

Sperm whales from the Miocene of the North Sea: a re-appraisal

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Abstract

A review of the sperm whales (Cetacea, Odontoceti, Physeteroidea) from the Miocene of the southern margin of the North Sea Basin is undertaken, mostly based on the cranial material of the area of Antwerp (north of Belgium) described for the first time by P.-J. Van Beneden, B. A. L. du Bus, and O. Abel more than a century ago. This work leads to the detailed redescription of the species *Eudelphis mortezelensis*, *Physeterula dubusi*, *Placoziphius duboisi*, and *Thalassocetus antwerpiensis*, the identification in the North Sea Basin of the eastern North American species *Orycterocetus crocodilinus*, and the description of a new undetermined physeterid. The stratigraphic information associated to some of these Miocene taxa is refined (*E. mortezelensis*, *O. crocodilinus*, and *P. duboisi*), whereas a more important incertitude persists for others. These results further emphasize the physeteroid diversity during the Miocene.

The performed phylogenetic analysis places *Eudelphis* as the most basal stem-physeteroid, displaying the most salient features of the superfamily (supracranial basin, strong asymmetry of the bony nares and premaxillae) but retaining enamel on teeth and a rather conservative skull morphology (deep maxillary alveoli, large left premaxillary foramen, distinct falciform process of the squamosal...). Together with *Orycterocetus*, *Placoziphius* is provisionally kept outside the family Physeteridae, defined as the clade grouping all the physeteroids more closely related to *Physeter* than to *Kogia*. The large species *Physeterula dubusi* is the most stemward physeterid, retaining functional upper teeth lacking enamel. Among the physeterids the new undetermined taxon is sister-group to the clade *Aulophyseter* + *Physeter*, sharing with these two genera the preorbital process distinctly lower than the lateral margin of the rostrum base. With a sagittal crest in its supracranial basin the small *Thalassocetus antwerpiensis* is confirmed as an archaic kogiid.

The evolutionary history of the supracranial basin and the oral apparatus are discussed. The parsimony analysis suggests that the spermaceti organ remained small in the supracranial basin of most physeteroids, the basin probably functioning as a parabolic structure for reflecting and focusing the echolocative sounds. It is proposed

that the spermaceti organ only considerably increased in size in the lineage of the Recent species *Physeter macrocephalus*, possibly as a sexually dimorphic sound transmitting organ. Preceded by the loss of enamel, the reduction of the upper dentition associated to a decrease of the size of the temporal fossa occurred in parallel in the physeterids and the kogiids, much likely related to a major change in diet and food processing.

Keywords: Odontoceti, Physeteroidea, sperm whale, Miocene, North Sea, phylogeny.

Résumé

La révision des cachalots (Cetacea, Odontoceti, Physeteroidea) du Miocène du bord sud du Bassin de la Mer du Nord est entreprise, principalement sur base du matériel crânien de la région d'Anvers (nord de la Belgique) décrit pour la première fois il y a plus d'un siècle par P.-J. Van Beneden, B. A. L. du Bus, et O. Abel. Ce travail mène à la redescription des espèces *Eudelphis mortezelensis*, *Physeterula dubusi*, *Placoziphius duboisi*, and *Thalassocetus antwerpiensis*, à l'identification dans le Bassin de la Mer du Nord d'*Orycterocetus crocodilinus*, espèce connue auparavant de la côte est des Etats-Unis, et à la description d'un nouveau physétéridé indéterminé. L'information stratigraphique associée à certains de ces taxons (*E. mortezelensis*, *O. crocodilinus*, et *P. duboisi*) est affinée, alors qu'une plus grande incertitude persiste pour les autres taxons étudiés. Ces résultats soulignent la diversité des physétéroïdés durant le Miocène.

L'analyse phylogénétique entreprise positionne *Eudelphis* comme le plus basal des 'stem'-physétéroïdés. Celui-ci montre les caractères principaux de la super-famille (bassin supracrânien, forte asymétrie des narines osseuses et des prémaxillaires), mais il conserve de l'émail sur les dents et une morphologie crânienne relativement archaïque (alvéoles maxillaires profondes, grand foramen prémaxillaire gauche, processus falciforme du squamosal développé...). Avec *Orycterocetus*, *Placoziphius* se place ici en dehors de la famille Physeteridae, définie comme le clade groupant tous les physétéroïdés plus proches parents de *Physeter* que de *Kogia*. La grande espèce *Physeterula dubusi* constitue le plus basal des physétéridés, conservant des dents fonctionnelles supérieures sans émail. Parmi les physétéridés, le nouveau taxon indéterminé est le groupe-frère du clade *Aulophyseter* + *Physeter*, partageant avec ces derniers le processus préorbitaire nettement plus bas que le bord latéral du rostre à sa base. Avec une crête sagittale dans son

bassin supracrânien, le statut de kogiidé archaïque de *Thalassocetus antwerpiensis* est confirmé.

L'histoire évolutive du bassin supracrânien et de la région orale sont commentés. L'analyse de parcimonie suggère que l'organe du spermaceti a conservé une taille réduite dans le bassin supracrânien de la plupart des physétéroïdés, le bassin fonctionnant probablement comme une structure parabolique permettant la réflexion et la focalisation des sons d'écholocalisation. La taille de l'organe du spermaceti n'aurait augmenté significativement que dans la lignée de l'espèce actuelle *Physeter macrocephalus*, peut-être comme organe de transmission des sons sexuellement dimorphique. Précédée de la perte de l'émail dentaire, la réduction de la dentition supérieure associée à la diminution de taille de la fosse temporale se produit en parallèle chez les physétéridés et les kogiidés, vraisemblablement en relation avec un changement majeur dans l'alimentation et le traitement de la nourriture.

Mots-clefs: Odontoceti, Physeteroidea, cachalot, Miocène, Mer du Nord, phylogénie.

Introduction

The three Recent sperm whale species roughly occupy the limits of the range of sizes for all the known physeteroids. *Physeter macrocephalus* is the largest, with adult males reaching 18 meters; the two species of *Kogia* are among the smallest, with a mean body length of only 2.7 meters in *Kogia simus* (CALDWELL & CALDWELL, 1989; RICE, 1989). Besides the lack of upper functional teeth and a diet mostly predominated by squid, the main cranial feature grouping these three species and differentiating them from all other odontocetes is the large supracranial basin, containing organs related to the production and transmission of sounds (review of the homologies with the forehead morphology of other odontocetes in CRANFORD *et al.*, 1996). The presence of a supracranial basin can be traced in the fossil record back to the early Miocene, with two species from Patagonia (MORENO, 1892; LYDEKKER, 1893). Older presumably physeteroid material, from the late Oligocene of Azerbaijan is too fragmentary to infer the presence of a supracranial basin (MCHIDLIDZE, 1970).

Besides the dental and fragmentary non-diagnostic material (e.g. *Scaldicetus carretti* DU BUS, 1867, *S. grandis* DU BUS, 1872, *Prophyseter dolloi* ABEL, 1905), four physeteroid species from the Miocene of Antwerp, north of Belgium, southern margin of the North Sea Basin, were described on the basis of more diagnostic skull elements: the large *Physeterula dubusi* VAN BENEDEN, 1877, the moderate size *Eudelphis mortezelensis* DU BUS, 1872, the smaller *Placoziphius duboisi* VAN BENEDEN, 1869, and the

even smaller *Thalassocetus antwerpiensis* ABEL, 1905. The main specimens were found during the building of fortifications around the city of Antwerp, mostly between 1861 and 1863 (VAN BENEDEN, 1861; DU BUS, 1867; VANDEN BROECK, 1874; ABEL, 1905) in several localities of the south-east suburbs of the city (Fig. 1).

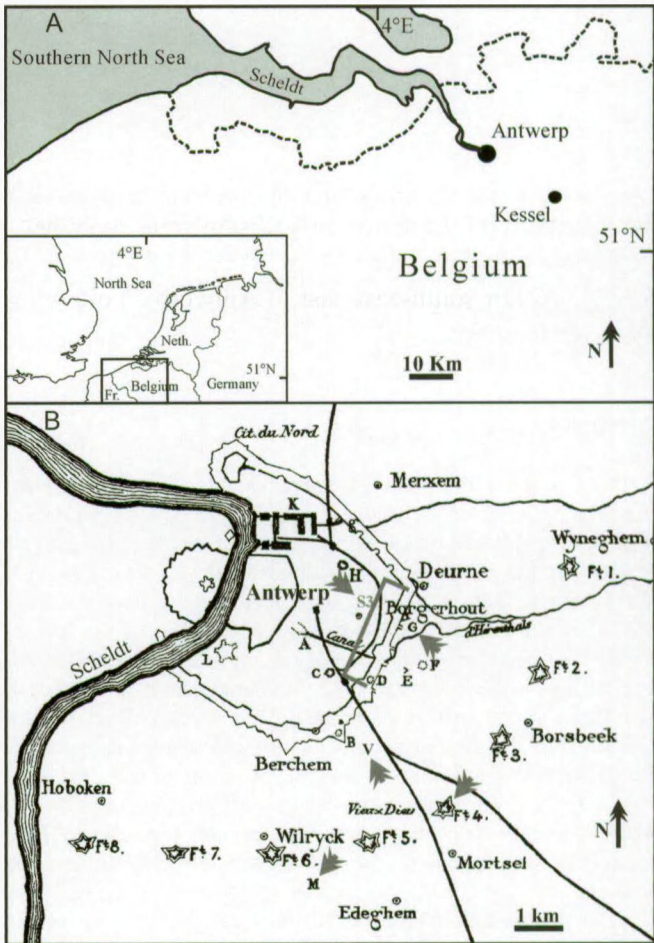


Fig. 1 – A. Map of the north of Belgium giving the position of Antwerp and Kessel on the southern margin of the North Sea Basin. B. Map of Antwerp and its suburbs with the two fortification rings dating from the 19th century (modified from VANDEN BROECK, 1874). The Miocene localities where physeteroid remains were found are indicated by arrows: Ft 4. Fort n°4, Oude God (Vieux-Dieu), Mortsel (*Eudelphis mortezelensis*). G. Ancien fortin n°1 (*Physeterula dubusi*). M. Briqueterie de la société Pauwels, Edegem (*Placoziphius duboisi*). S3. 3^{ème} section (inner fortification ring) (Physeteridae indet. IRSNB M.1937). V. Veldekens, Berchem (*Placoziphius duboisi*). One locality (Veldekens) yielded remains some years ago, whereas the others were exploited during the years 1861-1863.

These species have been the subject of comments in various works dealing with other physeteroids (KELLOGG, 1925, 1927, 1965; MUIZON, 1991; HIROTA & BARNES, 1995; KAZÁR, 2002; BIANUCCI & LANDINI, 2006), but most authors were reluctant to use them (or part of them) as comparison material or in phylogenetic analyses of the superfamily Physeteroidea, probably for two main reasons: (1) the lack of good quality illustrations and detailed descriptions in the original papers and (2) the relatively fragmentary state of the type material (actually needing also some re-preparation work). An additional weak side of these specimens is the lack of precise stratigraphic data associated. This last point can be partly solved with a revision of the stratigraphy of the old localities and with the addition of more recently discovered specimens from new localities (Veldekens, Berchem and fort of Kessel, 16 km south-east-east to Antwerp). Following the re-preparation of the specimens the aims of this paper are therefore: (1) to redescribe in detail these specimens, with correct illustrations, (2) to compare them with more recently described physeteroid taxa, (3) to clarify the stratigraphy for some of the species, and (4) to include these species in a phylogenetic analysis of the superfamily Physeteroidea. These systematic and phylogenetic sections will be followed by comments on functional anatomy, mostly focused on the sound producing area (supracranial basin) and the feeding apparatus.

