie du crâne est commentée, en particulier pour un étrange spécimen muni d'un basicrâne asymétrique interprété comme la conséquence d'une pathologie. Grâce à des spécimens récemment découverts, l'extension stratigraphique de *Xiphiacetus cristatus* pourrait être prolongée dans le Miocène supérieur, allongeant la distribution des Eurhinodelphinidae préalablement limitée à un intervalle Oligocène supérieur – Miocène moyen.

La description chez *X. cristatus* de plusieurs structures liées au 'téléscopage' du crâne, à l'audition, et à l'appareil nutritif, considérées comme dérivées par rapport aux autres eurhinodelphinidés, permet quelques suggestions à propos de tendances évolutives au sein de la famille.

Une analyse cladistique est entreprise afin d'examiner les relations de parenté entre les genres les mieux connus d'eurhinodelphinidés. Les résultats principaux de l'analyse sont une relation de groupes-frères entre *Schizodelphis* + *Xiphiacetus* et *Ziphiodelphis* + (*Mycteriacetus* + *Argyrocetus*), et une position plus basale pour *Eurhinodelphis*. Cette topologie permet quelques hypothèses concernant l'évolution de l'habitat des eurhinodelphinidés. Un appendice contient quelques remarques à propos du statut systématique de plusieurs taxa habituellement inclus dans, ou apparentés à, la famille Eurhinodelphinidae.

Mots-clefs: Eurhinodelphinidae, taxinomie, *Xiphiacetus cristatus*, tendances évolutives, phylogénie

Introduction

In 1872, du Bus shortly described several species in the genera of long-snouted dolphins *Eurhinodelphis* du Bus, 1867 and *Priscodelphinus* Leidy, 1851 (Cetacea, Odontoceti, Eurhinodelphinidae), from the Miocene of Antwerp (North of Belgium), among them, the species *Priscodelphinus productus* and *P. cristatus*. The new combination *Eurhinodelphis cristatus* was proposed by Abel (1902) on the basis of eight skulls and partial skulls referred to these species; the holotype of *E. cristatus* is associated with all the cervical and several thoracic vertebrae and ribs. Later, the presence of the species was suspected in the Miocene of Portugal (Mata, 1962-63), and recognized in the Miocene of the eastern coast of the USA, Calvert Formation (Myrick, 1979, unpublished thesis; Muizon, 1988a), and of Italy (Bianucci *et al.*, 1994).

Additional specimens from Belgium and a comparison with specimens from the Calvert Formation allow a more detailed description and a systematic revision of *E. crista-*

tus (*sensu* Abel, 1902). As suggested by Lambert (2004), this species is referred here to a new genus together with *E. bossi* Kellogg, 1925. The asymmetry of the skull is discussed, especially for a strange individual with an asymmetric basicranium. The stratigraphic data obtained with several recently found Belgian skulls might lead to a refining of the stratigraphic range of the species.

Comments are given about evolutionary trends observed among the eurhinodelphinids. The general phylogenetic study of the odontocetes by Muizon (1991) briefly commented the relationships inside the family Eurhinodelphinidae; a more detailed study, using parsimony software, is undertaken, taking account of the new taxonomy within the family.

Material and methods

Abbreviations. **IRSNB**: Institut royal des Sciences naturelles de Belgique, Brussels; **M**: Fossil mammals collection of types and figured specimens from the IRSNB; **MGPD**: Museo di Geologia e Paleontologia dell'Universita di Padova, Italy; **MNHN**: Muséum national d'Histoire naturelle, Paris, France; **MP**: Museo di Storia Naturale e del Territorio Certosa di Calci dell'Università di Pisa, Italy; **USNM**: United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA; **YPM**: Peabody Museum of Natural History, Yale University, New Haven, USA; **ZMA**: Zoölogisch Museum Amsterdam, The Netherlands.

Terminology. The terminology for cranial, ear bones and vertebral anatomy is mainly taken from: Fordyce (1994), Kasuya (1973), Muizon (1984, 1988a), and Rommel (1990). The orientations of the tympanic bulla and periotic are simplified in the descriptions compared to the actual anatomical position on the basicranium. The long axis of the tympanic is considered as anteroposterior, with ventral surfaces of inner and outer posterior prominences indicating the horizontal plane. The anterior direction of the periotic is given by the longitudinal axis of the anterior process, and the horizontal ventral plane by the surface contacting the most ventral points of pars cochlearis and anterior process.

Schematic drawings illustrating the measurements on the skull of eurhinodelphinids are in Lambert (2004, fig. 1).

Taxonomy

Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Superfamily Eurhinodelphinoidea Muizon, 1988a
Family Eurhinodelphinidae Abel, 1901
Xiphiacetus n. gen.

Etymology. From *Xiphias*, swordfish, and *cetus*, whale in ancient Greek; *Xiphiacetus* because of a rostrum longer than the mandible, a feature characterizing the swordfish. Gender: masculine.

Type species. X. cristatus (du Bus, 1872)

Included species. X. cristatus and *X. bossi* (Kellogg, 1925)

Diagnosis. Eurhinodelphinid genus differing from:

- the closest genus *Schizodelphis* Gervais, 1861 in: more robust skull with more progressive elevation of the premaxillae towards the vertex; medial plate of the maxilla along the vertex less concave and less erected; thicker supraorbital process; rostrum generally relatively wider at its base; longer fossa for the postorbital lobe of the pterygoid sinus, usually longer than half the width of the orbit roof.
- *Ziphiodelphis* Dal Piaz, 1908 in: narrower and thicker triangular part of the premaxilla medially to the premaxillary foramen, lacking the more regular flatness and lateral slope seen in *Ziphiodelphis*; mesorostral groove widely open at that level; posterolaterally shorter plate of the maxilla along the vertex, giving the posterodorsal outline of the skull a more rounded aspect in lateral view; longer and narrower vertex (width less than 30 per cent of the postorbital width); nasal longer than wide lacking an anterodorsal projection.
- *Eurhinodelphis* du Bus, 1867 (*sensu* Lambert, 2004) in: maxillary part of the rostrum relatively shorter; dorsomedian portion of the supraoccipital shield concave; less elevated and wider paroccipital process of the exoccipital with lower occipital condyles (ventral margin of the condyles much lower than the level of the floor of the temporal fossa); distinctly concave premaxillary sac fossa; zygomatic process of the squamosal flatter in lateral view and wider in ventral view; presence of a fossa for the postorbital lobe of the pterygoid sinus on the ventral surface of the supraorbital process; pars cochlearis of the periotic anteromedially rounded; inner posterior prominence of the tympanic distinctly narrower than the outer prominence.
- *Argyrocetus* Lydekker, 1893 in: relatively wider face (ratio between the bizygomatic width of the skull and the length of the cranium from the antorbital notch to the occipital condyles > 1); more elevated vertex with nasal longer than wide, at the same level or lower than the frontal; more erected supraoccipital shield (Appendix 1 for comments about the content of the genus *Argyrocetus*).
- *Macrodelphinus* Wilson, 1935 in: more elevated and more transversely compressed vertex with nasal as long as wide or longer than wide, and frontal as long as, or shorter than the nasal; supraoccipital shield closer to the vertical.
- *Mycteriacetus* Lambert, 2004 in: relatively wider cranium (ratio between the bizygomatic width of the skull and the length of the face from the antorbital notch to the occipital condyles > 1); more elevated vertex with nasal at the same level or lower than the frontal, and frontal as long as, or shorter than the nasal; more erected supraoccipital shield.

Comment. The holotype of *Xiphiacetus cristatus* was originally referred by du Bus (1872) to *Priscodelphinus*, but that genus is now restricted to its type-species and holotype – a series of six undiagnostic vertebrae from New Jersey (*P. harlani*, Leidy, 1851) – and considered as Odontoceti *incertae sedis* (e.g., Fordyce & Muizon, 2001).

Xiphiacetus cristatus (du Bus, 1872)

* 1872 *Priscodelphinus cristatus* du Bus, p. 497.
v. 1880 *Priscodelphinus cristatus* Van Beneden & Gervais, p. 495.
v. 1902 *Eurhinodelphis cristatus* Abel, pl. 15, figs 1, 2; pl. 16; pl. 17, fig. 3.
v. 1931 *Eurhinodelphis cristatus* Abel, pl. 19, fig. 3; pl. 20, figs 1, 2, 18-20; pl. 21, figs 2, 3, 9; pl. 22, figs 1, 2; pl. 23, figs 8-10.

Emended diagnosis. This species differs from *Xiphiacetus bossi* in the following combination of characters: major thickening of the maxilla on the supraorbital process; posterior margin of the maxilla on the cranium notched by a forwards indentation of the frontal and the supraoccipital laterally to the vertex; vertex acute and short in lateral view constituted by the posterodorsal edge of the frontals and the supraoccipital, vertical on its mediodorsal portion against the frontals; trapezoid dorsal surface of the frontals on the vertex plane and anteriorly sloping; relatively lower temporal fossa (less than 20 per cent of the bizygomatic width); deep and long fossa for the postorbital lobe of the pterygoid sinus.

Holotype. IRSNB 3234-M.361, a partial skull lacking teeth, ear bones and basicranium, associated with the seven cervical vertebrae, seven thoracic vertebrae, and several ribs (found between 1861 and 1863, individual 1 in Abel, 1902, pl. 15, figs 1, 2; several post-cranial elements are figured in Abel, 1931, pl. 19, fig. 3; pl. 20, figs 1, 2, 18-20; pl. 21, figs 2, 3, 9; pl. 22, figs 1, 2; pl. 23, figs 8-10).

Locus typicus. The holotype was found in Antwerp (Fig. 1), and the locality cited by Abel (1902) is '? 4^{e} Section'. This locality corresponds to a portion of the fortification belt built in the 1860's around Antwerp (see map in Vanden Broeck, 1874), north of Berchem, south-eastern suburb of Antwerp. However, the question mark of Abel lowers the interest of that information.

Stratum typicum. No data are available for the holotype. However, several skulls from Antwerp and the skulls from the Calvert Formation (east coast of USA) are accompanied by more precise stratigraphic information. The species is limited to the Miocene, mainly Middle Miocene, with a possible extension in the Belgian Upper Miocene (see stratigraphic remarks below).

Referred Belgian specimens. IRSNB 3241-M.1893, a well preserved partial skull (found in '4^{e} Section', Antwerp; individual 2 in Abel, 1902, pl. 16); IRSNB 3242, fragments of skull (found in '? 4^{e} Section', Antwerp, 1861-1863; individual 4 in Abel, 1902, pl. 17, fig. 3); IRSNB 3237-M.1894, partial skull (found in '? 4^{e} Section', Antwerp, 1861-1863; individual 5 in Abel, 1902); IRSNB 3240-M.1895, partial skull (found in '4^{e} Section', Antwerp, 1861-1863; individual 6 in Abel, 1902); IRSNB M.1896, partial skull (found in 1978 by G. Paredis in Borgerhout, eastern suburb of Antwerp, near the Stenen Brug bridge, during the construction of the motorway around the city); IRSNB 3227-M.1897, partial skull (with a label '*Eurhinodelphis cristatus*, Abel, 1904'); IRSNB 3236, partial skull (found in Antwerp area); IRSNB 8243-M.1898, partial skull (with a label '*Eurhinodelphis cristatus* – Et.: Anversien, lettre M,

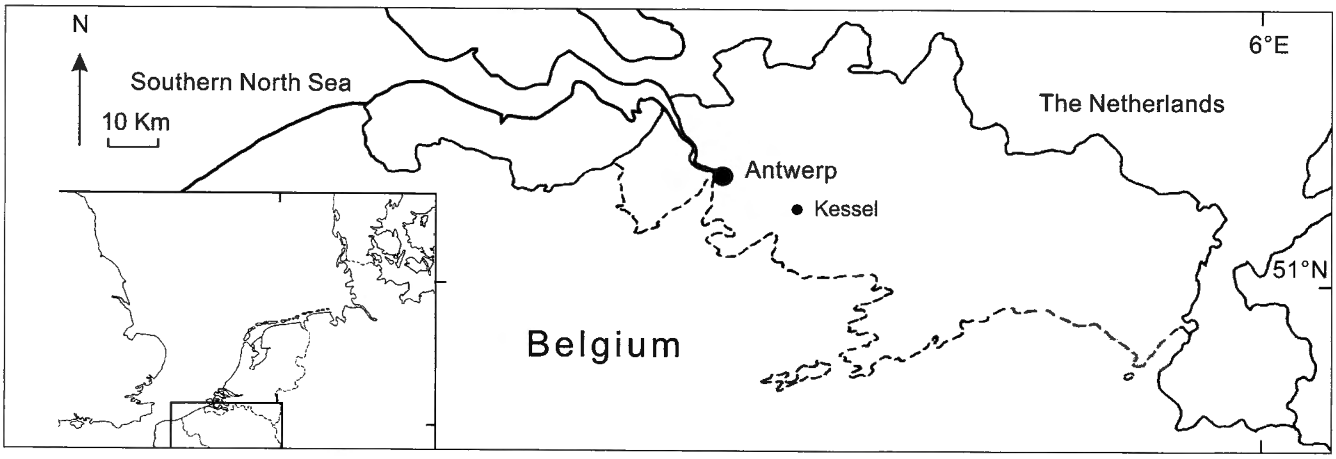

Fig. 1 — Map of northern Belgium and location of the two localities of the Belgian specimens of *Xiphiacetus cristatus*, Antwerp and Kessel. Inset: southern North Sea Basin. Dashed line: southern limit of Neogene deposits in Belgium (modified after Tavernier & de Heinzelin, 1963).

Loc.: Kessel – Expl. fév., mars, 1910 – Reg. – I. G. 8243'; Kessel: Prov. Antwerp); IRSNB 8243', vertex and left supraorbital process (with a label 'isolé – Terrain Boldérien – Loc. Kessel – le 18 mars 1910 – I. G. n° 8243'); IRSNB 3589, a fragment of the right side of the vertex (found in the Antwerp area); IRSNB M.1899, the maxillary part of a right supraorbital process (found in the Antwerp area); IRSNB M.1900, a right supraorbital process (found in the Antwerp area); IRSNB M.1901, a right supraorbital process (found in the Antwerp area); IRSNB 3245, fragmentary rostrum [found in Antwerp, 1861-1863, individual 17 of *Eurhinodelphis longirostris* (*sensu* ABEL, 1902)]; IRSNB M.1902, a fragmented right tympanic (found associated to a partial skull in 1974 by L. Peeters, near the locality of IRSNB M.1896 (Deurne bridge)].

Referred American specimens. The skulls from the Calvert Formation referred by MYRICK (1979) to *Eurhinodelphis cristatus*: USNM 21303, USNM 171067, USNM 13470, USNM 24856, USNM 167675, USNM 13436, USNM 21363, and USNM 21360; *E. whitmorei*: USNM 25666; *E. ashbyi*: USNM 244401 and USNM 244411 (partially suggested in MUIZON, 1988a; detailed in LAMBERT, 2004).

Further comments on specimens previously reported to the species. IRSNB 3243-M.367 is a partial skull lacking the apical part of the rostrum, nasals and ear bones, from '4e Section, Vieux-Dieu' (= Oude God, Mortsel). It is the holotype and only specimen of *Priscodelphinus productus sensu* DU BUS 1872, figured by VAN BENEDEN & GERVAIS (1880, pl. 58, fig. 3), and revised by ABEL (1902) in *Eurhinodelphis cristatus* (individual 3, pl. 18, fig. 3). It is referred to *Xiphiacetus bossi*, as well as the fragments of skull IRSNB 3497 ['4e Section', also placed by ABEL (1902) in *Eurhinodelphis cristatus*, individual 7] (LAMBERT, in press).

IRSNB 3443-M.368, a right squamosal with the corresponding paroccipital process of the exoccipital (from '3e section', Antwerp, individual 8 of *Eurhinodelphis cristatus* in ABEL, 1902), is too fragmentary to be included in a defined species of eurhinodelphinid; it shows actually more similarities with *E. longirostris*, and is referred here to Eurhinodelphinidae aff. *Eurhinodelphis*. Its association with three vertebrae (two cervicals and one thoracic) is judged doubtful.

The partial skull of an odontocete from the late Miocene of Portugal referred to *Eurhinodelphis* cf. *cristatus* by MATA (1962-63, fig. 1, pl. 1-3) lacks all diagnostic characters of the species and shares affinities with the kentriodontids (ESTEVENS, 2003; LAMBERT, 2004).

BIANUCCI *et al.* (1994) identified a partial skull from the Miocene of the "Pietra leccese" (Apulia, Italy) as *Eurhinodelphis cristatus*. Its state of preservation precludes a specific attribution; it is referred here to *Xiphiacetus* aff. *bossi*, according to the observations in LAMBERT (2004).

Description

Skull (Pl. 1, Pl. 2, Figs 1-3, Pl. 3, Fig. 1; Figs 2-4)

Premaxilla. The premaxilla is longer than the maxilla anteriorly, a feature observed on the small skull IRSNB M.1896: the premaxilla-maxilla suture reaches the ventral margin of the rostrum 450 mm anteriorly to its base (Pl. 1, Fig. 2). However, this rostrum lacks its anterior portion, and consequently the length of the premaxillary portion cannot be evaluated. On better-preserved skulls from the Calvert Formation, the premaxilla-maxilla suture is completely fused anteriorly, precluding a quantification of the relative lengths of the maxilla and the premaxilla on the rostrum. In particular, the large skull USNM 21363 has a nearly complete rostrum with a rostral length of 970 mm, and a total length of the skull of 1170 mm (Fig. 2; Table 1), but without indications of the anterior part of the premaxilla-maxilla suture. A deep longitudinal groove follows the rostral maxilla-premaxilla suture from *ca.* 15 mm anterior to the antorbital notch, at the exit of a dorsal infraorbital foramen; the groove

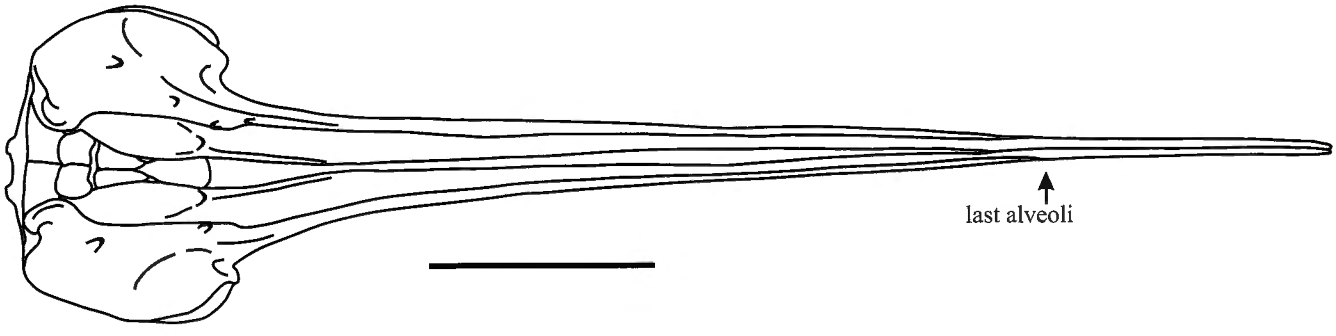

Fig. 2 — Reconstruction of the skull of *Xiphiacetus cristatus* in dorsal view, mainly based on the nearly complete specimen USNM 21363, from the Calvert Formation, Middle Miocene of the east coast of the USA. Scale bar = 200 mm.

Table 1 — Measurements (mm) on the skulls of *Xiphiacetus cristatus* from IRSNB and USNM. 'e' indicates estimate, '+' nearly complete and '–' no data. The numbers of the measurements refer to Lambert, 2004, fig. 1.

	Holotype IRSNB 3234-M. 361	IRSNB 3241-M.1893	IRSNB M.1896	IRSNB 3227-M.1897	IRSNB 8243-M.1898	IRSNB 3237-M.1894
1. total length skull	–	–	–	–	–	–
2. length base rostrum-anterior maxilla	–	–	+450	–	–	–
3. length anterior orbit-posterior skull	–	187	–	–	–	–
4. length anterior supraoccipital-anterior orbit	130	134	e128	–	149	–
5. length orbit	+84	82	57	–	80	e77
6. length temporal fossa	–	e71	–	–	–	–
8. width base rostrum	e123	–	e123	–	103	–
9. width premaxillae at base rostrum	e80	e76	e62	–	–	–
10. width skull at level of postorbital processes	e240	–	–	–	224	e208
11. width skull at level of zygomatic processes	–	228	–	e258	–	179
12. width bony nares	–	32	e30	e43	29	33
13. width nasals	e34	e33	e31	–	41	37
14. maximal posterior premaxillary width	e113	e90	–	e93	84	–
15. minimal posterior distance between maxillae	46	e40	e43	44	40	44
16. width between ventromedial margins exoccipitals	–	118	91	e166	–	113
17. width between lateral margin of occipital condyles	–	90	78	96	–	81
18. width between inner margins of occipital condyles	–	35	38	42	–	34
19. height cranium	–	175	–	–	–	–
21. height base rostrum	–	71	e47	–	e51	–
22. height temporal fossa	–	45	–	–	–	–
23. height ventral margin of occipital condyles	–	32	36	53	–	31
24. height occipital condyles	–	51	46	e48	–	44

	USNM 21363	USNM 24856	USNM 13436	USNM 21303	USNM 171067	USNM 21360	USNM 167675	USNM 244411	USNM 244401	USNM 25666
1.	+1170	–	–	–	–	–	–	–	–	–
2.	–	–	–	–	–	–	–	–	–	–
3.	e200	–	186	–	171	–	188	–	–	–
4.	166	153	138	120	124	–	128	100	129	166
5.	89	–	72	–	56	–	67	e61	–	70
6.	e77	–	e65	–	e62	–	58	–	–	–
8.	157	e135	150	101	–	–	–	118	100	114
9.	83	70	86	61	–	–	76	70	e51	57
10.	275	258	251	181	194	–	231	205	202	226
11.	263	–	233	–	204	–	222	–	–	–
12.	36	38	36	32	e28	21	35	27	25	22
13.	54	57	e49	e31	e39	37	–	e38	40	39
14.	99	e92	100	85	79	84	–	91	e83	97
15.	57	52	48	36	46	36	57	e34	30	41
16.	e133	–	125	–	95	–	e130	–	–	–
17.	–	–	96	–	78	–	96	–	–	–
18.	–	–	37	–	35	–	39	–	–	–
19.	182	–	171	–	155	–	157	–	–	–
21.	79	–	75	–	–	–	70	–	–	66
22.	37	–	e32	–	32	–	28	–	–	–
23.	–	–	46	–	37	–	40	–	–	–
24.	–	–	50	–	45	–	51	–	–	–

nearly reaches the apex of the rostrum. Additionally to the eurhinodelphinids, a similar groove is present in other groups of Miocene long-snouted dolphins (e.g., platanistids, eoplatanistids) and in extant river dolphins (e.g., *Platanista*, *Pontoporia*), innervating/vascularizing the anterior of the rostrum.

The slight posterior widening of the premaxilla on the rostrum increases 100-150 mm before the base of the rostrum, together with a considerable flattening of the bone. In this widened area, the median portion of the premaxilla is often depressed relatively to the lateral portion; the degree of medial deepening is however variable. The premaxillary sac fossa is usually well excavated, and its elevation towards the vertex is only pronounced from the mid-length of the orbit. The posterior apex of the premaxilla contacts the frontal, as a thin process between the nasal and the median margin of the maxilla. The premaxilla is sometimes thick and wide at the level of the posterior margin of the bony nares.

Maxilla. The maxilla is poorly exposed in dorsal view of the rostrum, with a slight lateral bulge *ca.* 200 mm anteriorly to the base of the rostrum. The lateral margins of the maxillae diverge towards the antorbital notches, widening the base of the rostrum; the lateral margin of the maxilla is extended on the supraorbital process by a short longitudinal crest, medial to the antorbital notch.

On the skull USNM 21363, alveoli with a mean diameter of 8 mm and separation septa of 5-7 mm are present on the first 740 mm of the rostrum, interrupting 240 mm before the apex. This condition confirms that the apex of the rostrum was only constituted by the edentulous premaxillae, as it is the case in *Eurhinodelphis cocheteuxi* DU BUS, 1867, *E. longirostris* DU BUS, 1872, and *Xiphiacetus bossi*. Number and spacing of the alveoli are intraspecifically variable; for instance, on the smaller IRSNB M.1896, the bases of the crowns of successive anterior teeth nearly contact, with a diameter of 5 mm for the alveoli. This variability might be related to the age of the individuals.

A striking feature of *Xiphiacetus cristatus* is the frequent strong thickening of the maxilla on the supraorbital process, forming a longitudinally elongated dome, posterolateral to the antorbital notch. The development of the dome is variable, rarely absent, and sometimes reaching 25-30 mm of height in lateral view (e.g., IRSNB M.1899, Pl. 1, Figs 7-8). This structure stresses the median depression of the face due to the medial slope of the flat dorsal surface of the premaxillae. The dome shows similarities with the elevated frontal at the level of the supraorbital process on the Miocene platanistid *Pomatodelphis*, wider and lower than in the other Miocene platanistid *Zarhachis* (see KELLOGG, 1924, 1959). This dome might correspond to an area of origin for rostral and facial muscles as seen in *Hyperoodon*; the very high maxillary crest medial to the antorbital notch provides to this extant ziphiid genus a different orientation for the rostral and pars anterointernus muscles, inserting on the melon (SCHENKKAN, 1973). ABEL (1905, p. 118) suspected the elevation of the maxilla on the supraorbital processes of *Xiphiacetus cristatus* to be linked to a sexual dimorphism (males with thicker maxillae, in a way somewhat similar to *Hyperoodon*). MYRICK (1979) could not find specimens lacking the thickened maxilla among American specimens that he referred to *X. cristatus*. Therefore, either all the American specimens represent males, or there is no sexual dimorphism for that feature. MYRICK (1979) could however detect a good correlation between the relative age of the specimen and the elevation of its maxilla. Concerning the Belgian specimens, the maxilla is distinctly thicker in larger animals; the smallest skulls IRSNB M.1896 and IRSNB 3237-M.1894 lack a clear elevation, and the largest IRSNB 3241-M.1893 and IRSNB 3227-M.1897 have a high maxillary dome. The maxillary crests of *Hyperoodon* are also known to increase in size allometrically (HEYNING, 1989).

The posterior margin of the maxilla goes barely beyond the anterodorsal margin of the supraoccipital; the acute transverse crest is thus roughly rectilinear. This crest, made of the compression of the maxilla and frontal against the supraoccipital shield, is notched by a distinct indentation of the supraoccipital and frontal on the dorsal edge of the maxilla, laterally to the vertex (= maxillary fold *sensu* MYRICK, 1979). This structure, absent in other eurhinodelphinid taxa, is present on all the skulls of *Xiphiacetus cristatus* for which this area is preserved, including USNM 25666 and USNM 244401, respectively holotypes of *Eurhinodelphis whitmorei* and *E. ashbyi* *sensu* MYRICK (1979). The maxilla sends a slightly concave median strip towards the frontal part of the vertex, which pinches, with the nasal, the posterior projection of the premaxilla. This median plate of the maxilla is less straightened up and more covering than in *E. cocheteuxi*, for which it reaches a vertical position.

Nasal. The morphology of the nasal is variable; it is either longer than wide, or roughly square, always narrower and lower than the frontal. Its dorsal surface progressively curves anteroventrally, without distinct angle. The posterior vertical plate of the mesethmoid projects only weakly dorsally from the ventral margin of the nasals, which are therefore only partially retained anteriorly.

Frontal. The dorsal surface of the frontal on the vertex is smooth and flat, anteriorly sloping, often with an acute and high posterodorsal edge, continuous with the transverse crest on the maxilla/supraoccipital. The degree of penetration of the frontals between the nasals is variable.