Material and methods

Institutional abbreviations. IRSNB: Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MNHN: Muséum national d'Histoire naturelle, Paris, France; USNM: United States National Museum of Natural History, Washington DC, USA; ZMA: Zoölogisch Museum Amsterdam, The Netherlands.

Measurements. Due to the fragmentary and dislocated state of preservation of most of the specimens the few measurements that could be taken are placed directly in the text of the description.

Taxonomic names. In a way to lighten the text the species names for monospecific genera are omitted. In the genus *Orycterocetus* only the species *O. crocodilinus* was considered for comparison. Additionally author names of fossil physeteroid species from localities outside the North Sea mentioned in the text are provided here: *Aprixokogia kelloggi* WHITMORE & KALTENBACH, 2008; *Aulophyseter morricei* KELLOGG, 1927; '*Aulophyseter*'

rionegrensis GONDAR, 1975; *Brygmophyseter shigensis* (HIROTA & BARNES, 1995); *Diaphorocetus poucheti* (MORENO, 1892); *Idiophyseter merriami* KELLOGG, 1925; *Idiorophus patagonicus* (LYDEKKER, 1893); *Orycterocetus crocodilinus* COPE, 1868; *Praekogia cedrosensis* BARNES, 1973; *Scaphokogia cochlearis* MUIZON, 1988; *Zygophyseter varolai* BIANUCCI & LANDINI, 2006. For further details on the age and locality of these species, see the review in BIANUCCI & LANDINI (2006).

Non-diagnostic material from Antwerp area. Based on three fragments of the anterior part of a large rostrum, ABEL (1905) erected the species *Prophyseter dolloi*. The author provided two arguments to identify this species as a sperm whale: the transverse compression of the anterior of the rostrum and the first step towards a reduction of the upper teeth, indicated by the partial occlusion with bony outgrowths of the alveoli (specially the premaxillary alveoli). Even if, mostly because of the size, the physeteroid hypothesis is better supported, a similar trend towards the reduction of the upper (and lower) teeth is observed in Ziphiidae (MUIZON, 1991; LAMBERT, 2005). Furthermore several ziphiids display a transversely compressed rostrum. As this specimen does not match the dimensions of the rostrum and/or alveoli of other known physeteroids from the North Sea, *P. dolloi* is considered Odontoceti aff. Physeteroidea and it will not be considered in detail farther in the text.

The status of the tooth-based species *Scaldicetus caretti* DU BUS, 1867 (type species) and *S. grandis* (DU BUS, 1872) is briefly commented on in the section Systematic palaeontology. More recently, a fragmentary physeteroid skeleton from the Miocene of Antwerp has been described (PETERS & MONTEIRO, 2005), but due to the limited information available only rough similarities with *Orycterocetus crocodilinus* and *Physeterula dubusi* could be noted. Even more recently an isolated tooth from the Neogene of Antwerp previously identified as a pinniped canine (*Paleophoca nystii* VAN BENEDEN, 1859) was corrected as a physeteroid tooth (KORETSKY & RAY, 2008).

Systematic palaeontology

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1867

Superfamily Physeteroidea GRAY, 1821

Genus *Eudelphis* DU BUS, 1872

Type species: *E. mortezelensis* DU BUS, 1872

Diagnosis. The diagnosis is the same as for the only included species.

***Eudelphis mortezelensis* DU BUS, 1872**

Figs 2-6

1872 — *Eudelphis mortezelensis* DU BUS, p. 500.1874 — *Eudelphis mortselensis* VAN DEN BROECK, p. 146.1898 — *Delphinus mortezelensis* TROUËSSART, p. 1032.1905 — *Scaldicetus mortselensis* ABEL, p. 66; fig. 5.2006 — *Eudelphis mortselensis* BIANUCCI & LANDINI, p. 104.**Holotype**

IRSNB M.523, the skull of a young individual, associated with two teeth, missing mostly elements of the supracranial basin.

Type locality

Fort n°4, Oude God (Vieux-Dieu), Mortsel, 6 km south-west to Antwerp city (Fig. 1). Geographic coordinates: 51°10'25"N-4°27'36"E.

Type horizon

Berchem Formation, Antwerpen Sands Member. This member is dated by dinoflagellates from Langhian (possibly latest Burdigalian) to middle Serravalian (LOUWYE *et al.*, 1999, 2000; LOUWYE, 2005).

Emended diagnosis

Eudelphis mortezelensis is a moderate size physeteroid somewhat larger than *Orycterocetus crocodilinus*. It differs from all the other members of the superfamily in: the presence of a large left premaxillary foramen, the vomer widely exposed in ventral view, and the postglenoid process of the squamosal ventrally elongated. It differs from all the other physeteroids except *Zygophyseter* in the plate-like falciform process of the squamosal, from all the other physeteroids except *Scaphokogia* in the rostrum more progressively narrowing forwards, from *Brygmophyseter* and *Zygophyseter* in the proportionally smaller teeth, from *Zygophyseter* in the shorter zygomatic process of the squamosal, from *Idiorophus* and *Scaphokogia* in the widely dorsally open mesorostral groove, from *Aulophyseter*, *Idiophyseter*, *Kogia*, *Orycterocetus*, *Physeter*, and *Scaphokogia* in the presence of at least 10 deep maxillary alveoli, from *Aulophyseter*, *Kogia*, *Orycterocetus*, *Physeter*, and *Physeterula* in the enamelled crown of the teeth, and from *Aulophyseter*, *Orycterocetus*, *Physeter*, and *Physeterula* in the low supraoccipital shield.

Comments

The species name was changed in *E. mortselensis* by VANDEN BROECK (1874), following the label associated to the skull. As there is no clear evidence of an

inadvertent mistake as defined by the ICZN (1999), this change is not supported and the original spelling should be preserved.

When revising the sperm whales described by DU BUS (1867, 1872) and VAN BENEDEN (1869, 1877), ABEL (1905) proposed to refer this species to the genus *Scaldicetus*, together with the tooth-based *S. caretti* (type species) and *S. grandis*. BIANUCCI & LANDINI (2006) correctly restricted the genus and species names of the two latter to the original material of du Bus, considering isolated teeth as not diagnostic, and re-evaluating the original genus name *Eudelphis* for the species *S. mortezelensis*. Two separate works (BIANUCCI & LANDINI, 2006; KIMURA *et al.*, 2006) suggested a change for the genus name of the Japanese species *Scaldicetus shigensis*. As the revision of Kimura *et al.*, proposing the new genus name *Brygmophyseter* Barnes, was published in the time interval between the acceptance and the publication of the work of Bianucci and Landini, it has the priority on the latter for this taxonomic change. Justifying the change in genus name by the fact that the type species of *Scaldicetus*, *S. caretti* is based on isolated teeth, KIMURA *et al.* (2006) propose that ‘*Scaldicetus* is probably a grade taxon, not a natural biological grouping’. Nevertheless, in the same work they continue to refer fragmentary physeteroid specimens to the genus *Scaldicetus*.

ABEL (1905, fig. 6) referred to *E. mortezelensis* an isolated atlas IRSNB M.524 from the Miocene of the area of Anwerp (possibly Fort n°1, east of Antwerp). This complete vertebra, with a maximum width of 226 mm and a maximum width of the anterior articular facets of 157 mm, approximately matches the size of the occipital condyles of the holotype of *E. mortezelensis*, somewhat larger with a more developed transverse process than the atlas of the holotype of *Placoziphius duboisi*, and distinctly smaller and more slender than the atlas of the holotype of *Physeterula dubusi* (see below). As noted by ABEL (1905) its general morphology is similar to *Physeter*, particularly the high transverse process with a rectilinear dorsomedially directed lateral margin. This isolated atlas is referred here to *Physeteroidea* indet.

Description of the holotype of *Eudelphis mortezelensis*

With most of the bones of the rostrum unfused, this skull likely belongs to a relatively young individual. Most of the elements of the rostrum, including two teeth, and of the basicranium are preserved, whereas the walls of the supracranial basin and the supraorbital processes are much more fragmentary. The total length of the skull as preserved is 852 mm. No more than 100 mm of the apex

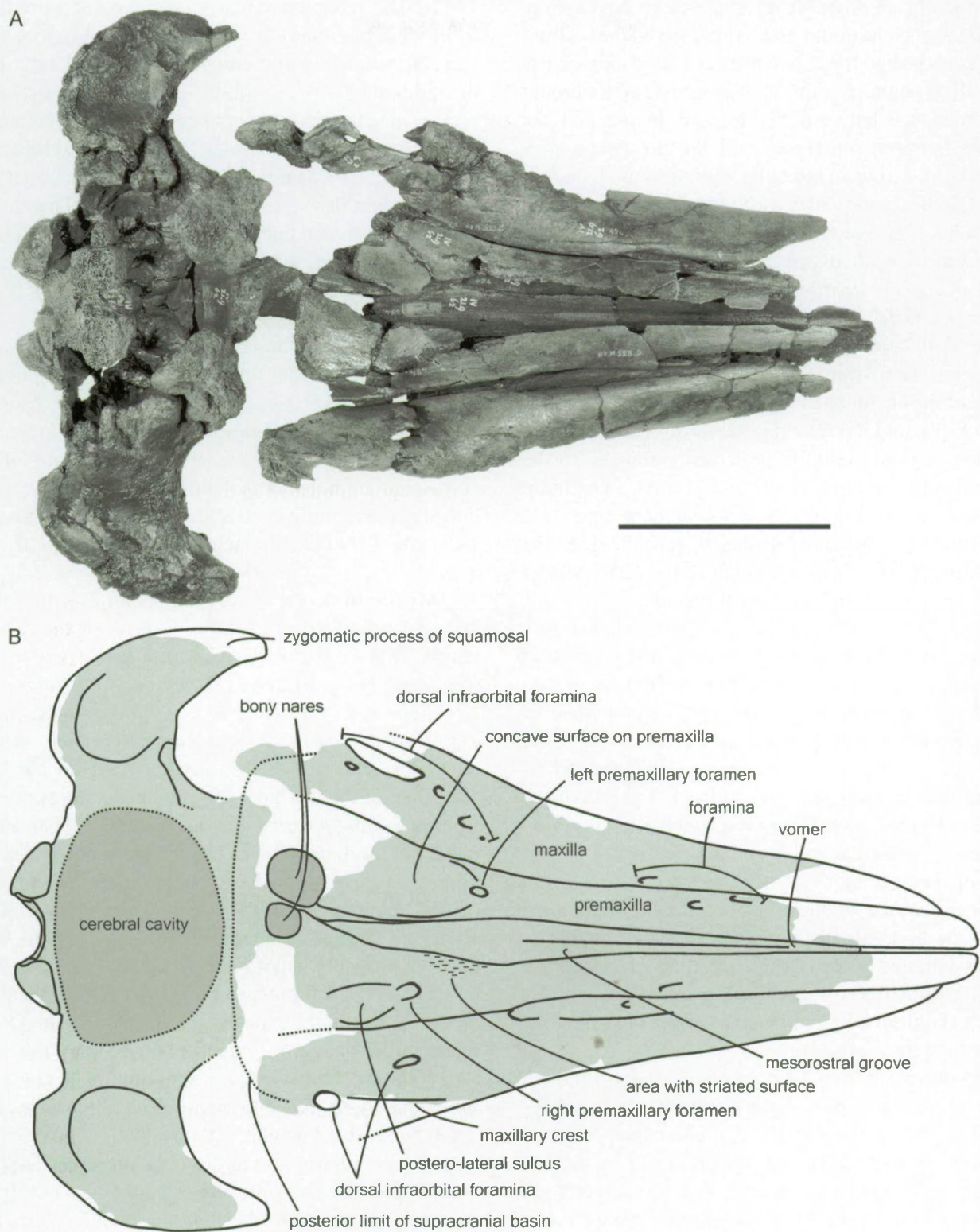


Fig. 2 – Skull of *Eudelphis mortezelensis* IRSNB M.523 (holotype), Miocene of Antwerp. **A.** Dorsal view. **B.** Schematic reconstruction of the skull in dorsal view. The shaded areas represent the preserved elements. Scale bar for A-B equals 200 mm.

of the rostrum are probably missing (see reconstruction, Fig. 2B). As no antorbital notch is preserved the rostrum length is estimated to ca. two thirds of the condylobasal length. Bizygomatic width is 592 mm. Taking account of the distance between the glenoid fossae and the distance between one fossa and the preserved apex of the rostrum, the mandibular bluntness index sensu WERTH (2006: mandibular width/length) was originally not much larger than 0.5. The dimensions of the skull are intermediary between *Diaphorocetus poucheti* / *Orycterocetus crocodilinus* (smaller) and *Aulophyseter morricei* (larger).

The skull's long axis, mostly determined by the direction of the rostrum, is roughly perpendicular to the surface of the occipital condyles (Fig. 3), whereas in the Recent *Kogia* and *Physeter* this axis is directed ventrally, indicating a skull ventrally projected compared to the body axis (CRANFORD, 1999); the primitive condition of *Eudelphis* is also observed in *Orycterocetus* and *Zygophyseter*, whereas *Praekogia* (considering the orientation of the occipital condyles) and *Scaphokogia* already have a rostrum ventrally projected.

Premaxilla. From the proportions of the premaxilla and maxilla at the preserved anterior end the premaxilla was likely anteriorly longer (Fig. 2). A thin plate of the premaxilla nearly completely covers dorsally the anterior part of the mesorostral groove; the mesorostral opening widens until the level of the left premaxillary foramen. The mesorostral groove is dorsally closed by the joined premaxillae in *Idiorophus*, *Scaphokogia*, and a part of the specimens of *Aulophyseter morricei*. On the dorsal surface of the right premaxilla, a foramen pierces the bone along the suture with the maxilla at 230 mm anterior to the right premaxillary foramen; on the left premaxilla, two similar foramina are slightly anterior. From a median slope on the anterior two thirds, the dorsal surface of the premaxilla changes to a lateral slope 65 mm anterior to the right premaxillary foramen; this level might approximately indicate the anterior limit of the supracranial basin. A premaxillary foramen is present on both right and left premaxillae; the left foramen is 60 mm more anterior than the larger right foramen (width: 14 mm versus 11 mm for the left). The right premaxillary foramen is followed posterolaterally by a sulcus (= postero-lateral sulcus). The sulcus laterally margins a triangular depressed and convex surface of the premaxilla. Interestingly the anterior part of this depression is marked by a striated surface that might correspond to the area of origin for the nasal plug muscle observed anterior to the premaxillary sac fossa in other odontocetes (e.g. the ziphiids, see HEYNING,

1989). The left premaxillary foramen, not as reduced as in most physeteroids, opens posteriorly into a wide and concave area with a smooth surface, just anterior to the left bony naris. The more conservative aspect of the premaxillae in this area compared to other physeteroids (a feature seemingly present in *Diaphorocetus*, Bianucci, pers. comm., 2008) might have been accompanied by a similarly less derived soft tissue anatomy. Therefore it cannot be excluded that *Eudelphis* retained well-formed premaxillary sacs, structures present in all the Recent odontocetes except *Kogia* and *Physeter*, in which only incipient or vestigial pockets are observed (HEYNING, 1989; CRANFORD *et al.*, 1996).

Both premaxillae are nearly complete postero-medially but their posterolateral portion is lost. The posterior widening and elevation of the right premaxilla is however sketched, from the anterior limit of the corresponding bony naris. Considering the slope of the dorsal surface of the bone at that level, the supracranial basin could not extend much farther backwards.

Maxilla. In dorsal view, the maxilla is more robust and wider than the premaxilla on most of the rostrum length. It lacks the proximal abrupt narrowing seen in *Aulophyseter morricei*, *Diaphorocetus*, *Idiorophus*, *Orycterocetus*, *Physeterula*, *Placoziphius*, and *Zygophyseter*. Several foramina pierce each maxilla along the suture with the rostrum (two on the right side, one on the left side) but the open sutures prevent from providing accurate diameters (Fig. 2). The lateral margin of the maxilla raises towards the antorbital notch, giving a nearly vertical orientation to the lateral wall of the supracranial basin. One large anteroposteriorly elongated foramen (length 32 mm) pierces the right maxilla probably anteromedial to the lost antorbital notch. A second foramen is 85 mm backwards, at the top of the lateral slope of the supracranial basin. On the left maxilla at least one small foramen, three moderate size foramina and one large longitudinally elongated foramen (length > 57 mm) are located in the area of the lost left antorbital notch.

Deep maxillary alveoli are only preserved on their medial side. The first posterior right alveolus is 150 mm anterior to the level of the right premaxillary foramen. However, as the surface of the maxilla is damaged posteriorly, more posterior alveoli might have been originally present. 10 alveoli are preserved on a length of 272 mm for the right maxilla, and 10 on 280 mm for the left maxilla (Fig. 3D). The total tooth count was however certainly higher, with several anterior alveoli missing (at least three), but it did not reach the count of *Idiorophus patagonicus* (22 teeth on each side of

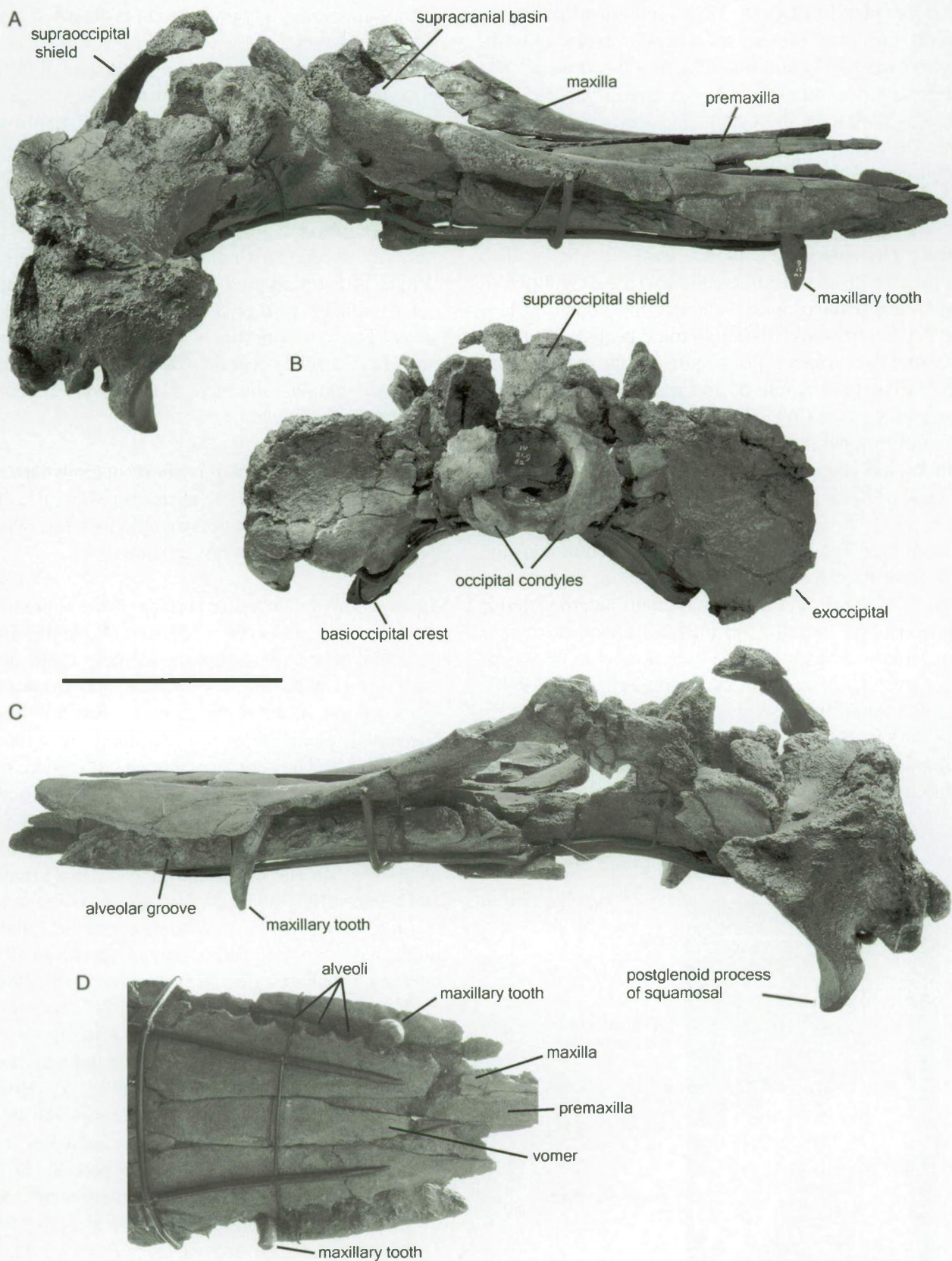


Fig. 3 – Skull of *Eudelphis mortezelensis* IRSNB M.523 (holotype), Miocene of Antwerp. **A.** Right lateral view. **B.** Posterior view. **C.** Left lateral view. **D.** Ventral view of the palate. Scale bar for A-D equals 200 mm.

the upper jaw; LYDEKKER, 1893). Individualized upper alveoli are also present in *Diaphorocetus* (13-14), *Zygophyseter* (13) and possibly *Brygmophyseter*. The anteroposterior diameter of the alveoli ranges from 20 to 29 mm, with short septa and a mean depth of 30 mm. The ventral surface of the maxilla is nearly flat, subhorizontal, and wide. A palatine foramen is located 80 mm anterior to the tip of the right palatine.

Vomer. The anteriorly complete vomer is shorter than the premaxilla and maxilla, contrary to the condition in *Kogia* and *Scaphokogia*. Ventrally the vomer widens and flattens forwards. Being no more keeled, it forms a wide and flat surface exposed between the maxillae and premaxillae on a length of 240 mm, with a maximum width of 45 mm (Fig. 3D). Such a wide exposure of the vomer is possibly related to the young age of the animal (see young *Physeter macrocephalus* figured in KELLOGG, 1925, pl. 6).

Mesethmoid. The morphology of the mesethmoid is the only indication for the asymmetry of the bony nasal tracts. The right tract has a maximum anteroposterior diameter of 37 mm; the left tract has a diameter larger than 56 mm. The keel of the mesethmoid between the two nares is distinctly tilted on the left side (30-40° from the vertical).

Palatine. The two palatines are partly preserved as unfused simple plates, somewhat thickened posteriorly.

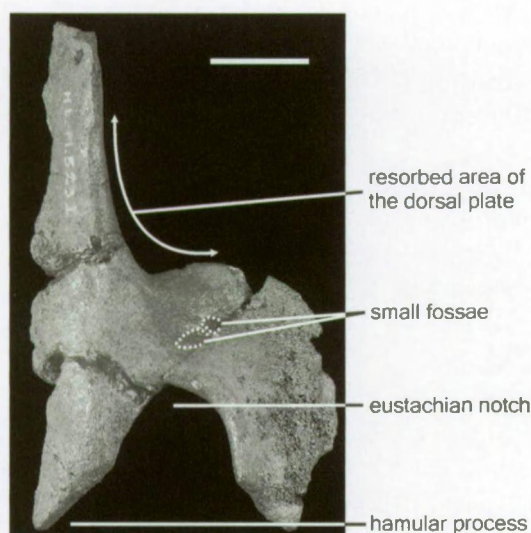


Fig. 4 – Left pterygoid of *Eudelphis mortezelensis* IRSNB M.523 (holotype), Miocene of Antwerp, in ventral view. Scale bar equals 30 mm.