In ventral view, a deep and long fossa for the postorbital lobe of the pterygoid sinus incises the frontal along the posterior wall of the optic canal, in an anterolateral direction. Laterally, this fossa ends 30-40 mm before the lateral margin of the supraorbital process. In some specimens, the fossa is so deep in the frontal (up to 10 mm) that it nearly reaches the maxilla dorsally. If present, the fossa is usually shallower in *Xiphiacetus*

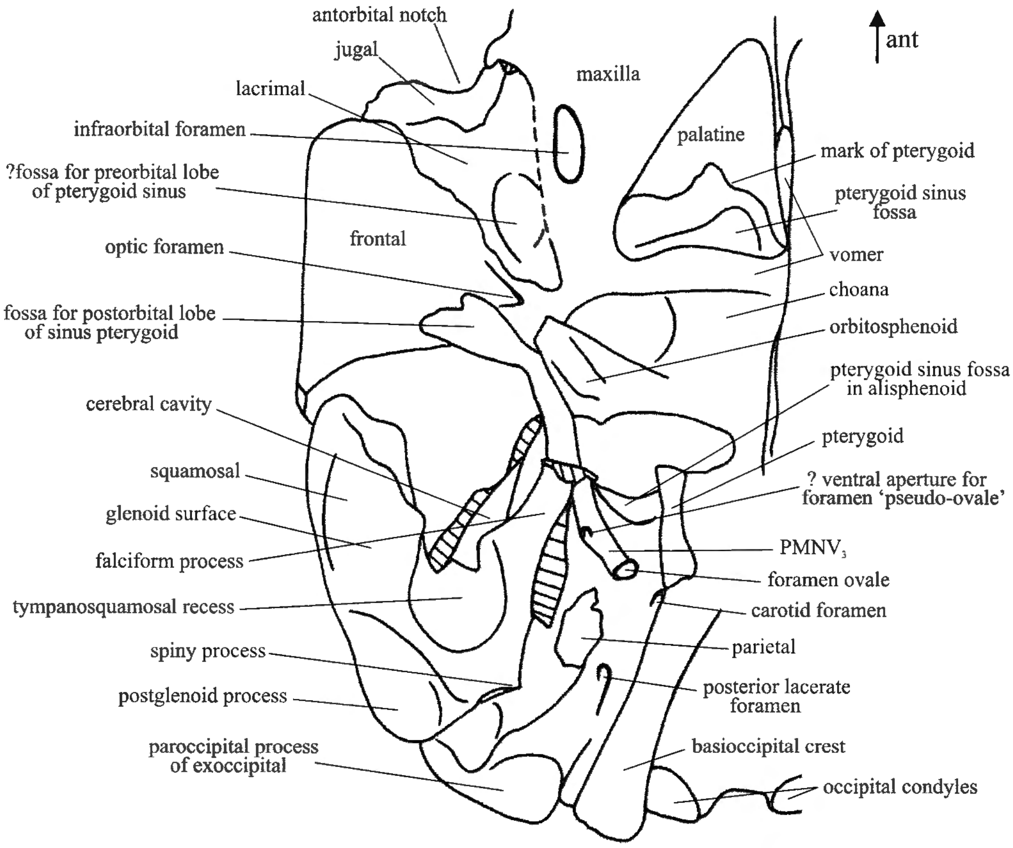

Fig. 3 — Schematic drawing of the right side of the basicranium of *Xiphiacetus cristatus* IRSNB 3241-M.1893, Miocene of Antwerp, in ventral view.

bossi, and laterally shorter in *Schizodelphis* spp. and *Ziphiodelphis* spp., never as developed as in *X. cristatus*; it is absent in *Eurhinodelphis* spp.

Palatine. The anterior margin of the palatine is either wide and blunt, *ca.* 40 mm anterior to the antorbital notches, or slightly longer and more pointed. The lateral margin is roughly rectilinear.

Pterygoid. The pterygoid sinus fossa excavates the pterygoid roughly until the level of the antorbital notches (with intraspecific variation; the fossa ends sometimes just posterior to the notches). The lateral lamina of the pterygoid is complete and strong, contacting the falciform process of the squamosal. No hamular process of the pterygoid is preserved on any of the specimens of this species.

Jugal-lacrimal. The jugal-lacrimal complex is visible in lateral view, anterior to the preorbital process of the frontal, and sending a short posterior process between frontal and maxilla. In ventral view, the complex forms the U-shaped ventral part of the antorbital notch. The posterolateral suture between lacrimal and frontal follows the anterior margin of the poorly individualized and narrow optic groove. The lacrimal is excavated by a shallow fossa, which might have held the preorbital lobe of the pterygoid sinus.

Supraoccipital. The dorsomedian portion of the supraoccipital is vertically applied on the elevated posterior margin of the frontals. More ventrally, this concave plate is less inclined, posteroventrally bending towards the occipital condyles. The lateral parts of the bone are convex, more protuberant.

Exoccipital. The paroccipital process of the exoccipital is wide and low, giving a low position to the occipital condyles compared to *Eurhinodelphis* spp.; their ventral margin is much lower than the level of the floor of the temporal fossa.

Basioccipital. The basioccipital basin is deep, limited by basioccipital crests forming an angle of about 55°. The posteroventral extremity of the basioccipital crest is thick, and reaches the ventral level of the exoccipital.

Squamosal. The zygomatic process of the squamosal is high and long; the elongated postglenoid process is slightly more robust, with a rounded apex. The temporal fossa is reduced, longer than high, with the roof roughly at the same vertical level than the roof of the orbit. In ventral view, the glenoid surface is wide and medially margined by a deep tympanosquamosal recess. The recess extends for a short distance dorsally to the glenoid surface, and dorsally to the base of the falciform process. The long anterior portion of the recess is supported by the zygomatic process, which is anteromedially widened. The falciform process of the squamosal is anteromedially directed, differing from the more laterally bent process in *Eurhinodelphis cocheteuxi*.

Alisphenoid. The foramen ovale, anterolateral to the carotid foramen at the posterior margin of the alisphenoid, is anterolaterally followed by the path for the mandibular nerve V$_3$ (PMNV$_3$). This PMNV$_3$ is a deep groove, which leads to a foramen piercing the falciform process of the squamosal in a laterodorsal direction, and emerging in the base of the temporal fossa (= foramen 'pseudo-ovale' *sensu* FORDYCE, 1994). This last part of the path is variable: for instance, on the skull IRSNB 3241-M.1893 (Pl. 2, Fig. 1C; Fig. 3) the sulcus shows a bifurcation, with a second branch more anteriorly directed, probably exiting in the temporal fossa ventrally to the lateral lamina of the pterygoid. The PMNV$_3$ ventrally overhangs a dorsoposteriorly extended round and smooth fossa on the alisphenoid (pterygoid sinus fossa in alisphenoid *sensu* FORDYCE, 1994). This fossa, laterodorsally deepening, is connected to the fossa for the postorbital lobe of the pterygoid sinus on the frontal, confirming the functional interpretation of this latter.

Parietal. Several small foramina pierce the parietal posteriorly to the foramen ovale, but their position and number are variable and the correlation with the foramina identified by FORDYCE (1994) in *Waipatia* was not successful.

Asymmetry. The vertex is distinctly asymmetric: the suture between the frontals is posteriorly deflected on the left side. Asymmetry is also observed on the relative development of the two maxillae along the vertex. For instance, the large fragmentary skull IRSNB 3227-M.1897 has a right maxilla much higher and wider than the left, forming a large transverse protuberance between the vertex and the indentation of the supraoccipital and frontal described above. Furthermore, the deflection of the suture between the frontals is much pronounced on that skull; the left frontal is strongly narrowed posteriorly, and its posterodorsal edge is deeply excavated, forming a wide valley (Pl. 3, Fig. 1A; Fig. 4). On this skull, the strong asymmetry of the vertex is curiously associated to asymmetric squamosals, an unusual feature in the odontocetes (MEAD, 1975; HEYNING, 1989). In lateral view, the left zygomatic process is more than 10 mm shorter than the right (measured from the rostral apex of the zygomatic process to the ventral tip of the postglenoid process); it is also narrower in ventral view, and the roof of the tympanosquamosal recess is open on its anterior part, isolating the zygomatic process from the lateral wall of the cerebral cavity (Pl. 3, Fig. 1B). HOWELL (1925) suggested that the asymmetry observed in some pinnipeds, at the level of the shape and size of bony elements involved in the insertion of masseter and temporal muscles, could be caused by injury or disease, producing a weakening of these muscles on one side of the skull relatively to the other. The earlier in the life of the animal the injury occurs, the more the asymmetry is pronounced. On IRSNB 3227-M.1897, the clear difference of size and shape between the two squamosals, bones implied in the articulation of the mandible and in the insertion of masticatory muscles, might be explained by the development, before the end of the growth, of a deficiency of the masticatory muscles of the left side. In that case, the pathological asymmetry of the basicranium would be independent from the asymmetrical vertex.

Teeth (Pl. 2, Figs 3A-3C)
Nine distal teeth are attached to the maxillae of the small skull IRSNB M.1896. The teeth have an average total length of 16 mm (6 mm for the root), and a maximal width at the base of the crown of 5 mm. The teeth nearly contact each other by the tip of the root and the base of the crown. The root is strongly flattened transversely with a roughly rectangular profile in lateral view, and an elongated dorsoposterior corner projecting towards the preceding tooth. The base of the crown is a slightly longitudinally elongated thick ring, quickly distally narrowing. The rest of the crown is longitudinally flattened. The median margin of the crown is rectilinear, sometimes slightly concave on the distal portion, while the lateral margin is parallel to the median for the first third of the crown, followed by a distinct angle towards the tip.

Among extant odontocetes, the teeth of *Pontoporia blainvillei* show the most striking resemblances; for example, loose maxillary teeth from *P. blainvillei* ZMA 15518 (Pl. 2, Fig. 4) show several characters in common with *Xiphiacetus cristatus*: small and numerous teeth

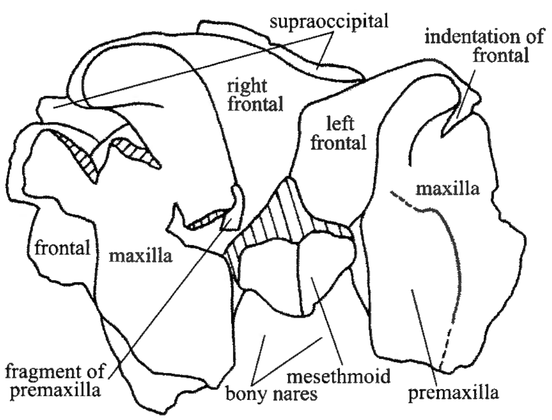

Fig. 4 — Posterior part of the cranium of *Xiphiacetus cristatus* IRSNB 3227-M.1897, Miocene of Antwerp, in anterodorsal view, showing the strong asymmetry of the bones of the vertex. The nasals are lost.

close one to the other (some of them were still attached with each other by the base of the crown); strongly transversely flattened root with a rectangular lateral aspect and a posterodorsal projection; thickened base of the crown; crown longitudinally flattened with the median margin rectilinear and an angle on the lateral margin. The similarities at the level of the teeth between those two species, both bearing an elongated rostrum and an individualized neck, might have a palaeoecological meaning (feeding behaviour), and should probably be interpreted as homoplasies.

Ear bones (Pl. 3, Figs 2-5; Fig. 5)
The partial skull USNM 21360 is associated with a periotic, the skull USNM 21363 with a fragment of periotic, and the skull USNM 244401 (considered by MYRICK, 1979 as *Eurhinodelphis ashbyi* and referred here to *Xiphiacetus cristatus*) with a tympanic bulla. A recently discovered Belgian skull is also associated with a right tympanic bulla IRSNB M.1902.

Periotic. The right periotic USNM 21360, only lacking the medioposterior part of the pars cochlearis, has a total length of 35 mm. Its general morphology is close to *Eurhinodelphis cocheteuxi*, except its slenderness. A wide and deep articular facet, laterally and medially limited by longitudinal crests, excavates the ventral surface of the anterior process; the median crest is more pronounced. An anteroexternal sulcus is posterolaterally curving, incising the anterior process before the large lateral tuberosity. The latter bears a large mallear fossa, anterior to a shallow but well-defined fossa incudis. The hiatus epitympanicus is pronounced, deeply cutting the lateral margin of the bone, without any articular rim. The dorsal protuberance of the anterior process is separated from the pars cochlearis by a transverse depression leaving from the median contact between the anterior process and the pars cochlearis towards the hiatus epitympanicus, on the dorsal face of the bone. The median surface of the anterior process is slightly depressed, cut by two small longitudinal sulci along the anterior articular facet (anterointernal sulci *sensu* FORDYCE, 1994), and pierced by numerous tiny apical foramina.

The anteromedial corner of the pars cochlearis is rounded in ventral view, and the anterior portion is narrower in medial view than in *Eurhinodelphis cocheteuxi*. The partially preserved internal auditory meatus, including the tractus spiralis foraminosus and the foramen singulare, is anteriorly pointed; its tip contains the dorsal opening of the facial canal; it is extended anteriorly by a narrow fissure nearly reaching the contact between the pars cochlearis and the anterior process.

The posterior process is relatively long beyond the posteromedian limit of the stapedial muscle fossa, with a length corresponding to 70 per cent of the length of the pars cochlearis (measured from the anterior wall to the posteromedian limit of the stapedial muscle fossa). The concave posterior articular facet is posterolateroventrally curved. The dorsal face of the posterior process is roughly keeled: a wide longitudinal protuberance runs from the tip of the process until the internal auditory meatus.

Only the posterior process and the posterior part of the pars cochlearis are preserved on the right periotic associated with the skull USNM 21363. This fragment fits the periotic USNM 21360 for the shape of the pars cochlearis and the base of the posterior process, but the posterior process, which is complete, is much shorter, less than 37 per cent of the length of the pars cochlearis, and associated to a stronger posteroventral curve of its dorsal margin (Pl. 3, Fig. 3; Fig. 5). The length of the posterior process is thus variable among the individuals of this species. A similar condition may also be present in *Xiphiacetus bossi*: the periotic USNM 167629 has a long posterior process (73 per cent of the length of the pars cochlearis), and the periotic USNM 23086 has a short posterior process (26 per cent of the length of the pars cochlearis). The progressive loss of bony contact between the periotic and the basicranium among the Delphinida (*sensu* MUIZON, 1988b), leading to a better isolation of the ear bones from the skull, is related to the shortening of the posterior process that contacts the squamosal and exoccipital on more stemward groups of Cetacea. The reduction of the process is for instance particularly pronounced among the families Pontoporiidae and Iniidae (about 28 per cent of the length of the pars cochlearis in *Pontoporia* and 15 per cent in *Inia*).