Pterygoid. Both pterygoids are also detached from the skull. The general shape of the bone is similar to *Kogia* and *Physeter*, except for a strong reduction of the dorsal plate usually covering the ventrolateral surface of the palate (Fig. 4). This reduction is much likely related to the development of the pterygoid sinus in the palate area (see the illustration of *Kogia* in FRASER & PURVES, 1960, pl. 16), a trend documented, but in a lesser extent, in other physeteroids (MUIZON, 1984; pers. obs.). Actually, several small and deep fossae on the median lamina of the pterygoid just anterior to the eustachian notch indicate further development of the pterygoid sinus. The posterior tip of the unexcavated hamular process is medial, differing from the laterally directed tip in *Aulophyseter morricei*, *Kogia*, *Orycterocetus*, and *Physeter*.

Frontal. The deeply worn portions of frontal preserved at the posterior wall of the supracranial basin only give a faint idea of the abrupt elevation of this wall; the dorsal extent of the basin is unknown.

Supraoccipital. The outer surface of the supraoccipital shield is only preserved on 55 mm above the foramen magnum, where it is slightly convex; more dorsally the bone is abraded. Nevertheless, the slope on this short portion, at an angle no more than 50° from the horizontal plane, allows a comparison with other physeteroids. The supraoccipital shield is more erected with a concave surface in *Aulophyseter morricei* (see comment in KIMURA *et al.*, 2006), *Orycterocetus*, *Physeter*, and *Physeterula*, whereas the condition in *Diaphorocetus* and *Brygmophyseter*, with a lower slope and a generally convex or flat surface, is more similar to *Eudelphis*. A small to moderate size occipital crest might have limited posteriorly the supracranial basin, but not on such an extent as in *Orycterocetus*, *Physeter*, or *Physeterula*.

Squamosal. On both sides, the zygomatic process of the squamosal is incomplete (Fig. 5). However, the orientation of the ventral surface of the process, continuous with the glenoid fossa, indicates a short triangular apex of the zygomatic process no more than 140 mm anterior to the anterolateral margin of the exoccipital, shorter than in *Brygmophyseter*, *Diaphorocetus*, *Orycterocetus*, *Physeterula*, and *Zygophyseter*. The anteroposteriorly flattened post-glenoid process forms a wide plate anteroventrally curved. The ventral tip, triangular in anterior view, is considerably longer ventrally than the post-tympanic process, separated from the latter by a deep and wide

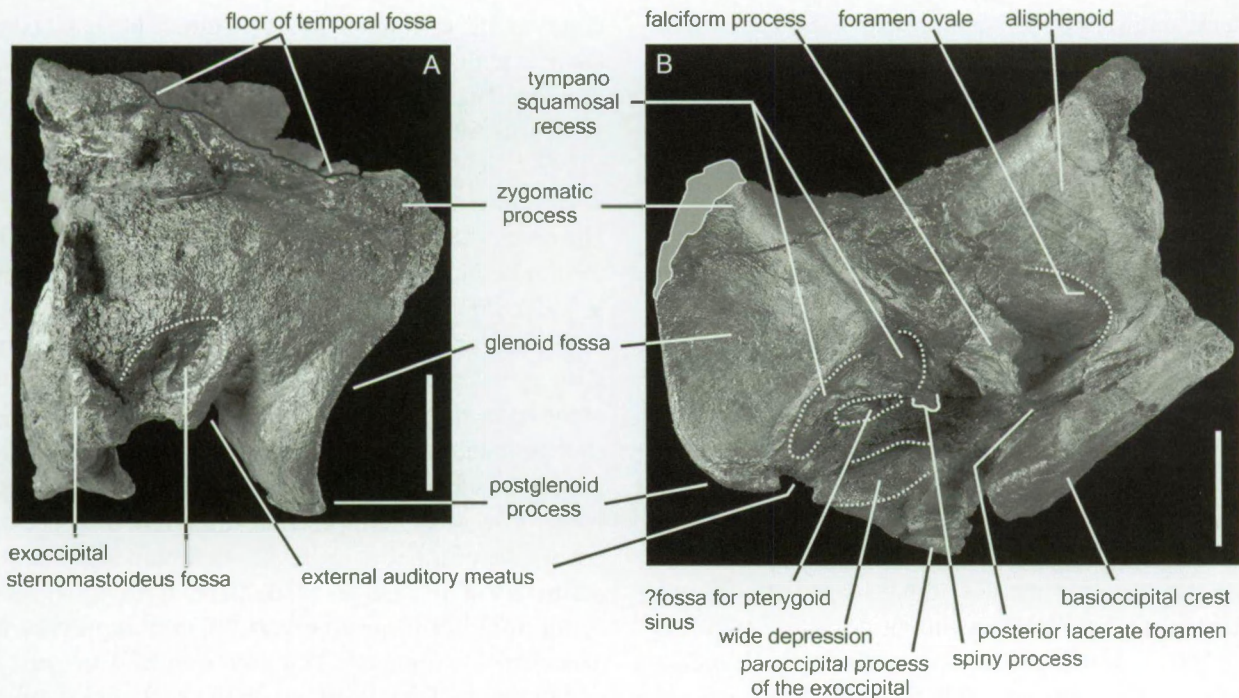


Fig. 5 – Right squamosal, exoccipital, and basioccipital of *Eudelphis mortezelensis* IRSNB M.523 (holotype), Miocene of Antwerp. **A.** Lateral view. **B.** Anteroventral view. Scale bar for A-B equals 50 mm.

external auditory meatus. This condition is similar to the archaeocete *Zygorhiza* TRUE, 1908 and basal odontocetes as *Agorophius* COPE, 1895 and *Squalodon* GRATELOUP, 1840. The postglenoid process is shorter in all other physeteroids for which this area is preserved. An oval sternomastoideus fossa excavates the lateral surface of the post-tympanic process.

The triangular glenoid surface is anteromedially and posteromedially limited by a depression (= tympanosquamosal recess), especially deep towards the postglenoid process. The falciform process is a thin and moderately large plate nearly ventrally facing, separated from the glenoid surface by a series of fossae corresponding to the medial part of the tympanosquamosal recess. The condition in *Zygophyseter* seems similar. In *Orycterocetus*, *Physeter*, *Physeterula*, *Placoziphius* (see below), and the kogiids *Kogia* and *Praekogia*, the falciform process is either reduced to a slender projection, or to a short bud, or is even absent. In Recent physeteroids as well as in Recent ziphiids the pterygoid sinuses are proportionally much larger than in other odontocetes (FRASER & PURVES, 1960); more voluminous air spaces surrounding the ear bones would be necessary for keeping an acoustically isolating thin air layer around the ear bones during deep diving (for binaural hearing or to allow efficient operation of the ossicular chain), when increasing

pressure strongly squeezes the air sacs (FRASER & PURVES, 1960; CRANFORD *et al.*, 2008). It is proposed here that the reduction of the falciform process of the squamosal in the physeteroids from the condition in *Eudelphis* is directly related to the enlargement of the pterygoid sinus, this enlargement being possibly associated to the shift to deeper foraging areas in more crownward taxa.

The ear bones of the holotype are lost, suggesting that these were better isolated from the rest of the basicranium than in e.g. the archaic odontocete *Simocetus* FORDYCE, 2002. However, a roughly cylindrical bony element striated with longitudinal grooves, is transversely directed along the posterior margin of the left external auditory meatus (not preserved on the right side), from the spiny process of the squamosal to the lateral margin of the post-tympanic process; it might correspond to a part of the enlarged posterior process of the tympanic bulla, partly fused with elements of the squamosal in physeteroids and ziphiids (KASUYA, 1973; MUZON, 1984). Between the posterior meatal crest and this hypothetical element of the tympanic bulla is an elongated fossa likely corresponding to a diverticle of the pterygoid sinus fossa, extending posterodorsally to the external auditory meatus.

The floor of the temporal fossa is wide (180 mm from the lateral margin of the cerebral cavity to

the lateral margin of the squamosal). The supraorbital and postorbital processes of the frontal being lost, the dimensions and shape of the temporal fossa cannot be assessed; the fossa is posteriorly longer than in *Physeter* and likely anteriorly shorter than in *Brygmophyseter* and *Zygophyseter*.

Alisphenoid. A large foramen ovale opens laterally on the alisphenoid, followed on a short length by a wide and shallow sulcus (path for mandibular nerve V3).

Exoccipital. The laterally extended exoccipital is dorsally overhung by the floor of the temporal fossa (Fig. 3C). In ventral view, the anterior surface of the exoccipital is excavated by a wide depression, posterolaterally elongated along the surface of contact between the posterior process of the tympanic bulla and the squamosal (Fig. 5B). In a similar position FORDYCE (1994, 2002) describes in *Simocetus* and *Waipatia* FORDYCE, 1994 a narrow cleft that might correspond to a ventral exit for the facial nerve. The outline of the depression in IRSNB M.523 seems however to fit better with a posterior extension of the pterygoid sinus. In this case, the posterior process of the tympanic bulla would have been margined both anterolaterally (fossa described above on the squamosal) and posteromedially by extensions of the peribullary sinus. No clue for a posterior sinus, identified along the anterior surface of the paroccipital process in most Recent odontocetes but not in physeteroids (FRASER & PURVES, 1960), could be found.

Basioccipital. The diameter of the foramen magnum is 67 mm and the width across the robust occipital

condyles is estimated to 164 mm. The basioccipital basin is widely open posteroventrally. The jugular notch is wide. The posterior lacerate foramen has a reduced size (greatest diameter 15 mm).

Teeth. Two teeth were found associated to the skull. However, their exact position along the alveolar groove cannot be guaranteed. The tooth in the posterior fourth left alveolus is the best preserved (Fig. 6). This 88 mm high tooth is generally cylindrical, moderately curved, with a low crown (11 mm long). The section is circular at the base of the crown (diameter 10 mm). Apically the root is anteroposteriorly flattened with a longitudinal groove on the anterior surface; proximally the flattening twists to a more lateromedial direction. The proximal narrowing of the root is weak; maximum and minimum diameters at mid-height section and at proximal section of the root are respectively 24/17 mm and 20/14 mm. The crown is separated from the root by a marked step due to the thickened cement on the root, and is covered with a smooth cap of enamel, as mentioned by ABEL (1905). The diameter of the crown smaller than the root diameter at their boundary, also seen on the second tooth preserved, is rather unusual in enamel-bearing fossil physeteroids; on most of the isolated teeth observed, the enamel layer is either thicker than, or form a continuous surface with, the adjoining cement of the crown. A constriction, much shallower than the constriction at the cement-enamel boundary, marks the apical two-fifths of the crown. The second tooth, located in the posterior sixth right alveolus, is poorly preserved with a crown height of 9 mm for a total height of 93 mm. In *Idiorophus* the enamelled crown is proportionally higher, approximately one third of the total height of the tooth (LYDEKKER, 1893), whereas the teeth of *Brygmophyseter* and *Zygophyseter* are proportionally larger and more swollen on the distal portion of the root. The physeteroid species from the Neogene of the North Sea defined on the basis of enamelled teeth, *Hoplocetus ritzi* HAMPE, 2006, *Scaldicetus caretii*, and *S. grandis* (see material and methods for the status of the two latter species), differ significantly in the more robust, swollen root, with a stronger proximal reduction of the section.

The pulp cavity of these two teeth is hollow, confirming the young age of the animal. However, substantial apical wear is already present and a groove along the posterior surface of the left tooth corresponds to the contact with the opposite lower tooth. Besides the indication of a weaned animal, the wear proves that the teeth were functional and associated to similar mandibular teeth.