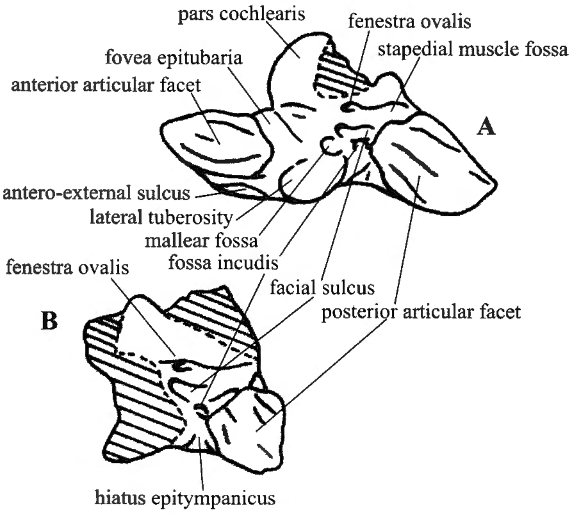

Fig. 5 — Periotics of *Xiphiacetus cristatus* from the Calvert Formation, Middle Miocene of the east coast of the USA. A. ventral view of the right periotic USNM 21360, with a portion of the pars cochlearis missing. B. ventral view of the right periotic USNM 21363, lacking most of its pars cochlearis and anterior process, and showing the shortened posterior process.

Tympanic bulla. None of the two known tympanic bullae of *Xiphiacetus cristatus* is complete: on both of them the posterior process is lacking. The left tympanic USNM

244401, although lacking a part of the outer lip and the sigmoid process, is better preserved in its anterior part. It has a total length of 35 mm and a maximal width of 21 mm, slightly smaller than IRSNB M.1902, with a width of 23 mm (Pl. 3, Figs 4,5). The anterior extremity is rounded and wide in ventral view, similarly to *Ziphiodelphis abeli*, *Z. sigmoideus*, and *Mycteriacetus bellunensis* (DAL PIAZ, 1977, pl. 3, figs 6-14; PILLERI, 1985, pl. 45, fig. a, pl. 48, fig. c), wider and less pointed than the one of *Eurhinodelphis cocheteuxi*. However, this character seems variable within the genus *Xiphiacetus*: tympanic bullae of *X. cristatus* IRSNB M.1902 and *X. bossi* USNM 16581 are relatively more pointed (Pl. 3, Fig. 4A; MUIZON, 1988a, fig. 6a). The distinct median groove is widening and shallowing anteriorly, anterolaterally turning, and ending after 25 mm. It separates the outer posterior prominence from a narrower and posteriorly shorter inner posterior prominence. In *E. cocheteuxi*, both prominences are sub equal in width, and the median groove is deeper. The condition of *Xiphiacetus*, also observed in *Mycteriacetus*, *Schizodelphis*, and *Ziphiodelphis*, might constitute a synapomorphy, differentiating those genera from *Eurhinodelphis* (see phylogeny below).

In medial view, the dorsal margin of the involucrum is high and parallel to the ventral margin for the posterior half of its length. After that, it is cut by a strong indentation, followed by a short platform and a progressive lowering until the anterior end of the bone. The ventral margin of the involucrum rises on the last anterior centimetre. The sigmoid process, only preserved in IRSNB M.1902, is transversely oriented, with a weakly angulated posteroventral corner.

Mandible

The partial skull USNM 244401 is associated to a fragment of mandible of 305 mm, including the anterior of the rami (one third of the total length) and the posterior of the symphysis. The width and height of the mandible at the symphysis respectively equal 38 and 24 mm. The alveolar groove contains about 45 alveoli on a length of 265 mm, with a diameter of 3-5 mm. The lateral surface of the mandible is hollowed by a deep longitudinal groove.

Post-cranial skeleton (Pl. 4)

The vertebrae associated to the holotype IRSNB 3234-M.361, seven cervicals and seven thoracics, were described and figured by ABEL (1931). The free cervicals bear long centra (Table 2), with proportions close to the extant river dolphins *Platanista* and *Inia*, indicating a long and flexible neck. The atlas is long and robust; the anterior articular surfaces are deeply concave; the dorsal transverse process is slightly longer and stronger than the ventral. The transverse process of the axis is robust; the neural spine is dorsally divided in a vertical thinner blade and a stronger dorsoposterior projection. The triangular neural arch of the five last cervicals bears a well developed pre- and postzygapophysis. The cervical c4 of *X. cristatus* IRSNB 3234-M.361 is close to the cervical (?c5)

Table 2 — Measurements (mm) on the cervical (c1-c7) and thoracic (t1-tx) vertebrae of *Xiphiacetus cristatus* IRSNB 3234-M.361 (holotype), Miocene of Antwerp region. The thoracic tx does not directly follow t6; at least one vertebra of the series is missing. 'e' indicates estimate, '+' nearly complete and '–' no data. Some of the measurements are illustrated on Plate 4. The centrum length on the atlas and the axis (c1, c2) is the maximum longitudinal length between anterior and posterior articular surfaces. On the six first thoracic vertebrae, the posterior centrum width is considerably larger than the anterior centrum width because of the presence of the diapophysis (articular surface with the tuberculum of the rib).

	c1	**c2**	**c3**	**c4**	**c5**	**c6**	**c7**	**t1**	**t2**	**t3**	**t4**	**t5**	**t6**	**tx**
1. centrum length	65	34	26	24	24	27	28	36	44	50	56	59	64	66
2. anterior centrum width	–	–	e62	61	60	60	55	55	+55	54	55	57	58	e63
3. anterior centrum height	–	–	43	47	48	47	47	e45	42	42	45	46	48	50
4. posterior centrum width	–	60	60	60	58	56	56	75	71	75	73	68	71	–
5. posterior centrum height	–	41	46	47	48	47	48	43	42	42	45	47	50	51
6. width across transverse processes	112	e134	e126	e126	e122	–	e133	140	e141	141	e134	128	124	e107
7. total height of vertebra	88	116	86	–	–	–	–	137	146	–	–	–	–	–
8. height neural arch	–	25	26	26	–	25	27	30	30	–	33	36	35	e29
9. height neural spine	–	53	–	–	–		–	+63	73	–	–	–	–	–

of *Xiphiacetus bossi* USNM 8842 figured by Kellogg (1925, pl. 6, figs 3, 6), but with a more dorsoventrally flattened centrum, and a longer transverse process with a lower parapophysis. The robust parapophysis of c6 is much elongated, 1.5 times longer than the parapophysis of c5, and more than twice longer than the plate-like parapophysis of c7. A similarly longer parapophysis of c6 is observed in the archaeocete *Dorudon atrox*; this parapophysis is one of the origins for the longus coli muscle, which inserts on the ventral side of the centra of the first cervicals, and which acts mainly as a flexor of the neck (Uhen, 2003). This condition further supports the high flexibility of the neck of *Xiphiacetus cristatus*. The thoracics are generally similar to *X. bossi* USNM 8842 (Kellogg, 1925, pl. 7-9), also with large pre- and postzygapophyses. The neural spine of t5 is slightly posteriorly projecting, contrary to the known anterior thoracics of *X. bossi*. Concerning the articulation of the ribs, the strong transverse process bears a wide parapophysis, and the centrum of at least the six first thoracics bears a diapophysis considerably increasing the posterior width of the centrum.

No forelimb element of *Xiphiacetus cristatus* is known, contradicting Abel (1931).

Remarks on the stratigraphic range of *Xiphiacetus cristatus*

The specimens of *Xiphiacetus cristatus* from the east coast of the USA were all found in the Calvert Formation, more precisely in the beds 12, 13, and 14 as defined by Shattuck (1904) (Myrick, 1979), dated from the Middle Miocene (Verteuil & Norris, 1996, fig. 4).

All the Belgian skulls of *Xiphiacetus cristatus* found during the 1860's were collected without precise stratigraphic and location data. None of them has a preservation similar enough to specimens of *Eurhinodelphis cocheteuxi*, from the Antwerp Sands (late Early to Middle Miocene), to imply a similar origin. The partial skulls IRSNB 8243-M.1898 and IRSNB 8243' were discovered in Kessel, 18 km southeast of Antwerp (Fig. 1), during the building of a fort, in February-March 1910. In the area of Kessel, the only Neogene unit recorded under the Quaternary layer is the member of the Antwerp Sands (see Huygebaert & Nolf, 1979, Kessel is close to the drilling GD 11 in figs 1, 3).

The specimens IRSNB M.1896 and IRSNB M.1902 were found in the 'Sables à Hétérocètes', the former more or less one metre above the upper *Glycymeris* layer of the Antwerp Sands (G. Paredis, pers. comm. 2002; L. Peeters, pers. comm. 2003). A section close to the place of discovery of the two skulls (Stenen Brug, I S. B.) was described by De Meuter *et al.* (1976, p. 10; fig. 16); no 'Sables à Hétérocètes' are described in that section, where the Antwerp Sands are overlaid with reworked Deurne Sands and Kattendijk Sands, respectively from the Upper Miocene and Lower Pliocene. However, IRSNB M.1896 is a fragile specimen, with slender fragments of the rostrum preserved, and several teeth *in situ*; it is therefore difficult to imagine this skull having undergone a phase of reworking. Non-reworked sediments might therefore be present above the Antwerp Sands, alternately with reworked Upper Miocene sediments, and under reworked Lower Pliocene deposits. The non-reworked deposits would correspond to the 'Sables à Hétérocètes'. Glibert & de Heinzelin (1955) and De Meuter & Laga (1976) include the 'Sables à Hétérocètes' in the Upper Miocene Diest Formation, a formation represented in Antwerp by the Deurne Sands. Even if microfossils from new samples of the non-reworked levels would help to clarify the problem, *Xiphiacetus cristatus* is probably recorded from levels at least younger than the Antwerp Sands.

The chronological range of the family Eurhinodelphinidae was usually proposed from the Late Oligocene to the Middle Miocene (Fordyce & Barnes, 1994; Fordyce & Muizon, 2001). Those newly identified Belgian skulls of *Xiphiacetus cristatus* might extend that range into the Late Miocene, pending additional stratigraphic information.

Evolutionary considerations

For several characters, *Xiphiacetus cristatus* seems particularly derived compared to other eurhinodelphinids.

The progressive telescoping of the skull, moving the bony nares posterodorsally, is a process that can be traced among the major lineages of odontocetes (Miller, 1923). In *X. cristatus*, the supraoccipital shield is nearly vertical against an elevated and acute posterior margin of the vertex, laterally followed by an acute transverse crest. This morphology indicates a pronounced posterodorsal shift of the bony nares, longitudinally pinching the vertex (Fig. 6).

The height of the temporal fossa of *X. cristatus* is reduced compared to other eurhinodelphinids and taxa probably related to the family (e.g., *Eoplatanista* Dal Piaz, 1916 and *'Argyrocetus' joaquinensis* Kellogg, 1932) (Fig. 6). When calculating the ratio between the height of the temporal fossa and the bizygomatic width of the skull among eurhinodelphinoid taxa (Eurhinodelphinidae + Eoplatanistidae, Muizon, 1988a), the following trend is observed (Fig. 7). The ratio varies between 0.44 and 0.35 among the two species of *Eoplatanista*, and equals 0.37 for the holotype of *'Argyrocetus' joaquinensis*. It decreases to 0.28 for the holotypes of *Eurhinodelphis longirostris* and *Mycteriacetus bellunensis*, between 0.28 and 0.26 for *Ziphiodelphis* (*Z. abeli* and *Z. sigmoideus*), 0.25 for the holotypes of *Eurhinodelphis cocheteuxi* and *Schizodelphis sulcatus*, a mean of 0.22 for the specimens of *Schizodelphis* from the USNM (specific taxonomy not always resolved and several specimens slightly dorsoventrally compressed) and for *Xiphiacetus bossi*, and finally no more than 0.20 for *X. cristatus*. As previously mentioned, few data are available about the total length of the mandible for the eurhinodelphinids.

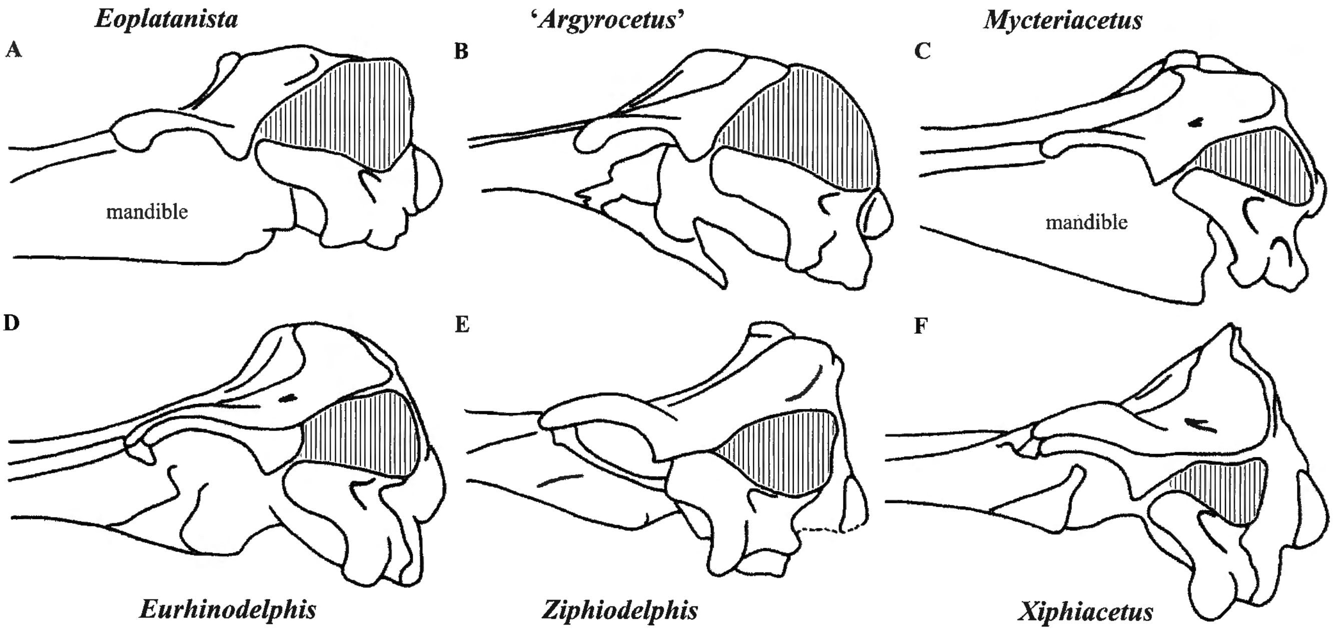

Fig. 6 — Schematic left lateral view of the cranium for several long-snouted dolphins, showing the variation of the degree of telescoping and of the height of the temporal fossa. A. *Eoplatanista gresalensis* MGPD 26409. B. *'Argyrocetus' joaquinensis* USNM 11996 (mod. from KELLOGG, 1932). C. *Mycteriacetus bellunensis* MGPD 26404. D. *Eurhinodelphis cocheteuxi* IRSNB 3252-M.294. E. *Ziphiodelphis sigmoideus* MGPD 26396. F. *Xiphiacetus cristatus* IRSNB 3241-M.1893. Not to scale.

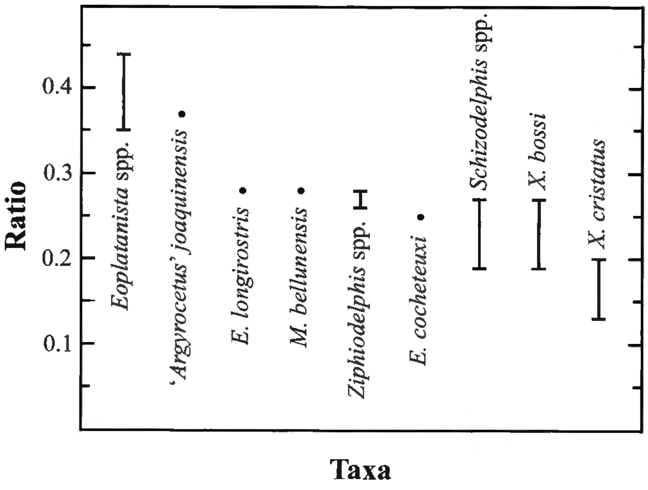

Fig. 7 — Diagram illustrating the trend towards a decrease of the ratio between height of temporal fossa and bizygomatic width among eurhinodelphinoid taxa. Interval bars indicate more than one specimen: *Eoplatanista* spp. (5), *Ziphiodelphis* spp. (4), *Schizodelphis* spp. (11), *Xiphiacetus bossi* (5), and *X. cristatus* (5). For *'Argyrocetus' joaquinensis*, *Eurhinodelphis longirostris*, *E. cocheteuxi*, and *Mycteriacetus bellunensis*, only the holotype was included. Several skulls from the USNM were too compressed dorsoventrally to be adequately used.

Nevertheless, the ratio between bizygomatic width of the skull and length of the mandible increases from *Eoplatanista* spp. (mandible as long as rostrum) to *Xiphiacetus* spp., with *Argyrocetus patagonicus* and *Mycteriacetus bellunensis* as intermediaries. Because the temporal fossa is the main area of origin for the temporalis muscles, elevating the mandible, the reduction of the size of the temporal fossa, probably associated to less powerful muscles, might be partially related to the shortening of the mandible. However, it is likely that the way the animal feeds – size and type of prey, kind of grasping process – is another factor related to the muscular development, and thus to the size of the temporal fossa. For example, suction feeding upon squids asks for a less powerful mandible than predation upon marine mammals. The temporal fossa of the extant ziphiid *Ziphius cavirostris*, suspected to feed by sucking in the preys (HEYNING & MEAD, 1996), is considerably reduced compared to the large fossa of the killer whale *Orcinus orca*.

The shortening of the posterior process of the periotic in *Xiphiacetus* is discussed above, and this feature, linked to a better isolation of the ear bones relatively to the basicranium, is derived compared to the condition in *Eurhinodelphis*, *Schizodelphis*, and *Ziphiodelphis*.

At the level of the pterygoid sinuses, *Xiphiacetus cristatus* is the eurhinodelphinid species with the deepest and longest fossa for the postorbital lobe of the sinus: the sinus does not reach the roof of the orbit in *Eurhinodelphis* – or does not excavate it, the fossa is laterally shorter in *Schizodelphis* and *Ziphiodelphis*, and it is shallower in *Xiphiacetus bossi*. The expansion of the pterygoid sinus in the orbit and the temporal fossa is a character used by MUIZON (1991) to group the superfamily Eurhinodelphinoidea with the Delphinida *sensu* MUIZON, 1988b. It is suggested here that this feature progressively appears within the family Eurhinodelphinidae, together with the shortening of the posterior process of the periotic; those two characters should therefore be considered as homoplasies, occurring independently in at least two different lineages (Eurhinodelphinidae and Delphinida).

Another character particularly specialized in *X. cristatus* is the shape of the teeth. The condition, probably ontogenetically variable, is close to the extant *Pontoporia*, and is likely derived, even if only few data are available on the teeth of other eurhinodelphinids.

All those anatomical observations, from diverse areas of the skull, most of them functionally related to the acoustic and feeding systems, indicate that *Xiphiacetus cristatus* is more specialized among eurhinodelphinids. The stratigraphic data and the palaeontological record are fragmentary and lack precision, but a correlation between the more derived features of that species and its possibly longer fossil record might be informative.

Phylogeny

Analysis

The only previous phylogenetic study illustrating the eurhinodelphinid relationships is the one of MUIZON (1991), isolating the crownward *Schizodelphis* + (*Ziphiodelphis* + *Eurhinodelphis*) from *Argyrocetus* by the sub vertical occipital shield, and *Ziphiodelphis* + *Eurhinodelphis* by the wider occipital shield and shorter cerebral skull.

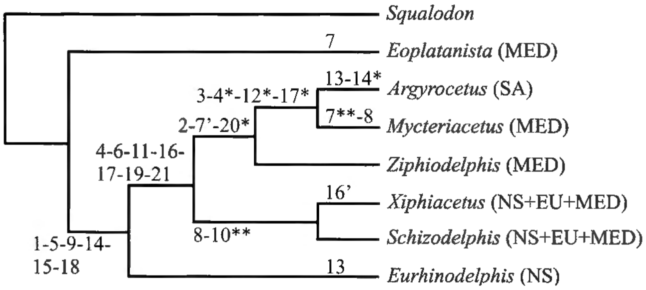

Fig. 8 — Most parsimonious cladogram illustrating the relationships between eurhinodelphinid genera. Tree length 32 steps; C.I. 0.75; R.I. 0.73. Numbers at each node refer to characters discussed in the text and listed in Appendix 2. Change from state 0 or 1 to state 2 ('); reversal from state 1 to state 0 (*); reversal from state 2 to state 1 (**). Abbreviations between brackets indicate the region of origin: EU, east coast of the USA; MED, Mediterranean; NS, North Sea Basin; SA, east coast of South America.

Taking into account the systematic revision inside the family (LAMBERT, 2004; this study), a cladistic analysis examining the phylogenetic relationships between the best-known eurhinodelphinid genera *Eurhinodelphis* (*E. cocheteuxi* and *E. longirostris*), *Mycteriacetus* (*M. bellunensis*), *Schizodelphis* (*S. morckhoviensis*, ?*S. barnesi*, and *Schizodelphis* sp. from the USNM), *Xiphiacetus* (*X. cristatus* and *X. bossi*), and *Ziphiodelphis* (*Z. abeli* and *Z. sigmoideus*), the more fragmentarily known *Argyrocetus patagonicus*, and the eoplatanistid *Eoplatanista* was carried out with the parsimony program PAUP, version 4.0 beta 10 (SWOFFORD, 1998). A matrix of 21 characters (excluding uninformative characters and all treated as unweighted and unordered, see Appendix 2 for the description of the characters) for the seven taxa (Table 3) was built on the basis of direct observations of most of the specimens, except the holotype of *Argyroce-*

Table 3 — Data matrix of 21 characters for one outgroup and seven analysed taxa. All characters with multiple states are treated as unordered. Primitive state, '0'; derived states, '1', '2'; variable between 0 and 1, 'a'; missing character, '?'. Description of the characters in Appendix 2.

	Characters																				
Taxa					5					10					15						21
Squalodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eoplatanista	0	a	a	0	0	0	1	0	0	2	0	1	0	0	0	0	?	0	0	1	0
Argyrocetus	1	?	1	0	?	?	2	0	1	?	?	0	1	0	?	?	?	?	?	?	?
Mycteriacetus	1	1	1	0	1	1	1	1	1	2	1	0	0	1	1	?	0	?	?	0	1
Ziphiodelphis	1	1	0	1	1	1	2	0	1	2	1	1	0	1	1	1	1	1	1	0	1
Xiphiacetus n. gen.	1	0	0	1	1	a	0	1	1	1	1	1	0	1	1	2	1	1	1	a	1
Eurhinodelphis	1	0	0	0	1	0	a	0	1	2	0	1	1	1	1	0	0	1	0	1	0
Schizodelphis	1	0	0	a	1	1	a	a	1	a	1	1	0	1	1	1	1	1	1	1	1

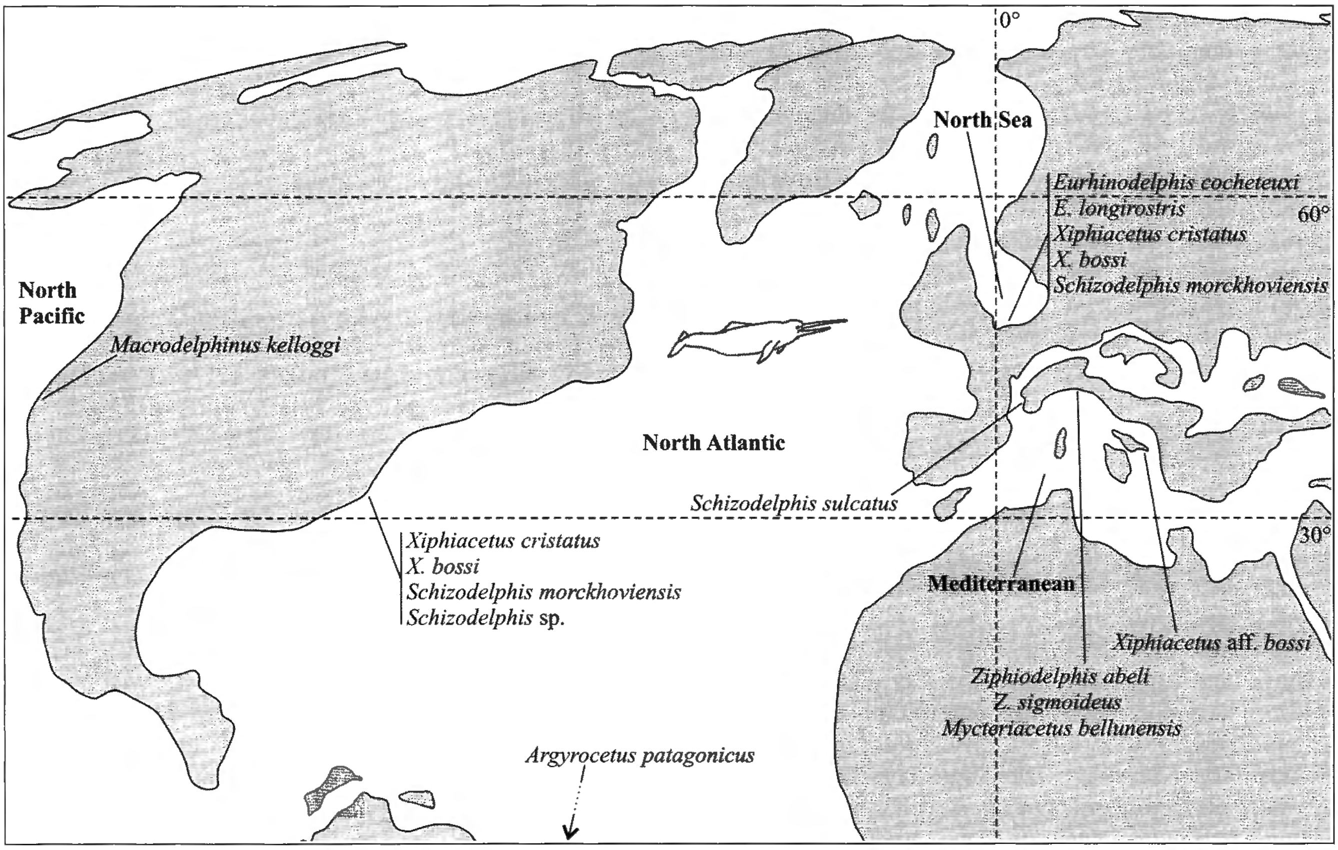

Fig. 9 — Palaeogeographic map of the North Atlantic and Mediterranean realms during Middle Miocene (mod. from SMITH *et al.*, 1994), with the main eurhinodelphinid localities. Several of the species placed on the map are dated from Early or Late Miocene; at those times, the outline of the coasts differed a while from the reconstruction presented here. The locality of *Argyrocetus patagonicus* is outside the map, in the Early Miocene of Patagonia, Argentina.

tus patagonicus (figured in LYDEKKER, 1893). One outgroup was chosen *a priori*: the squalodontid *Squalodon*. The poorly known large eurhinodelphinid *Macrodelphinus* WILSON, 1935 and the two species usually thought to belong to the same genus than *Argyrocetus patagonicus*, '*A.*' *joaquinensis* KELLOGG, 1932 and '*A.*' *bakersfieldensis* (WILSON, 1935), were not included in the analysis and their status is briefly discussed in Appendix 1.

The result of the performed heuristic search is a unique minimal cladogram of 32 steps (C.I. 0.75; R.I. 0.73), presented in Figure 8. The main features of that cladogram are a sister-group relationship between *Schizodelphis* + *Xiphiacetus* and *Ziphiodelphis* + (*Mycteriacetus* + *Argyrocetus*), and a more stemward *Eurhinodelphis*. The close relationship between *Mycteriacetus bellunensis* and *Argyrocetus patagonicus* was already suggested by MUIZON (1988a), COZZUOL (1996), and BIANUCCI & LANDINI (2002), while the general topology of the cladogram differs from the tree of MUIZON (1991) because of a larger number of characters and modifications concerning the generic allocation of the different species. This cladogram also differs from the consensus tree of LAMBERT (in press), giving hypothetical relationships between most of the Neogene odontocete families; in that study, using a larger number of characters, and only including three eurhinodelphinid taxa and no eoplatanistid, Eurhinodelphinidae is not monophyletic: *Eurhinodelphis cocheteuxi* is a more crownward, sister-group of the ziphiids.