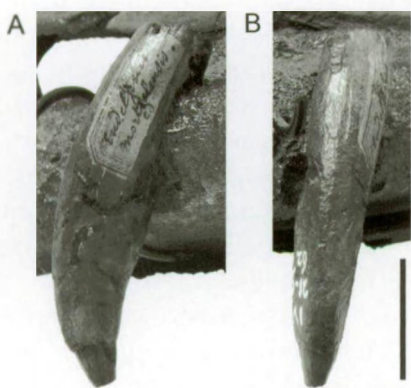


Fig. 6 – Maxillary tooth of *Eudelphis mortezelensis* IRSNB M.523 (holotype), Miocene of Antwerp. **A.** Posterolateral view. **B.** Anterolateral view. Scale bar for A-B equals 30 mm.

Discussion

Besides the presence of a supracranial basin, asymmetric bony nares, and a widened and posteriorly longer right premaxilla, i.e. the main characters defining the superfamily Physeteroidea, *Eudelphis mortezelensis* is characterised by a set of features that could be interpreted as primitive for a physeteroid. The left premaxillary foramen is not as reduced as in other physeteroids; the falciform process of the squamosal remains well developed, a feature likely related to the lesser development of the pterygoid sinus around the ear bones; and the postglenoid process is ventrally long. Furthermore, the teeth retain a cap of enamel on the crown, as in *Brygmophyseter*, *Idiorophus*, and *Zygophyseter*; more than 10 maxillary teeth are lodged in deep alveoli, a feature shared at least with *Brygmophyseter*, *Diaphorocetus*, *Idiorophus*, and *Zygophyseter*; and the slope of the supraoccipital shield is low.

In addition to these plesiomorphic characters, the rostrum of *E. mortezelensis* has maxillae wider in dorsal view than in most other physeteroids, lacking an abrupt narrowing at mid-length. The exposed ventral surface of the vomer is wide and not keeled, a feature possibly age-related.

Genus *Placoziphius* VAN BENEDEN, 1869

Type species: P. duboisi VAN BENEDEN, 1869

Diagnosis. The diagnosis is the same as for the only included species.

Placoziphius duboisi VAN BENEDEN, 1869

Figs 7-8

- 1869 — *Placoziphius duboisii* VAN BENEDEN, p. 11; pl. 1-2.
- 1880 — *Placoziphius duboisii* VAN BENEDEN & GERVAIS, pl. 27, figs. 11-12.
- 1905 — *Placoziphius duboisii* ABEL, p. 87.
- 2002 — *Placoziphius duboisii* KAZÁR, pl. 1, figs. 1-2.

Holotype

IRSNB M.530 (old number 1718), a fragmentary skull including most of the rostrum, fragments of the supraorbital processes and of the supracranial basin, the two squamosal/exoccipital sets, and an associated fragment of atlas.

Type locality

Edegem, *briqueterie de la société Pauwels* (VAN BENEDEN, 1869), 400 m south-east to Fort n°6, 6 km

south to Antwerp (Fig. 1). Geographic coordinates: 51°09'38"N-4°24'50"E.

Type horizon

Berchem Formation, Edegem Sands Member. This member is dated by means of dinoflagellates to early Miocene, late or latest Aquitanian to early Burdigalian (LOUWYE *et al.*, 1999, 2000; LOUWYE, 2005). Two skull fragments tentatively referred to *P. duboisi*, namely a left exoccipital and the left side of a rostrum base, were recently found in the Antwerpen Sands Member, in the foundations of new buildings at the locality of Veldekens, Berchem, 3.5 km south-east to the centre of Antwerp (geographic coordinates: 51°20'24"N-4°26'17"E), possibly extending the range of the species in the middle Miocene.

Emended diagnosis

Placoziphius duboisi has a size close to *Diaphorocetus poucheti* and the smallest specimens of *Orycterocetus crocodilinus*, larger than all the kogiid species. It differs from all the other physeteroids for which the rostrum is known, except *Kogia* and possibly *Diaphorocetus* and '*Aulophyseter*' *rionegrensis*, in the premaxilla narrower than the maxilla on the whole length of the rostrum in dorsal view. It differs from *Eudelphis* in the abrupt narrowing of the rostrum on its proximal half, the reduced left premaxillary foramen and falciform process of the squamosal, and the narrower and keeled vomer in ventral view, from '*Aulophyseter*' *rionegrensis*, *Diaphorocetus*, *Eudelphis*, *Idiorophus*, *Orycterocetus*, and *Zygophyseter* in the loss of the posterior maxillary alveoli, from *Aulophyseter*, *Orycterocetus*, and *Physeter* in the lower slope of the maxilla-frontal suture on the supraorbital process, and from *Aulophyseter* and *Physeter* in the higher preorbital process compared to the lateral margin of the rostrum base. It differs from the kogiids in the widened posterior portion of the right premaxilla. It further differs from *Diaphorocetus* in the more laterally located right premaxillary foramen, from *Orycterocetus* in the wider dorsal surface of the supraorbital process lateral to the supracranial basin, and from *Thalassocetus* in the wider glenoid surface and the longer plate-like postglenoid process of the squamosal.

Remark

The species '*Aulophyseter*' *rionegrensis* is based on two skulls from the middle Miocene of Argentina, one of them rather complete and associated to the mandible and teeth, but poorly illustrated in the original work (GONDAR, 1975). COZZUOL (1996) and KAZÁR (2002)

estimated that the species differs significantly from members of the genus *Aulophyseter*, the second author finding more similarities for '*A.* *rionegrensis*' with *Diaphorocetus poucheti*. In addition the outline of the rostrum in dorsal view and the narrow premaxilla on the rostrum are also similar to the somewhat smaller *Placoziphius duboisi*. A detailed comparison of the three species and a re-illustration of the two Argentine species would allow a better understanding of their relationships.

Comments on the attribution of other specimens to Placoziphius duboisi

ABEL (1905) referred to the species another specimen from the area of Antwerp, still in a matrix of hardened sand. This specimen could not be further prepared and it will not be taken into account here.

More recently, KAZÁR (2002) referred two additional specimens to the species: a partial skeleton from the Miocene of Stotzing (Austria) and the fragmentary skull IRSNB M.525 from the area of Antwerp part of the syntype of *Thalassocetus antwerpiensis* sensu ABEL, 1905.

Besides similarities at the level of the rostrum, a few differences between the holotype of *Placoziphius duboisi* and the Stotzing specimen are noted. If the exoccipital is correctly identified on the lateral view of the Stotzing specimen (KAZÁR, 2002, pl. 4, fig. 1), either the postglenoid process of the squamosal is missing (not mentioned by the author), or it is much shorter ventrally than on the holotype of *P. duboisi*. The squamosal of the holotype of *P. duboisi* is not hidden by the exoccipital in posterior view, contrary to the Stotzing specimen. Among the characters listed in the diagnosis of *P. duboisi* by KAZÁR (2002), only two are observed in the holotype: (1) premaxillae not exceeding maxillae in width at any given point and (2) distal portion of the rostrum narrow. Both characters might be present in *Diaphorocetus*, the first character is seen in *Kogia*, and a narrow distal portion of the rostrum is rather common among physeteroids [e.g., *Orycterocetus* and part of the specimens of *Aulophyseter morricei* (see KIMURA *et al.*, 2006)]. The difficulty to find other comparison points between these two fragmentary skulls, with different preservation states, leaves open the question of the attribution of the Stotzing specimen to *P. duboisi*. In this work I prefer not to consider it in the species, pending new data from more complete specimens.

More conspicuous differences between the holotype of *P. duboisi* and IRSNB M. 525, part of the syntype of *T. antwerpiensis* sensu ABEL, 1905, are noted. As mentioned in KAZÁR (2002) IRSNB M.525 is

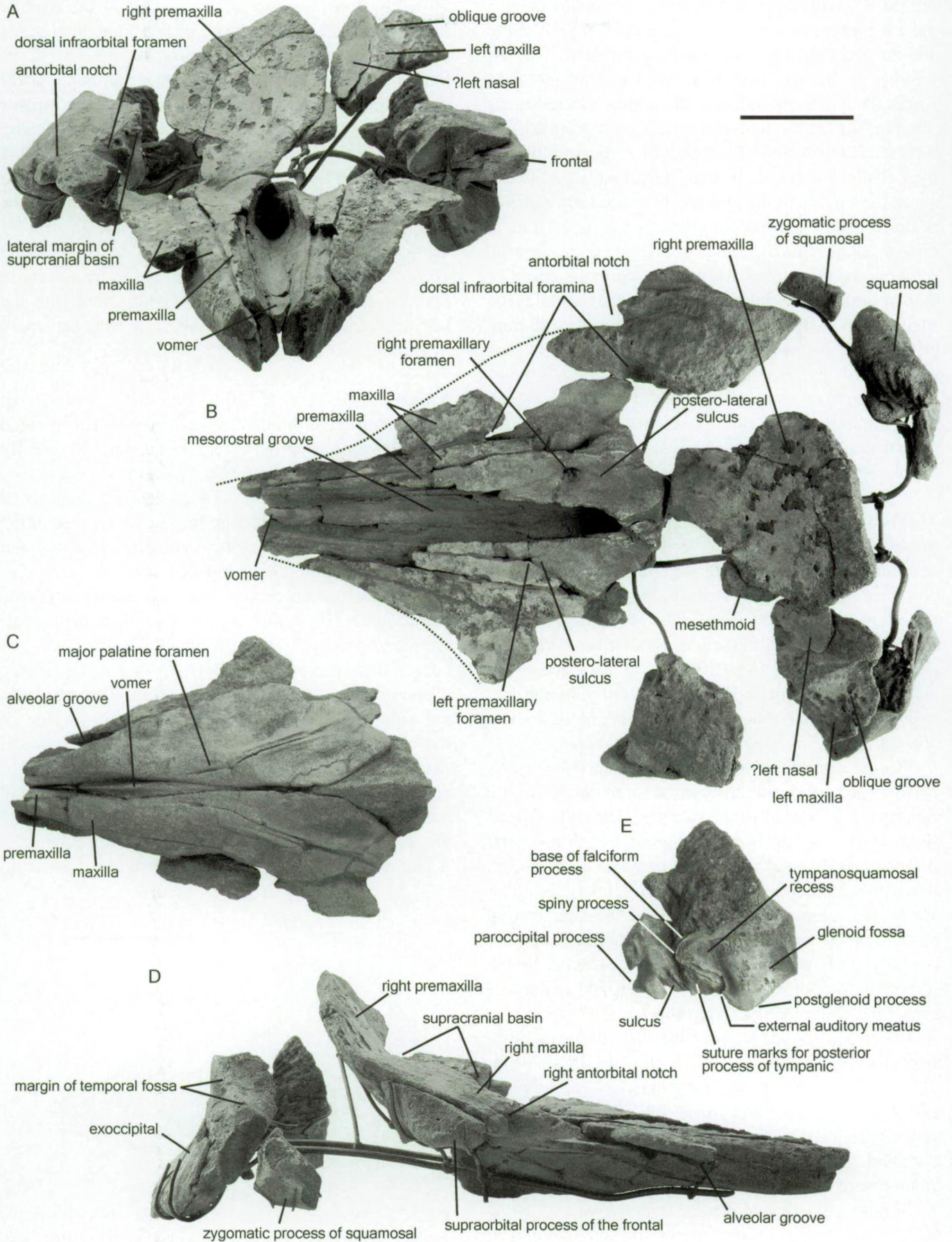
significantly smaller and its supraorbital region is not extremely thickened in lateral view. Furthermore, the supraorbital process of IRSNB M.525 is narrower in dorsal view; a sagittal crest covered by the right premaxilla is identified in its supracranial basin, not homologous to the crest covered by the left nasal in *P. duboisi*; and the squamosal of IRSNB M.525 differs considerably in the short, more nodular than plate-like postglenoid process, higher than the ventral margin of the exoccipital, and in the narrower glenoid surface. IRSNB M.525 is therefore excluded from the hypodigm of *P. duboisi* (see below).