Discussion

The relatively isolated basal position of *Eurhinodelphis* obtained here allows establishing an interesting parallel with the palaeogeography of the family. The two species of *Eurhinodelphis* are currently only known from the North Sea Basin. On the other hand, several species of *Schizodelphis* and *Xiphiacetus* are described from both sides of the North Atlantic: in the North Sea Basin and along the eastern coast of the USA; *Schizodelphis* and *Xiphiacetus* are also known from the Mediterranean (Fig. 9). Species of the phylogenetically closely related *Xiphiacetus* and *Schizodelphis* might share a more pelagic habitat compared to *Eurhinodelphis*. The ancestral habitat could therefore have been more coastal, or even estuarine [one of the oldest records of eurhinodelphinids is from fluvial-lacustrine deposits of the Late Oligocene of Australia (FORDYCE, 1983)], with a progressive invasion of wider areas of the continental shelf until the mid-Miocene climatic optimum. From a morphological point of view, the similarities of the eurhinodelphinids with the river dolphins at the level of the length of the rostrum, bearing a deep lateral groove, and of the length of the neck, support the hypothesis of relatively slow-swimming shallow-water dwellers. The sensitive edentulous anterior part of the rostrum, longer than the mandible, could correspond to an efficient tool used to forage by burrowing on the sediments of the bottom to detect and disturb preys. Similar arguments were produced to propose a burrowing behaviour for *Eurhinosaurus longirostris*, a Jurassic ichthyosaur with a rostrum twice as long as the mandible (RIESS, 1986; GODEFROIT, 1996).

Ziphiodelphis and *Mycteriacetus* are for now only known from Mediterranean. A more southern origin (Mediterranean) for the clade *Ziphiodelphis* + (*Mycteriacetus* + *Argyrocetus*), in warmer climate, could have made possible a later dispersion in the southern hemisphere (South Atlantic for *Argyrocetus patagonicus*).

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Appendix 1

Comments on several taxa previously included in, or related to, the family Eurhinodelphinidae (reviews by FORDYCE, 1981; MUIZON, 1988a, 1991; FORDYCE & MUIZON, 2001).

Iniopsis caucasica LYDEKKER, 1892
The study of the systematic affinities of that probable primitive eurhinodelphinid, from the Late Oligocene of Georgia and Azerbaidzhan, would necessitate direct observation of the specimens (especially the ear bones and the basicranium, see MCHEDLIDZE, 1976, pl. 9, 10).

Protodelphinus capellinii DAL PIAZ, 1977
The only species of the genus *Protodelphinus* was described by DAL PIAZ (1977) on the basis of a partial mandible MGPD 26182, small fragments of rostrum, a right periotic-tympanic bulla set MGPD 26184-26185 and several teeth from the Early Miocene of north-eastern Italy (Libano Sandstone, Bolzano quarry). In this paper, DAL PIAZ considered the species as a primitive member of the family Delphinidae, an attribution also supported by PILLERI (1985) who described a new mandibular fragment, possibly belonging to a new species from the same genus. The ear bones lead MUIZON (1991) to suggest that *Protodelphinus* might be a eurhinodelphinid (at least a eurhinodelphinoid, FORDYCE & MUIZON, 2001). Those ear bones show clear eurhinodelphinid affinities (e.g., the long and pointed anterior process of the periotic bearing an anterior articular facet and the indentation on the high dorsal margin of the involucrum of the tympanic), even if several differences (size, shape of the pars cochlearis of the periotic, proportions of the tympanic) with the known eurhinodelphinids from the Belluno Sandstone, *Ziphiodelphis* and *Mycteriacetus*, preclude a specific attribution. However, some characters of the mandible provide differences with the eurhinodelphinids: the lateral surface lacks a longitudinal groove, even at the beginning of the symphysis; the ventral margin is distinctly angulated at 50-60 mm anteriorly to the beginning of the symphysis, indicating a dorsal elevation of that margin; the forwards decrease of the height of the symphyseal portion is stronger than in eurhinodelphinids. These three characters might indicate a shorter symphyseal portion of the mandible compared to the known eurhinodelphinids. Mistakes could therefore be suspected in the associations of isolated bones suggested by DAL PIAZ (1916, 1977), as already discussed by MUIZON (1988a) concerning *Dalpiazina ombonii*. In a deposit relatively so concentrated in fossil odontocete fragments as the Bolzano quarry, an association of ear bones and a mandible, while the basicranium is lacking, seems rather doubtful. In the present case, as the mandible does not fit the diagnostic characters seen on the ear bones, the association should be rejected. It is suggested here to remove the ear bones MGPD 26184-26185 from the holotype, and to refer them to Eurhinodelphinidae *incertae sedis*. The mandible and the associated teeth show similarities with kentriodontid delphinoids. Therefore, the holotype of *Protodelphinus capellinii* is restricted to the mandible MGPD 26182-26183 and associated teeth MGPD 26186, and that species is provisionally referred to Odontoceti aff. Delphinoidea.

Argyrocetus LYDEKKER, 1893
The poorly diagnosed genus *Argyrocetus* is currently including three species: the type-species *A. patagonicus* LYDEKKER, 1893 from the Late Oligocene-Early Miocene of Patagonia, Argentina; *A. joaquinensis* KELLOGG, 1932 and *A. bakersfieldensis* (WILSON, 1935), both from the Early Miocene of California (see BARNES, 1976). Those species are less extensively known than the eurhinodelphinids from Europe and the east coast of the USA. Only one specimen is described for the species *A. patagonicus*; the anterior part of the rostrum is poorly preserved in *A. patagonicus*, and absent in both Californian species; no ear bones and no teeth are described for the genus; and the mandible is known for *A. patagonicus* only.

Argyrocetus patagonicus LYDEKKER, 1893
The species was first briefly described by LYDEKKER (1893), particularly stressing the shape of the nasals, projecting over the bony nares where they end with a nearly straight transverse edge. Additionally to a scale mistake in the pictures of LYDEKKER (1893, pl. 5) – the reduction is not of 2/3 but 1/2, CABRERA (1926) provided further information: while the rostrum is preserved anteriorly on a shorter distance than the mandible, he maintained that the premaxillae are anteriorly longer than the maxillae, estimating the premaxillary part of the rostrum at 200 mm for a total length of the skull of at least 854 mm. This premaxillary length corresponds to the distance between the anterior preserved extremity of the maxilla and the apex of the articulated mandible on the left side picture of LYDEKKER (1893, pl. 5). Thus the opinion of CABRERA (1926) is that the anterior preserved extremity of the maxilla corresponds to the real apex of that bone, and that the mandible was 200 mm longer than the maxillary part of the rostrum. CABRERA (1926) also proposed that this missing anterior premaxillary part of the rostrum did not bear teeth, because the corresponding portion of the mandible seems to lack individualized alveoli. With this incomplete and dorsoventrally crushed rostrum (exaggerating the dorsal opening of the vomerian gutter, following CABRERA, 1926), it is not possible to guess if the premaxillae were longer than the mandible, the condition observed in at least *Schizodelphis*, *Xiphiacetus*, and *Ziphiodelphis*. However, the probably edentulous premaxillae extending further anteriorly than the maxillae for a substantial distance maintain *Argyrocetus patagonicus* in the family Eurhinodelphinidae. The close relationship between *A. patagonicus* and *Mycteriacetus bellunensis* obtained in the above phylogenetic analysis further supports that hypothesis.

'Argyrocetus' joaquinensis KELLOGG, 1932
In his systematic discussion about this species, KELLOGG (1932) evaluated the similarities of the holotype of '*A.*' *joaquinensis sensu* KELLOGG, 1932 with the eurhinodelphinids known at that time; because of resemblances with *A. patagonicus* at the level of the supraoccipital shield, the elevation of the vertex, and the proportions of the skull, he tentatively referred ''with considerable hesitation'' the Californian skull to the same genus. The only areas that are well preserved in both *A. patagonicus* and '*A.*' *joaquinensis* are the supraoccipital shield and the nasals and frontals on the vertex. The supraoccipital seems roughly similar in both species, notwithstanding the more acute aspect of the lambdoid crest in '*A.*' *joaquinensis*. The strange vertex of the latter, however, strongly differs from that of *A. patagonicus*; following KELLOGG (1932), the nasals are much longer than wide, they are posteriorly thicker, and they do not overhang the bony nares – a feature considered by LYDEKKER (1893) as the main characteristic of *A. patagonicus*. The attribution to the genus *Argyrocetus* is therefore doubtful. Furthermore, when

comparing the holotype of '*A.*' *joaquinensis* to other eurhinodelphinid taxa, clear differences appear in lateral view: the large temporal fossa (see Fig. 6) is much more developed dorsoposteriorly, higher relatively to the vertex than in *Eurhinodelphis*, *Mycteriacetus*, *Schizodelphis*, *Xiphiacetus*, and *Ziphiodelphis*, and the zygomatic process is longer anterodorsally. This condition is interestingly similar to the Italian eoplatanistid *Eoplatanista* (*sensu* Muizon, 1988a; e.g., *Eoplatanista gresalensis* MGPD 26409 in Pilleri, 1985, pl. 57, fig. a). The latter differs however in the wider and flatter vertex, posteriorly followed by the nearly horizontal median portion of the supraoccipital. Because of the lack of information about the rostrum and the mandible, and the absence of obvious similarities with the known eurhinodelphinids, the holotype of '*A.*' *joaquinensis* should not be definitely included in that family.

Other specimens referred to '*A.*' *joaquinensis* by Barnes (1976), i.e. the holotypes of *Doliodelphis littlei* Wilson, 1935 and *Eurhinodelphis extensus* Wilson, 1935, do not provide more information about the systematic status of the species; they could even belong to another taxon [e.g., apart from its size, the holotype of *Doliodelphis littlei* seems more similar to '*Argyrocetus*' *bakersfieldensis* (Wilson, 1935)].

'Argyrocetus' bakersfieldensis (Wilson, 1935).
This species, first assigned to the genus *Acrodelphis* by Wilson (1935), was revised by Barnes (1976) in the genus *Argyrocetus*. '*A.*' *bakersfieldensis* shares with the type species *A. patagonicus* the anterodorsal projection of the nasals above the bony nares, with an acute anterior edge. The frontals are relatively longer on the more transversely compressed vertex (Fig. 10), but those differences might be easily explained by intrageneric variation. However, the shape of the supraoccipital shield differs significantly: in '*A.*' *bakersfieldensis*, after a small step at the contact with the frontal, the concave mediodorsal portion of the occipital becomes nearly horizontal. The shield is too incomplete to follow the slope more posteriorly, but that morphology, contradicting the schematic reconstruction of the supraoccipital proposed by Wilson (1935, fig. 11), differs from the roughly regularly sloping supraoccipital shield of *A. patagonicus*. The condition of '*A.*' *bakersfieldensis* reminds *Eoplatanista*, for which the anteromedian portion of the supraoccipital roughly follows the horizontal plane of the frontal on the vertex, often with a small step between the frontal and the supraoccipital (e.g., *E. gresalensis* MGPD 26409, Pilleri, 1985, pl. 55). This feature gives *Eoplatanista* a more convex posterodorsal area of the cranial skull, compared to the eurhinodelphinids (Fig. 6). The preserved fragments of the roof of the temporal fossa of the holotype of '*Argyrocetus*' *bakersfieldensis* indicate a high fossa, similar to *Eoplatanista* and higher than in known eurhinodelphinids. Other characters differentiating *Eoplatanista* from the eurhinodelphinids, as the narrower and thicker preorbital process and the high and acute palate keel, are however absent in '*Argyrocetus*' *bakersfieldensis*.

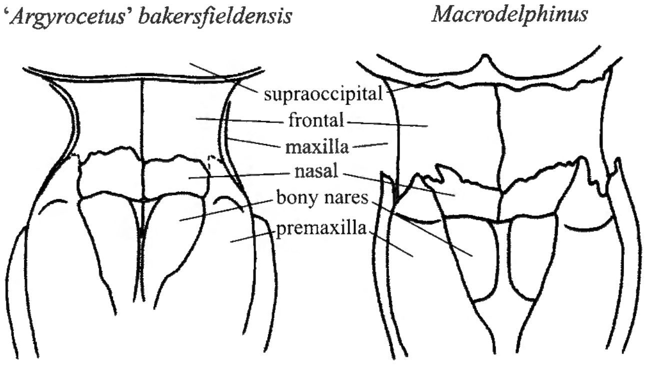


Fig. 10 — Schematic drawings of the vertex of '*Argyrocetus*' *bakersfieldensis* YPM 13406 and *Macrodelphinus kelloggi* YPM 13402. Not to scale.

To summarize, two of the three species usually included in *Argyrocetus*, '*A.*' *joaquinensis* and '*A.*' *bakersfieldensis*, are not enough similar to the type species to be referred to that eurhinodelphinid genus. Furthermore, because the specimens lack the areas of the skull where diagnostic characters of the family Eurhinodelphinidae are found, and because of similarities with the monogeneric family Eoplatanistidae, their familial attribution could not be resolved. Both of them are referred to Odontoceti aff. Eurhinodelphinoidea.

Macrodelphinus kelloggi Wilson, 1935
The holotype of this large Early Miocene Californian species is composed of the cranium, including the left preorbital process, the base of the rostrum, and a more anterior rostral portion bearing teeth. A right occipital condyle, an incomplete left tympanic bulla, a scapula, a fragment of atlas, and several additional vertebrae were tentatively referred to that specimen by Wilson (1935), who described a second specimen: the basal part of a rostrum associated with the left body of a mandible and several post-cranial bones. A left humerus, first identified by Wilson (1935) as belonging to a cetothere, was also referred to the species *Macrodelphinus kelloggi* by Barnes (1976).