Description of the holotype of Placoziphius duboisi

In addition to previous contributions (VAN BENEDEN, 1869; ABEL, 1905; KAZÁR, 2002), some elements of description are given here, based on the holotype specimen IRSNB M.530. The apex of the rostrum is missing (Fig. 7B); considering the thickness and orientation of the different elements at the preserved extremity, the rostrum was likely somewhat shorter than in *Orycterocetus*, but possibly longer than estimated in KAZÁR (2002). The distance between the right premaxillary foramen and the preserved apex of the rostrum is 280 mm. At the level of the right premaxillary foramen, the distance between the lateral margins of the premaxillae is 129 mm. As in other physeteroids the rostrum is wide at its base. The proximal narrowing is abrupt. More anteriorly the concave lateral margins indicate a more progressive narrowing.

Premaxilla. Even if the dorsal surface of both premaxillae is missing distally, these bones did not exceed the maxillae in width in dorsal view, as suggested by KAZÁR (2002), contrasting with *Orycterocetus*. A similar condition is present in *Kogia* and suspected in '*Aulophyseter*' *rionegrensis* and *Diaphorocetus*. The mesorostral groove is widely open on its whole length, with a maximum opening 37 mm wide. Contrary to the assumption of KAZÁR (2002) and as noted by Van BENEDEN (1869) and KELLOGG

Fig. 7 – Skull of *Placoziphius duboisi* IRSNB M.530 (holotype), Miocene of Antwerp. **A.** Anterodorsal view. **B.** Dorsal view with the reconstructed outline of the rostrum. **C.** Ventral view of the rostrum. **D.** Right lateral view. The relative position of the different elements in A-D is approximate. **E.** Left squamosal in anteroventral view. Scale bar for A-E equals 100 mm.



(1925), a small left premaxillary foramen (diameter 5 mm) is present in the holotype at a level slightly more anterior than the right premaxillary foramen. The left foramen is followed posteriorly by a narrow and short sulcus likely corresponding to the postero-lateral sulcus observed in most odontocetes. The right premaxillary foramen is much larger (diameter 14 mm) and followed by a shallow and wide postero-lateral sulcus. On both sides, the surface of the premaxilla is regularly concave posterior to the premaxillary foramen (Fig. 7A), as in *Orycterocetus*. From the level of the right bony naris the right premaxilla widens and raises to form the posterior wall of the supracranial basin, crossing the sagittal plane of the skull; the maximum width of the bone is 143 mm, at mid-height. Posterodorsally the right premaxilla is not vertical, more similar to *O. crocodilinus* USNM 14730 than to *O. crocodilinus* USNM 22926. Along the median margin of the right premaxilla and posterior to the bony nares, a plate-like fragment of the mesethmoid is preserved.

Maxilla. No alveoli are detected along the poorly preserved alveolar groove (Fig. 7C). However, taking account of the missing anterior elements, the shallow posterior alveoli in '*Aulophyseter*' *rionegrensis*, *Diaphorocetus*, and *Orycterocetus crocodilinus* USNM 22926, and the preservation similarities with *O. crocodilinus* USNM 14730, the possibility that anterior alveoli were present cannot be rejected, although this hypothesis is not better supported than a more derived alveolar groove as seen in *Aulophyseter morricei*.

60 mm anterior to the right premaxillary foramen a partly preserved dorsal infraorbital foramen pierces the right maxilla. Medial to the partly preserved U-shaped right antorbital notch is a large dorsal infraorbital foramen, partly subdivided by a lateral septum, and in line with a smaller posterior foramen. The two foramina are located along the lateral wall of the supracranial basin. On the left maxilla, the condition is similar, possibly with an additional foramen. Lateral to the foramina, the dorsal surface of the maxilla is flat and somewhat wider than in *Orycterocetus*.

In lateral view, the angle of the slope of the maxilla-frontal suture above the orbit is roughly 25-30° (Fig. 7D), probably close to '*Aulophyseter*' *rionegrensis* and *Diaphorocetus*, and lower than in *Aulophyseter* and *Orycterocetus*. Because the posterior portion of the maxilla is missing, the shape of the temporal fossa cannot be reconstructed.

Similar to *Orycterocetus crocodilinus* USNM 22926, an oblique groove marks the left maxilla on the posterolateral wall of the supracranial basin; this

groove isolates anteromedially a shelf of the maxilla partly covered by a thin sheet of flat bone, interpreted by comparison with *Orycterocetus* as the left nasal. Suture marks on the right side of this thin bone, likely indicating the contact with the right premaxilla, further support this identification. This shelf is superficially similar to the sagittal crest in *Kogia*, *Praekogia*, and possibly *Thalassocetus* (see below), but in the three latter taxa the surface is concave and covered by the right premaxilla.

Vomer. The nearly complete vomer is shorter anteriorly than the premaxilla and maxilla, contrasting with the kogiids. Ventrally the keeled vomer appears on a length of 190 mm.

Squamosal-Exoccipital. The zygomatic process of the squamosal is moderately elongated. The glenoid fossa is wide, approximately triangular, and nearly continuous with the shallow tympanosquamosal recess. The latter is only somewhat deeper along the external auditory meatus. Considering the preserved base of the falciform process, this element consisted in a thin and narrow projection, more reduced than in *Eudelphis*. The postglenoid process is a vertical anteroposteriorly compressed plate slightly longer ventrally than the post-tympanic process but proportionally shorter and less curved than in *Eudelphis*. As noted by KAZÁR (2002), elements of the posterior process of the tympanic bulla are still attached to the grooved ventral surface of the post-tympanic process, reaching the ventrolateral margin of the exoccipital. Differing from *Eudelphis*, no fossa separates this element from the external auditory meatus. Ventrolateral to the paroccipital process a narrow sulcus marks the exoccipital in a position similar to the depression mentioned above in

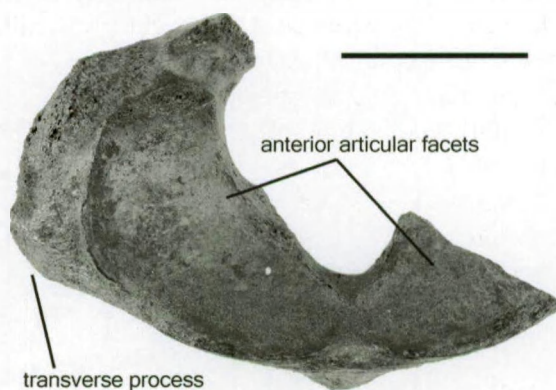


Fig. 8 – Atlas of *Placoziphius duboisi* IRSNB M.530 (holotype), Miocene of Antwerp, in anterior view. Scale bar equals 50 mm.

Eudelphis. The proportions of this sulcus, narrower than in *Orycterocetus*, better fit the description by FORDYCE (1994) of a narrow cleft possibly corresponding to the exit of the facial nerve in *Waipatia*.

Atlas. The fragmentary free atlas associated to the holotype skull (Fig. 8) has a maximum ventral length of 32 mm, proportionally shorter than in *Zygophyseter*. The maximum width is estimated to 186 mm. The long axis of the moderately concave anterior articular facet is, as noted by VAN BENEDEN (1869), more oblique from the vertical than in *Physeter* and *Zygophyseter*. The transverse process is shorter and more developed dorsoventrally than in *Zygophyseter*.

Discussion

The holotype of *Placoziphius duboisi* shares more similarities with *Orycterocetus*, '*Aulophyseter*' *rionegrensis*, and *Diaphorocetus* than with any other physeteroid, at the level of the size, the rostrum shape, the morphology of the premaxillae at the rostrum base and in the supracranial basin, and the supraorbital area of the maxilla.

Among the differences with *Orycterocetus* listed by KAZÁR (2002), only the narrowness of the premaxilla compared to the maxilla on the rostrum is seen in the holotype of *P. duboisi*. In addition, the rostrum of the smaller *P. duboisi* is likely shorter; at least the posterior alveoli are missing; the maxilla on the supraorbital process is wider, suggesting a narrower supracranial basin; and the elevation of the maxilla towards the occipital crest is less abrupt.

Considering the illustrations of *Diaphorocetus* in MORENO (1892, pl. 10), I disagree with the comment of KAZÁR (2002) about the outline of the rostrum in this species; the lateral margin is distinctly concave, as in *Orycterocetus*, *Placoziphius*, and several other physeteroids. *Diaphorocetus* has a right premaxillary foramen more medially located; it possibly possessed deeper maxillary alveoli, but the elongated braincase of the holotype might be related to the dorsoventral crushing of the skull. Despite obvious similarities, better preserved specimens of *Diaphorocetus* and *Placoziphius* would certainly allow a more detailed investigation of their systematic relationships with *Orycterocetus*.

Finally, *Placoziphius* shares a derived character with *Kogia*: the premaxilla narrower than the maxilla on the whole length of the rostrum. This hypothetical relationship could be tested with the description of new rostral material of *Aprixokogia* or *Praekogia*.

Genus *Orycterocetus* LEIDY, 1853

Type species: *O. quadratidens* (LEIDY, 1853)

Orycterocetus crocodilinus COPE, 1868

Figs 9-10

Referred specimen

IRSNB M.1936, a fragmentary skull found around 1910 during the construction of the fort of Kessel.

Locality

Fort of Kessel, Kessel, 16 km south-east-east to Antwerp (Fig. 1). Geographic coordinates: 51°09'02"N-4°37'44"E.

Horizon

Berchem Formation, Antwerpen Sands. This specimen displays the same preservation state as specimens of the ziphiid *Archaeoziphius microglenoideus* and the mysticete *Isocetus depauwi* from the same locality; dinoflagellate dating of sediment found around the skull of *I. depauwi* produced a middle Miocene, tentatively late Langhian to early Serravalian age (LAMBERT & LOUWYE, 2006).

Comments

As this work is not a revision of the genus *Orycterocetus*, *O. crocodilinus* being mostly known by more complete specimens from the east coast of USA (KELLOGG, 1965), I will only provide a brief description of the specimen from the North Sea and I will not discuss the definition and content of the genus. Such a work should indeed be centred on the American specimens (A. C. Dooley Jr., pers. comm., 2007).

Brief description of the referred specimen IRSNB M.1936

This skull is made of four fragments corresponding to both supraorbital areas and both squamosal-exoccipital sets. The size of the different elements falls within the size interval of three specimens of *Orycterocetus crocodilinus* provided by KELLOGG (1965), somewhat smaller than USNM 22926. Partly fused sutures, particularly on the basicranium, suggest a young individual.