In the description of the holotype, Wilson (1935, p. 29) gave the following indication: "The maxilla is broad at the base of the rostrum; and at the anterior extremity, as preserved, it descends abruptly laterally from the premaxilla." Taking account of the reconstruction of Wilson (1935, fig. 4) and of the height of the rostrum at the preserved extremity, the missing apical portion might be relatively long, and the abrupt descent might indicate that the maxilla was significantly shorter than the premaxilla. In addition, *M. kelloggi* exhibits premaxillae thick and wide at the level of the posterior margin of the bony nares. The surface occupied by the frontals on the vertex is larger, relatively to the short and wide nasals, than in any other eurhinodelphinid (Fig. 10). This condition reminds the vertex morphology of the more basal odontocetes *Waipatia* and *Squalodon*, and likely indicates a primitive state among eurhinodelphinids. The slope and concavity of the supraoccipital shield show rather good similarities with *Argyrocetus patagonicus*, and the nasals are slightly elevated anterodorsally. Apart from the absence of a clear indentation at mid-length of the dorsal margin of the involucrum, the description of the tympanic bulla of *Macrodelphinus kelloggi* follows the morphology of the eurhinodelphinid tympanics, with a broad, shallow and wide median groove, and the dorsal margin of the thick involucrum strongly anteriorly lowering. All those characteristics of the skull and the tympanic support the inclusion, first proposed by Barnes (1976), of *M. kelloggi* in the family Eurhinodelphinidae, probably in a basal position.

Appendix 2

List of the characters used in the cladistic analysis.

1. Anterior portion of the rostrum constituted by the only premaxillae, forming more than 10 per cent of the total length of the rostrum, and lacking alveoli: absent (0), present (1).
2. Mesorostral groove: widely open at the level of the antorbital notches (0) - nearly closed (1).
3. Proportions of the cranium: ratio between bizygomatic width and longitudinal distance from antorbital notch to occipital condyles $\geqslant 1$ (0) - < 1 (1).
4. Telescoping of the skull: ratio between longitudinal distance from anterior margin of the supraoccipital to the occipital condyles and bizygomatic width of the skull $\geqslant 0.30$ (0) - < 0.30 (1).
5. Preorbital process of the frontal in lateral view: abruptly dorsoventrally thickened (0) - weakly thickened, almost as thin as the supraorbital area (1).
6. Concavity of the premaxillary sac fossa: fossa flat or weakly concave (0) - strongly concave (1).
7. Dorsal surface of the nasal: lower or at the same level than the frontal on the vertex (0) - higher than the frontal without anterodorsal projection (1) - projecting anterodorsally (2).
8. Proportions of the nasal: wider than long (0) - as long as wide or longer than wide (1).
9. Relative length of the frontal on the vertex: distinctly longer than the nasal (0) - same length or shorter than the nasal (1).
10. Width of the vertex: ratio between minimum distance separating the maxillae across the vertex and postorbital width of the skull < 0.20 (0) - between 0.20 and 0.30 (1) - > 0.30 (2).
11. Dorsomedian portion of the supraoccipital shield: roughly flat or convex (0) - longitudinally concave (1). This character does not involve the degree of development of the more lateral lambdoidal crests.
12. Supraoccipital shield sub vertical on its portion above the occipital condyles: no (0) - yes (1).
13. Height of the occipital condyles: ventral margin of the condyles much lower than the floor of the temporal fossa (0) - approximately at the level of the floor of the temporal fossa (1). Additionally to *Eurhinodelphis* sp., *Argyrocetus patagonicus* seems to have the derived elevated condyles.
14. Roughly complete covering of the temporal fossa by the frontal-maxilla plate: no, squamosal widely visible in dorsal view (0) - yes (1).
15. Height of the temporal fossa: ratio between height of the fossa and bizygomatic width > 0.30 (0) - $\leqslant 0.30$ (1).
16. Fossa for the postorbital lobe of the pterygoid sinus on the orbit roof: no fossa reaching the orbit roof (0) - small fossa laterally limited (1) - longer fossa usually excavating at least half the width of the orbit roof (2).
17. Pterygoid sinus fossa in the alisphenoid dorsoposteriorly excavated above the base of the falciform process: no (0) - yes (1). This condition is often difficult to observe; it is at least present on some specimens of *Schizodelphis*, *Xiphiacetus*, and *Ziphiodelphis*.
18. Anterior articular facet of the periotic: nearly flat or weakly excavated (0) - wide and deep (1).
19. Shape of the pars cochlearis of the periotic: angulated outline, trapezoidal to rectangular in ventral view (0) - rounded, especially anteromedially (1).
20. Tymanic bulla anteriorly pointed in ventral view, with a progressive narrowing: no, abrupt narrowing (0) - yes (1).
21. Inner posterior prominence of the tympanic bulla: roughly as wide as the outer prominence in ventral view (0) - distinctly narrower (1). Even if the prominences are less distinct because of the lack of a deep median furrow in *Eoplatanista*, the widths are similar.

Explanation of plates

PLATE 1

Fig. 1 — Skull of *Xiphiacetus cristatus* IRSNB 3234-M.361 (holotype), Miocene of Antwerp region. Dorsal view. The labels on the skull are from ABEL (1902). f: frontal; me: mesethmoid; n: nasal; pmx: premaxilla; smx: maxilla.

Fig. 2 — *Xiphiacetus cristatus* IRSNB M.1896,?Late Miocene of Antwerp region. Detail of the rostrum in left lateral view, showing the descent of the maxilla-premaxilla suture.

Fig. 3 — *Xiphiacetus cristatus* IRSNB 3240-M.1895, Miocene of Antwerp region. Posterior part of the cranium in dorsal view.

Fig. 4 — *Xiphiacetus cristatus* IRSNB 3237-M.1894, Miocene of Antwerp region. Cranium in dorsal view.

Fig. 5 — *Xiphiacetus cristatus* IRSNB 8243-M.1898, Miocene of Kessel. Cranium in dorsal view.

Fig. 6 — Skull of *Xiphiacetus cristatus* IRSNB 3241-M.1893, Miocene of Antwerp region. Right lateral view. The labels on the skull are from ABEL (1902). f: frontal; pl: palatine; pmx: premaxilla; smx: maxilla; sq: squamosal; v: vomer.

Fig. 7 — Isolated supraorbital process of the right maxilla of *Xiphiacetus cristatus* IRSNB M.1899, Miocene of Antwerp region. Lateral view.

Fig. 8 — Isolated supraorbital process of the right frontal-maxilla of *Xiphiacetus cristatus* IRSNB M.1900, Miocene of Antwerp region. Lateral view.

Scale bars for Figs 1-8 = 50 mm.

PLATE 2

Fig. 1 — Skull of *Xiphiacetus cristatus* IRSNB 3241-M.1893, Miocene of Antwerp region. A. ventral view. B. posterior view. C. detail of the right side of the cranium in ventral view. Scale bar for A-C = 50 mm. The labels on the skull are from ABEL (1902). exo: exoccipital; pl: palatine; smx: maxilla; v: vomer.

Fig. 2 — Right supraorbital process of *Xiphiacetus cristatus* IRSNB M.1901, Miocene of Antwerp region. Ventral view showing the fossa for the postorbital lobe of the pterygoid sinus. Scale bar = 50 mm.

Fig. 3 — Maxillary teeth of *Xiphiacetus cristatus* IRSNB M.1896,?Late Miocene of Antwerp region. A. anterolateral view of a series of seven teeth. B. lingual view of the same series. Scale bar for A-B = 20 mm. C. posterior view of another tooth. Scale bar = 10 mm.

Fig. 4 — Maxillary teeth of *Pontoporia blainvillei* ZMA 15.518. The first on the left is in anterior or posterior view, the four others in lingual or labial view, all of them with the crown towards the top of the plate. Scale bar = 10 mm.

PLATE 3

Fig. 1 — Skull of *Xiphiacetus cristatus* IRSNB 3227-M.1897, Miocene of Antwerp region. A. posterior part of the cranium in anterodorsal view. B. partial basicranium in anteroventral view, showing the asymmetry of the squamosals (right larger than left). Scale bars = 50 mm.

Fig. 2 — Right periotic of *Xiphiacetus cristatus* USNM 21360, from the Calvert Formation, Middle Miocene of the east coast of the USA, with a portion of the pars cochlearis missing. A. lateral view. B. medial view. C. dorsal view. D. ventral view.

Fig. 3 — Posterior portion of the right periotic of *Xiphiacetus cristatus* USNM 21363, Calvert Formation, Middle Miocene of the east coast of the USA. Ventral view, showing the shortened posterior process.

Scale bar for Figs 2-3 = 10 mm.

Fig. 4 — Right tympanic bulla of *Xiphiacetus cristatus* IRSNB M.1902,?Late Miocene of Antwerp region. A. ventral view. B. medial view. C. dorsal view.

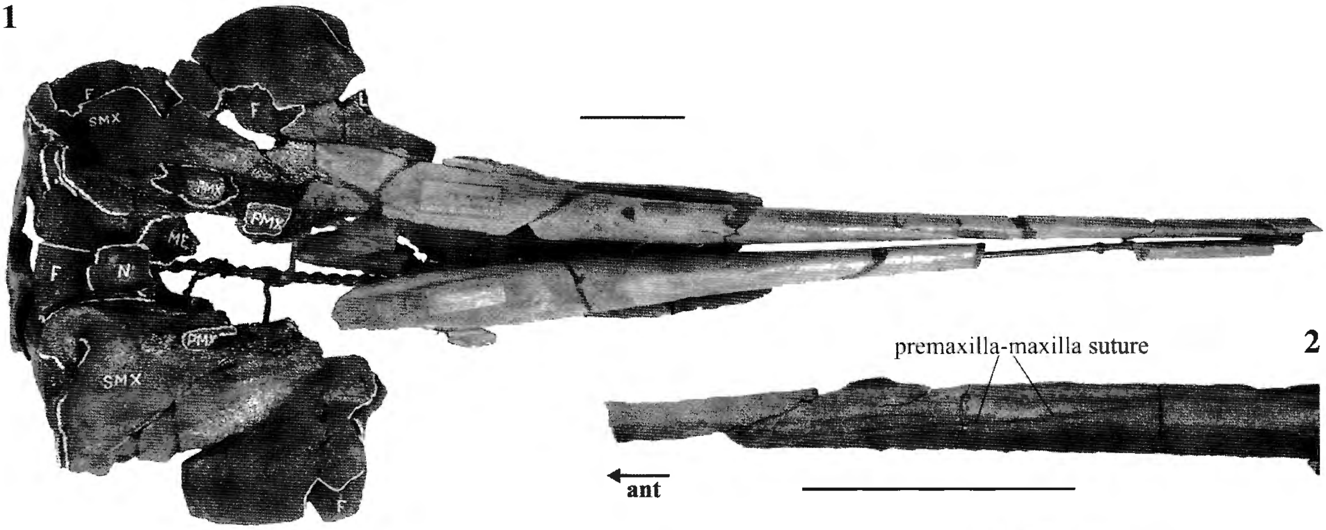
Fig. 5 — Left tympanic bulla of *Xiphiacetus cristatus* USNM 244401, Calvert Formation, Middle Miocene of the east coast of the USA. A. ventral view. B. medial view.

Scale bar for Figs 4-5 = 20 mm.

PLATE 4

Cervical and thoracic vertebrae of *Xiphiacetus cristatus* IRSNB 3234-M.361 (holotype), Miocene of Antwerp region. A. atlas (c1) in dorsal view. B. atlas in anterior view. C. seven cervicals (c1-c7) in left lateral view. Note the ventrolaterally elongated parapophysis of c6. D. axis (c2) in anterior view. E. third cervical (c3) in anterior view. F. six first thoracics (t1-t6) in left lateral view. G. first thoracic (t1) in left lateral view. H. first thoracic in anterior view, illustrating measurements 6-9. I. first thoracic in dorsal view.