The left supraorbital process of the frontal is roughly complete, as well as the covering maxilla. The pointed preorbital process of the frontal is barely thickened. A reduced space could contain a short extension (no more than 16 mm long) of the lacrimal between the maxilla and the frontal (Fig. 9B), more reduced

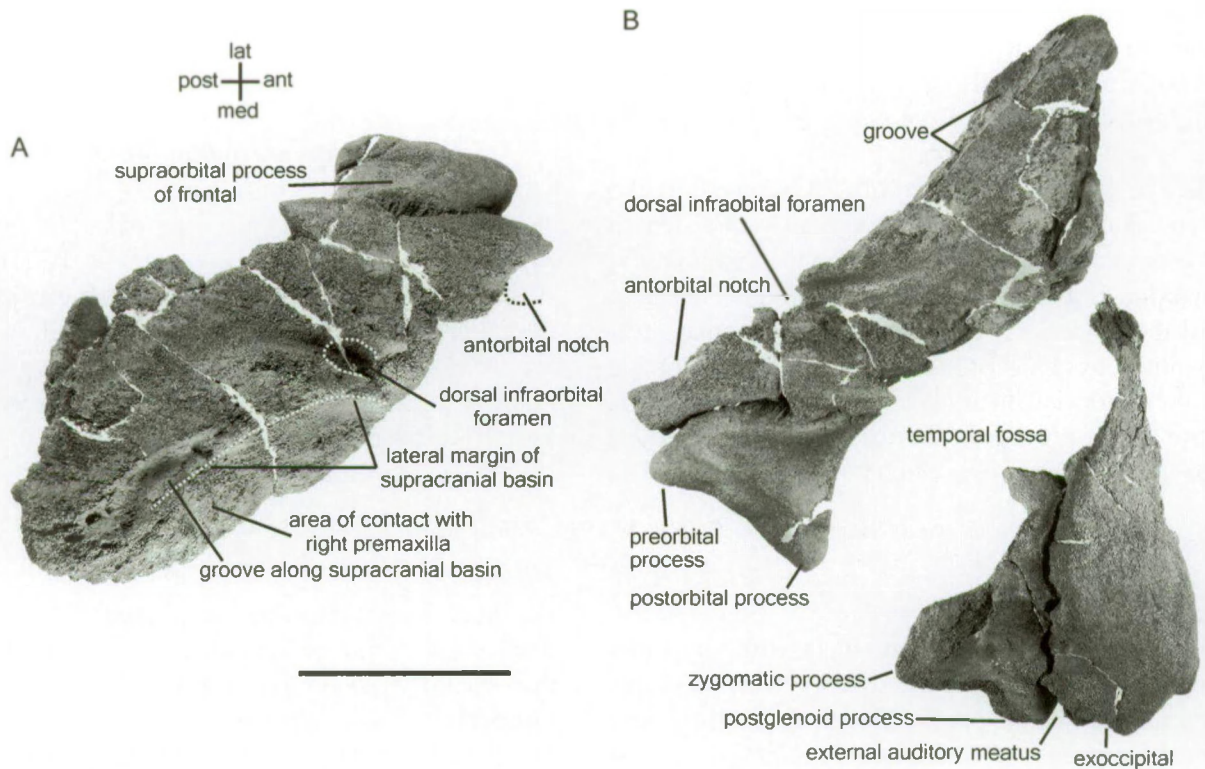


Fig. 9 – Skull of *Orycterocetus crocodilinus* IRSNB M.1936, Miocene of Kessel. **A.** Left supraorbital area in dorsal view. **B.** Left lateral view. The relative position of the different elements is approximate. Scale bar for A-B equals 100 mm.

than in the kogiids (see MUIZON, 1988, fig. 35). The triangular postorbital process is moderately elongated ventroposteriorly, less than in *O. crocodilinus* USNM 22926 and USNM 14730; its laterodorsal surface, not concealed by the maxilla in dorsal view, is concave. The length of the orbit is 121 mm. The elevation of the frontal towards the dorsal apex of the temporal fossa is abrupt, indicating together with the lateral outline of the exoccipital a high and anteroposteriorly compressed temporal fossa. On top of the temporal fossa, the frontal-maxilla suture is nearly vertical for a length of 95 mm.

The slightly medially sloping surface of the maxilla covering the supraorbital process of the frontal is narrower and more erected than in *Placoziphius*. 55 mm posterior to the partly preserved left antorbital notch a large foramen pierces the maxilla and is followed posterolaterally by a wide sulcus along the outer face of the lateral wall of the supracranial basin (Fig. 9A). On the inner wall of the basin a smooth concave surface gives the position of the apex of the left premaxilla. A wide longitudinal groove excavates the dorsal surface of the maxilla at its posterior end, less oblique than in *O. crocodilinus* USNM 22926. The more fragmentarily preserved dorsal surface of the right

maxilla only displays a large foramen similar to the foramen described on the left side and a wide concave surface for the large plate of the right premaxilla, along the inner wall of the supracranial basin.

Each squamosal lacks the apex of the zygomatic process; the anterior section is high, transversely flattened (Fig. 9B). More reduced than in *Placoziphius* the postglenoid process is anteroposteriorly flattened, thin and short, limiting a narrow external auditory meatus. The glenoid fossa is barely separated from the shallow tympanosquamosal recess (Fig. 10A). The falciform process is reduced to a small peg anterior to the spiny process, as in *O. crocodilinus* USNM 22926 and USNM 22931, smaller than in *Eudelphis* and *Placoziphius*. Suture marks on the post-tympanic process of the squamosal and on the anterior surface of the exoccipital likely indicate the contact with the elongated posterior process of the tympanic bulla. As in *Eudelphis*, an elongated depression margins this area posteromedially on the anterior surface of the exoccipital. Medial to this depression the anterior surface of the paroccipital process is hollowed by a small shallow circular fossa, possibly for the posterior sinus.

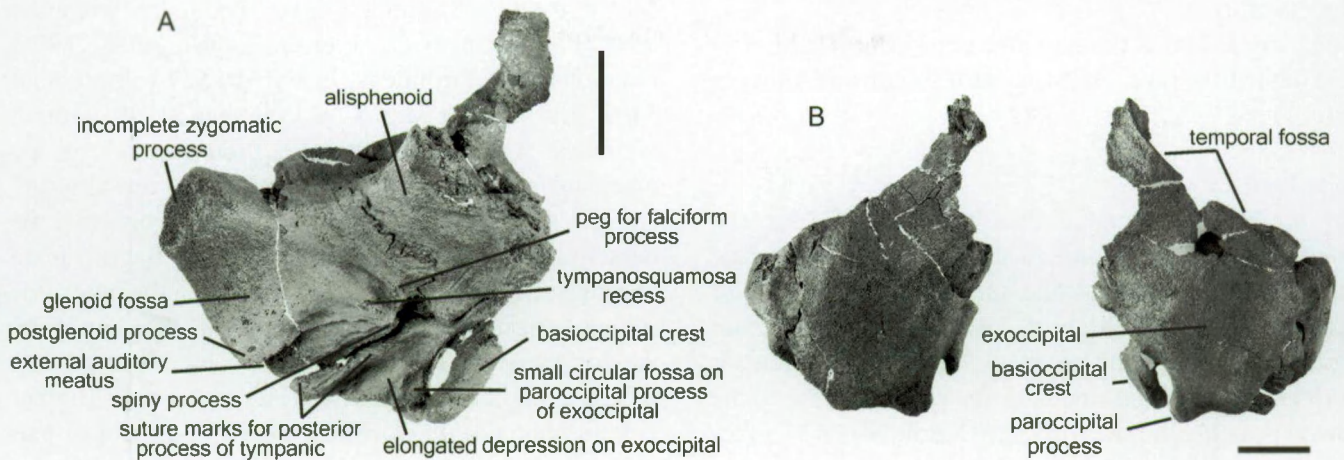


Fig. 10 – Skull of *Orycterocetus crocodilinus* IRSNB M.1936, Miocene of Kessel. **A.** Anteroventral view of the right squamosal. **B.** Posterior view of left and right portions of the basicranium. The relative position of the different elements is approximate. Scale bar for A-B equals 50 mm.

In posterior view the ventral margin of the exoccipital bears a distinct concavity (Fig. 10B). The ventral surface of the alisphenoid is concave medially; the foramen ovale is not preserved and only a faint groove indicates the path for the mandibular nerve V3.

Discussion

Besides slight differences, mostly at the level of the postorbital process of the frontal, this specimen perfectly fits the intraspecific variability within the Maryland and Virginia species *Orycterocetus crocodilinus*. From a stratigraphic point of view all the cranial material of *O. crocodilinus* (excluding isolated teeth) from the east coast of the USA was found in zones 9, 11, 12, and 13 of the Calvert Formation (KELLOGG, 1965), dated between latest early and early middle Miocene (VERTEUIL & NORRIS, 1996). This matches the Antwerpen Sands origin of IRSNB M.1936. It should be noted here that isolated teeth and ear bones from the Miocene of the *faluns de Tourraine et Anjou*, France, were tentatively referred to *Orycterocetus crocodilinus* (GINSBURG & JANVIER, 1971). The two other species of the genus *Orycterocetus* are based on more fragmentary material that cannot be compared to IRSNB M.1936 (see comments in KAZÁR, 2002; BIANUCCI *et al.*, 2004). BIANUCCI *et al.* (2004) attribute a mandible from the Miocene of Pietra leccese, southern Italy, to a larger species of *Orycterocetus*.

Family Physeteridae

Genus *Physeterula* VAN BENEDEN, 1877

Type species: P. dubusi VAN BENEDEN, 1877

Diagnosis. The diagnosis is the same as for the only included species.

Physeterula dubusi VAN BENEDEN, 1877

Figs 11-14; Table 1

- 1877 — *Physeterula dubusii* (part) VAN BENEDEN, p. 852; pl. 1, figs. 1-3.
- 1890 — *Kogia dubusii* COPE, p. 608.
- 1905 — *Physeterula dubusii* ABEL, p. 79; figs. 11-12.
- 2008 — *Physeterula dubusii* WHITMORE & KALTENBACH, fig. 89a.

Holotype

IRSNB M.527 (old number 3192), a fragmentary skull including rostral fragments of the premaxillae, parts of the supracranial basin and of the basicranium, with the associated mandible and 18 mandibular teeth, four additional detached teeth, the fragmentary atlas, four caudal vertebrae, one chevron, six rib fragments, and one fragment of the sternum. In the preliminary description of the species, VAN BENEDEN (1877, p. 852) designated this specimen as the '*type pour cette description*'. The mandible and isolated teeth are illustrated in VAN BENEDEN (1877) and the skull in ABEL (1905, p. 75, 77).

Type locality

Boundary between the communes of Deurne and Borgerhout (MOURLON, 1878), eastern suburbs of Antwerp (Fig. 1).

Type horizon

No precise stratigraphic data are available for the holotype. The appearance of the surface of the bones, mostly the premaxillae and the mandible, is similar to specimens of the ziphiid *Ziphirostrum marginatum* (colour, erosion, and possibly aborted invertebrate borings); this might indicate an origin in the same levels, possibly the late Miocene Deurne Sands Member (LAMBERT, 2005). This member is locally present at the boundary between the communes of Deurne and Borgerhout (DE MEUTER *et al.*, 1976).

Referred specimen

IRSNB M.528, fragments of the basicranium (see comment below). The label associated to the specimen provides the following information: *nouvelle enceinte, 3^{ème} section, vers le saillant du fossé du ravelin, face gauche de l'ancien fortin n°1, sous Deurne* (MOURLON, 1878). These indications correspond approximately to the geographic coordinates 51°13'6"N-4°27'7"E. Among the sections described in the area (DE MEUTER *et al.*, 1976), one mostly includes Antwerpen Sands Member (Stenen Brug), whereas the other (Rivierenhof) also includes the late Miocene Deurne Sands Member and the early Pliocene Kattendijk Formation.

Emended diagnosis

Physeterula dubusi is a large physeteroid with a skull size close to *Idiorophus patagonicus* and *Zygophyseter varolai*. It differs from the other physeterids *Aulophyseter* and *Physeter* in the retention of functional maxillary teeth, the shorter anterior extension of the supracranial basin, the preorbital process being at the same vertical level as the dorsolateral margin of the rostrum base, the frontal-maxilla suture less erected in lateral view, and more numerous dorsal infraorbital foramina. It further differs from *Physeter* in the maxilla being absent from the dorsal view of the rostrum for more than half its length, the elevated temporal fossa, the mandibular symphysis shorter than half the length of the mandible, and the fact that some of the caudal vertebrae are longer than wide. Finally it differs from *Aulophyseter* in the robust and shortened postorbital process of the frontal.