Scale bars for A, B, D, E, G, H, I = 20 mm, for C, F = 50 mm.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F
SMX
F
PMX
PMX
ME
F
N
PMX
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2
premaxilla-maxilla suture
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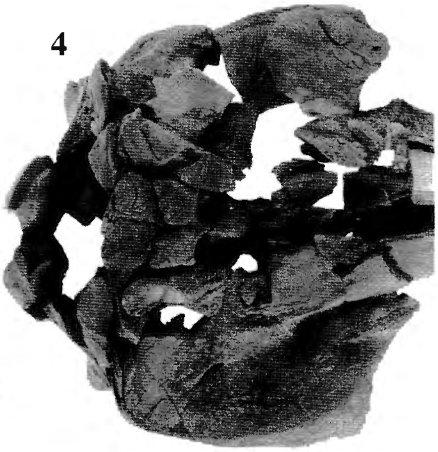
3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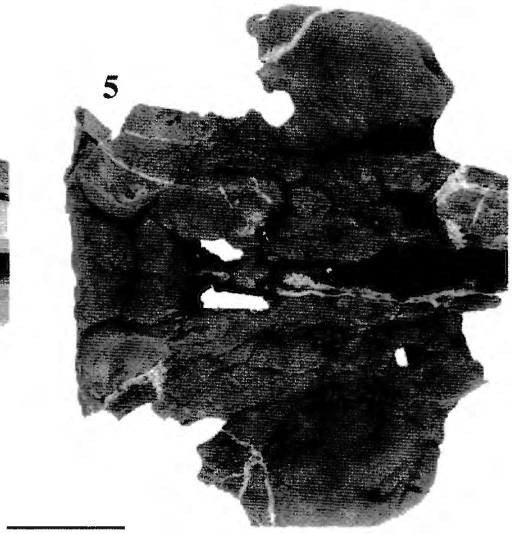
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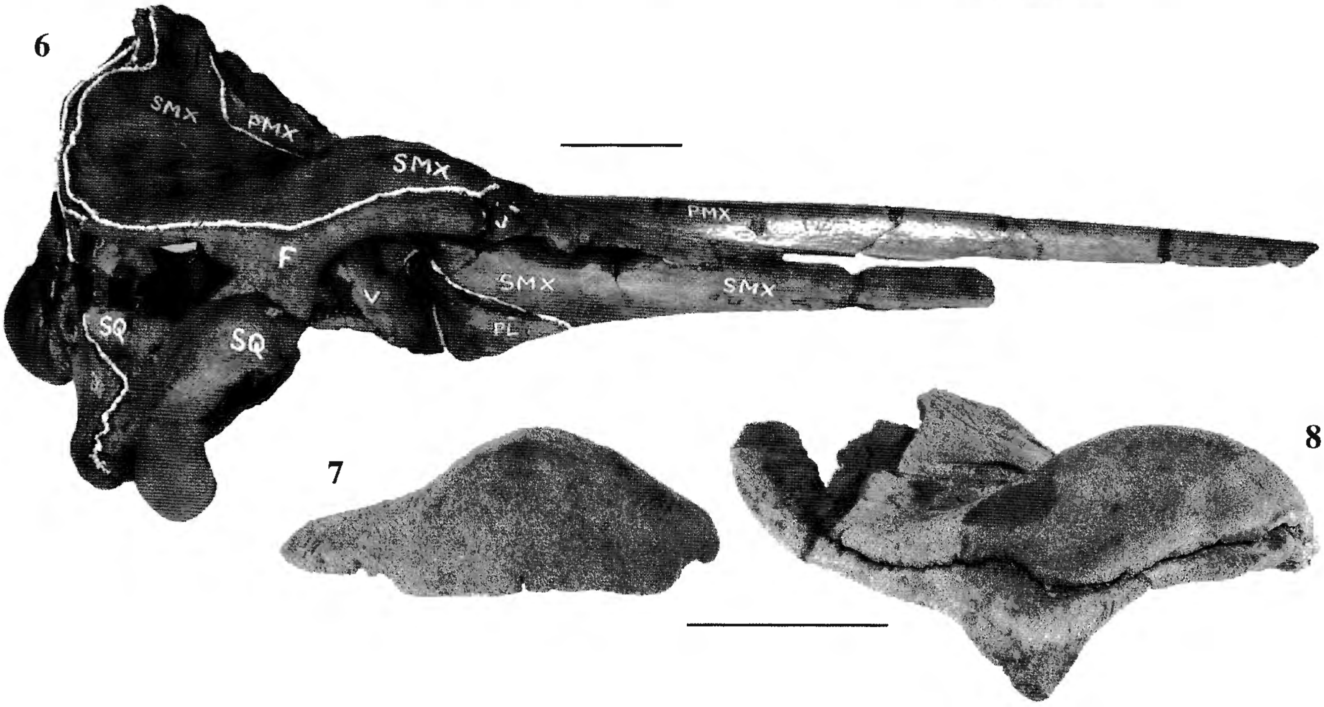
6
SMX
PMX
SMX
J
PMX
F
V
SMX
SMX
SQ
SQ
PL
7
8

PLATE 1

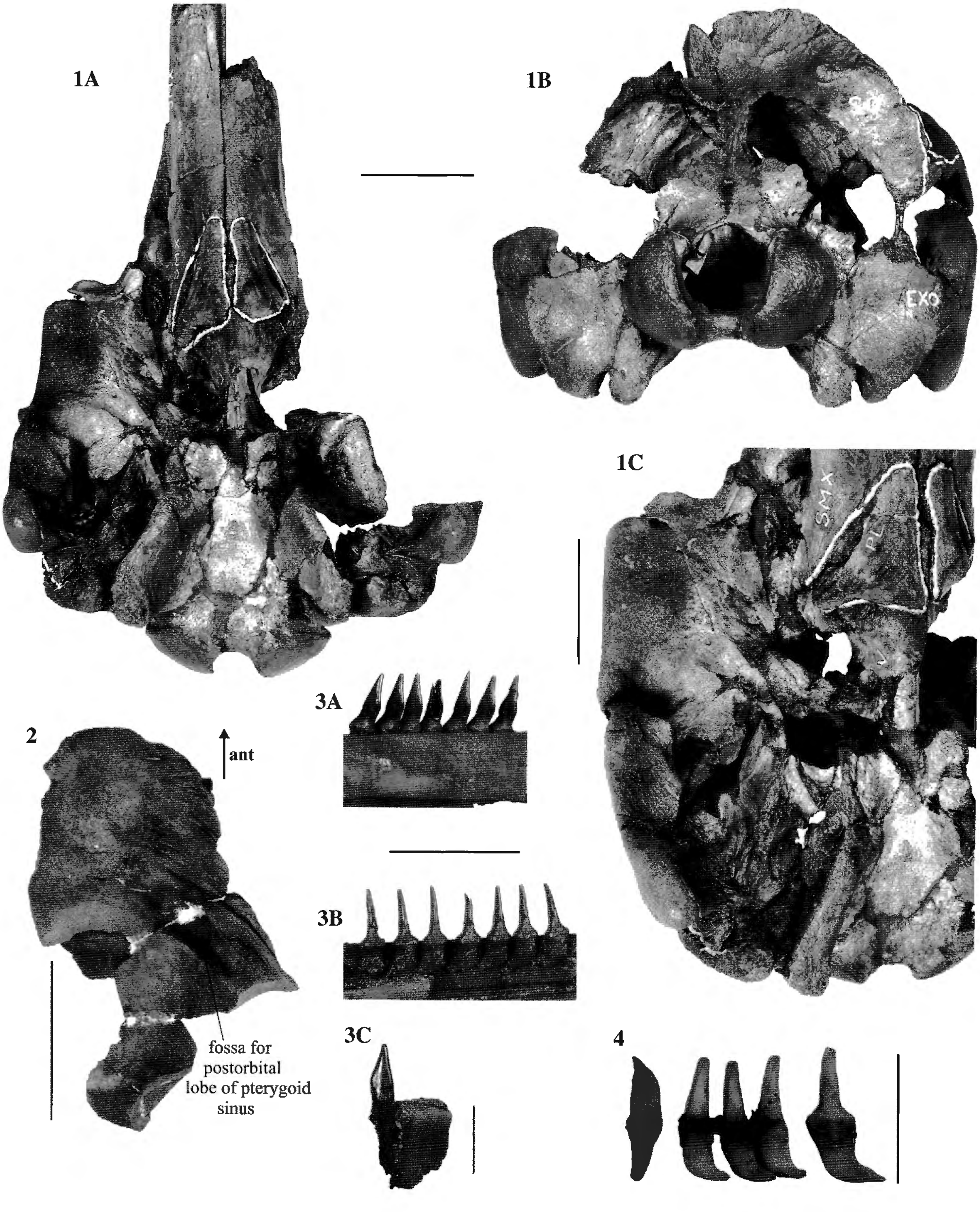
1A
1B
EXO
1C
SMX
PL
2
ant
fossa for postorbital lobe of pterygoid sinus
3A
3B
3C
4

PLATE 2

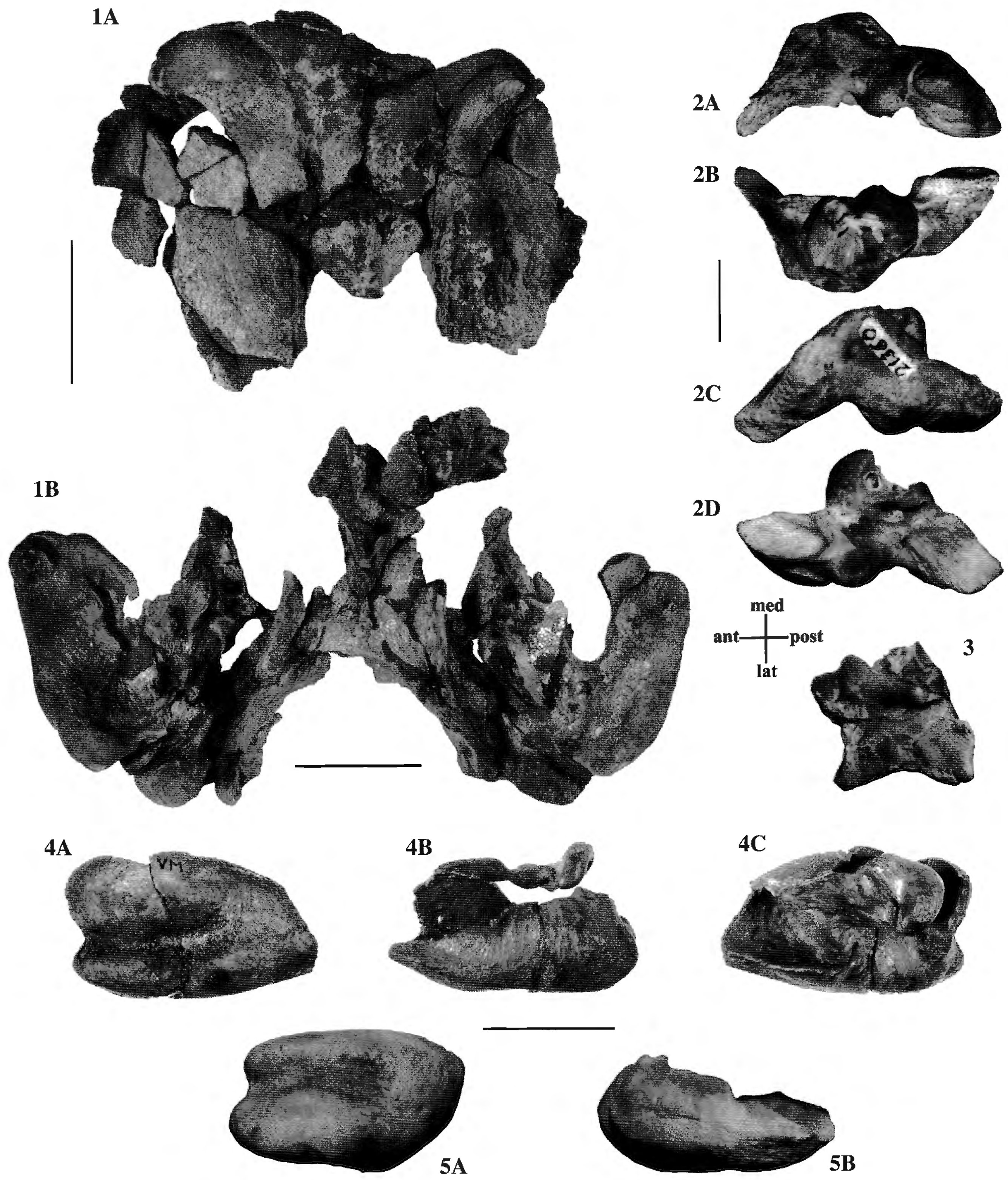

PLATE 3

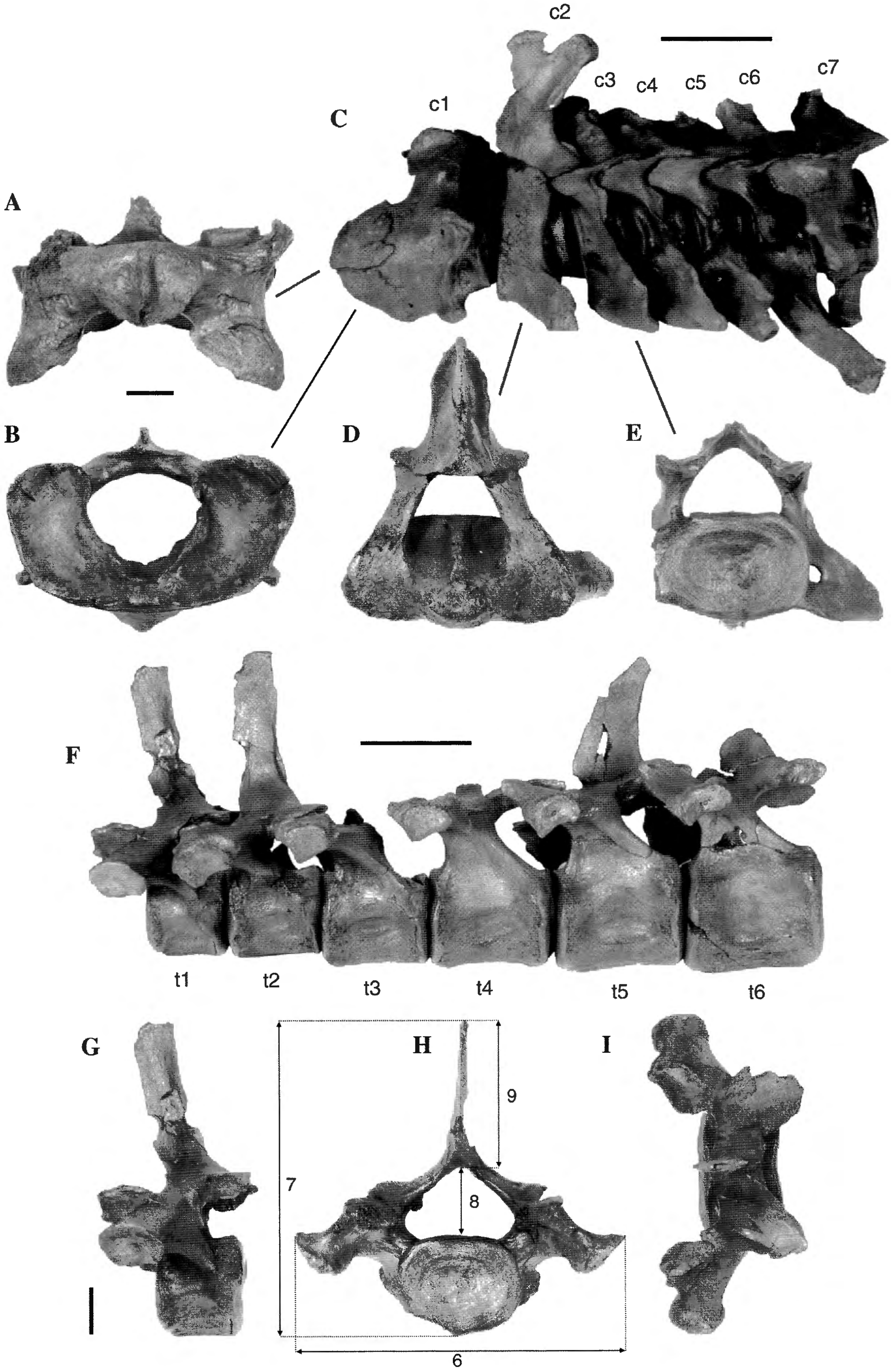

PLATE 4