Comments

Although VAN BENEDEN (1877), followed by

MOURLON (1878), refers three specimens from the area of Antwerp to *Physeterula dubusi*, ABEL (1905) only cites two specimens, IRSNB M.527 (old number 3192) and IRSNB M.528 (old number 3191), without argument. Considering the brief description of the elements preserved for each specimen by Mourlon and the size difference in IRSNB M.528 between the dorsal part of the skull and the mandible fragments on one side and the basicranium elements on the other side (much larger), an erroneous mix of two specimens by Abel is proposed. Furthermore, the mandible fragments have a completely different preservation type (lighter colour, bone deeply worn) compared to the dorsal part of the skull. As the basicranium and mandible elements do not bear any date of discovery, contrary to the dorsal elements, IRSNB M.528 is split in three. The basicranium roughly similar to the holotype is referred to *P. dubusi* whereas the referral of the mandible and dorsal elements to the species is rejected. The mandible is considered as *Physeteridae* indet. and a new collection number (IRSNB M.1937) is attributed to the supracranial elements, which are described farther in the text.

*Description**Skull*

Because the second specimen is only fragmentarily preserved the description is mostly based on the holotype. All the preserved elements of this large skull are dissociated, displaying no clear contacts, except for the vomer and the mesethmoid at the choanae and the exoccipital and the squamosal on both sides of the basicranium. Combining the preserved portion of the mandible and the basicranium, the condylobasal length of the skull is estimated at more than 1375 mm, probably close to *Brygmophyseter shigensis*, *Idiorophus patagonicus*, and *Zygophyseter varolai*.

Premaxilla. Considering the length of the mandible associated to the holotype, an important anterior portion of the premaxillae is missing. On the rostrum the premaxilla is wide (Fig. 11A), as in *Aulophyseter morricei*. Even if the degree of dorsal closure of the mesorostral cannot be estimated the separation between the two premaxillae is certainly narrower than illustrated in ABEL (1905, fig. 12). Although there is no firm contact between the right premaxilla and maxilla at the rostrum base, the correspondence between the slope of the premaxilla at the rostrum base and the slope of the maxillary lateral wall of the supracranial basin implies that the more anterior part of the same piece of

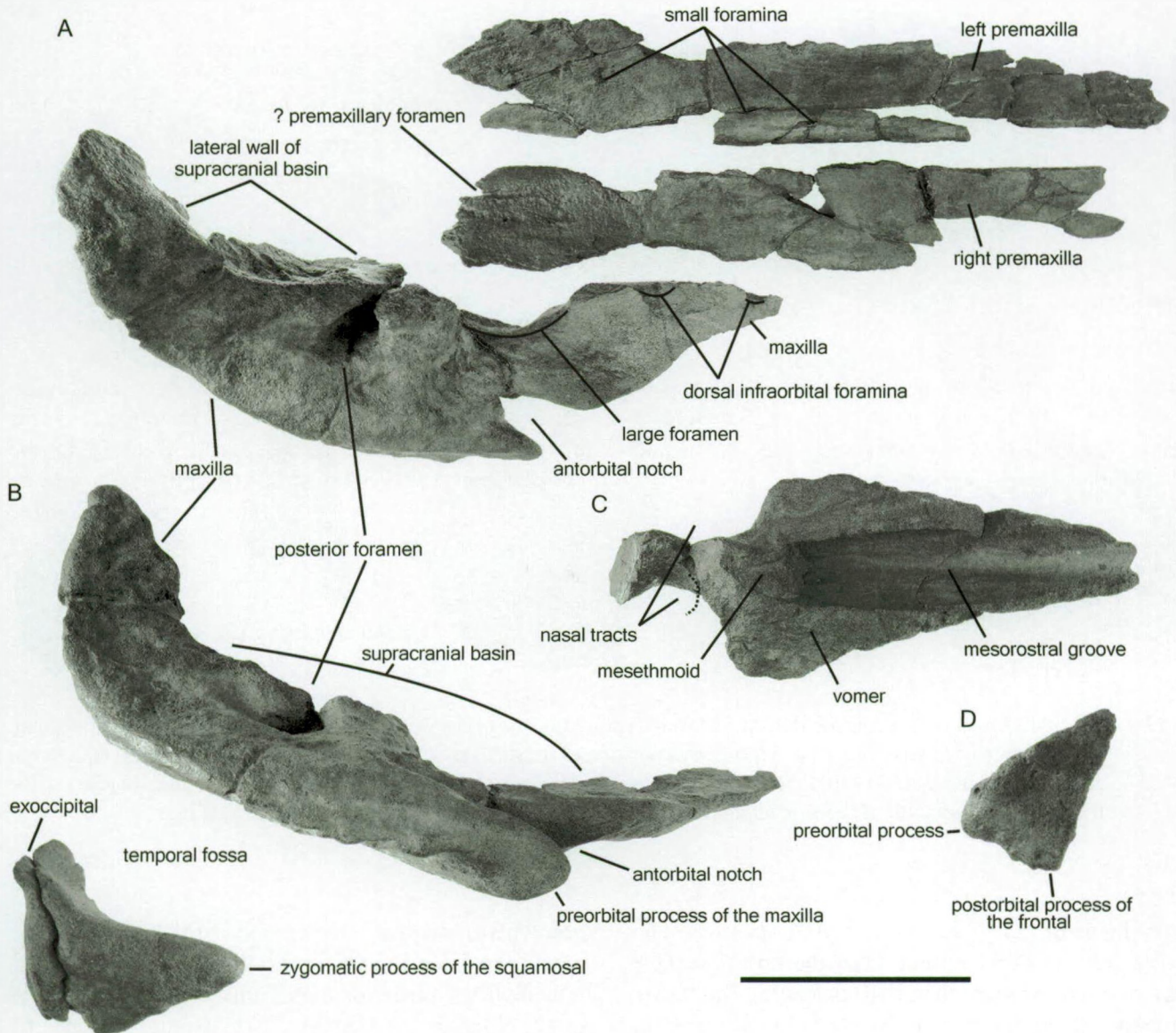


Fig. 11 – Skull of *Physeterula dubusi* IRSNB M.527 (holotype), Miocene of Antwerp. **A.** Fragments of premaxillae and right maxilla in dorsal view. **B.** Right maxilla, squamosal, and exoccipital in lateral view. The relative position of the different elements in A-B is approximate. **C.** Posterior part of the vomer and mesethmoid in dorsal view. **D.** Supraorbital area of the left frontal in lateral view. Scale bar for A-D equals 200 mm.

the premaxilla keeps a moderate median slope. This is a first argument supporting the idea that the supracranial basin was not as developed anteriorly in *Physeterula* as in *Physeter* and possibly *Aulophyseter*. At least three small foramina pierce the dorsal surface of the left premaxilla. Each foramen is followed anteriorly by a sulcus; none of them corresponds to the more posterior left premaxillary foramen of most odontocetes. One somewhat larger foramen is partly preserved at the posterior end of the fragment of right premaxilla; it might correspond to the main right premaxillary foramen.

The detached large posterior plate of the right

premaxilla (239 x 149 mm) displays only a slight concavity (Fig. 12D); it fits therefore entirely on the posterior wall of the supracranial basin, agreeing with the abrupt and important elevation of this posterior wall. As no firm clue of the right bony naris margin is seen on this isolated fragment, lacking its median margin, we cannot assess the degree of overlap of the right premaxilla on the left side of the basin.

Maxilla. The right maxilla is preserved from 250 mm anterior to the antorbital notch to the posterior wall of the supracranial basin. The lateral margin of the rostrum base diverges anteriorly for 75 mm, before a pronounced

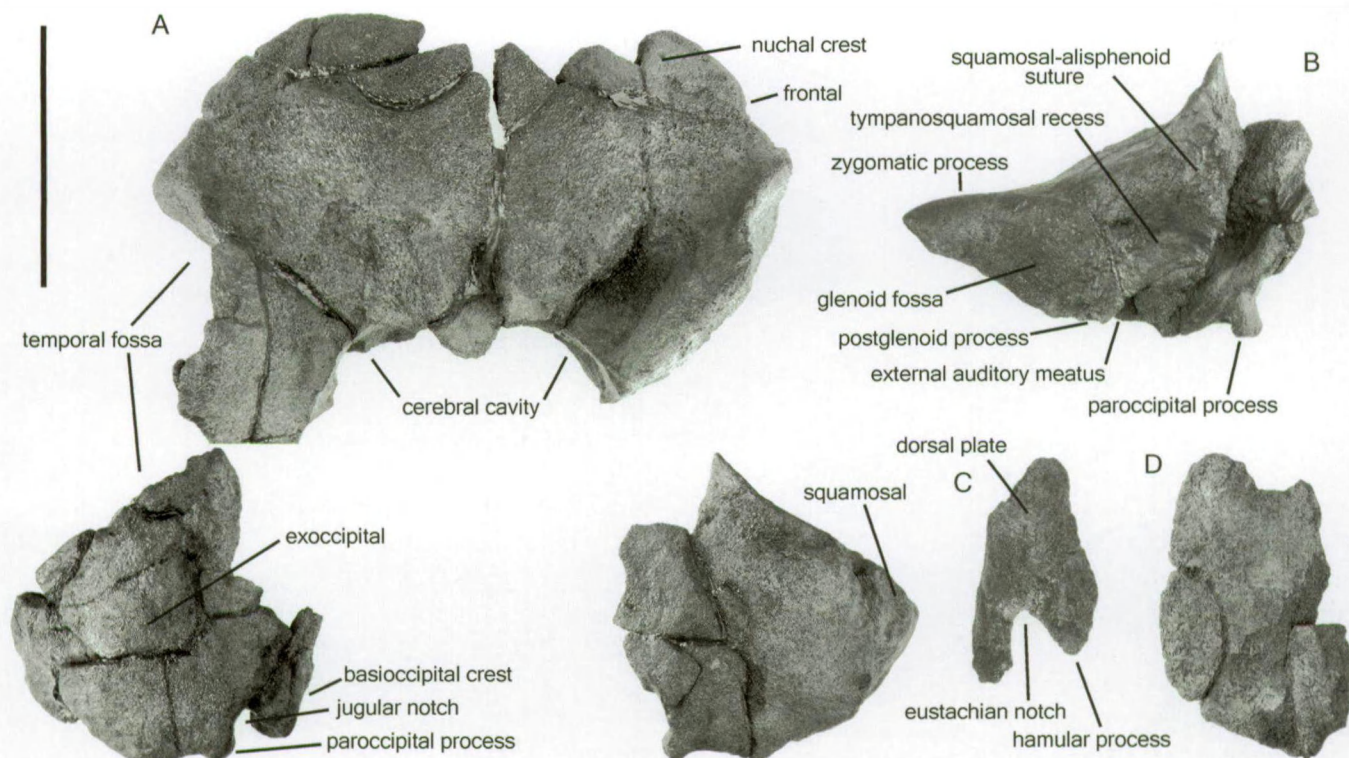


Fig. 12 – Skull of *Physeterula dubusi* IRSNB M.527 (holotype), Miocene of Antwerp. **A.** Frontals, exoccipitals, basioccipital, and squamosals in posterior view. The relative position of the different elements is approximate. **B.** Right squamosal and exoccipital in anteroventral view. **C.** Right pterygoid in ventral view. **D.** Posterior portion of the right premaxilla, from the posterior wall of the supracranial basin, in anterior view. Scale bar for A-D equals 200 mm.

narrowing (Fig. 11A) as seen in *Aulophyseter*. The maxilla was probably absent from the dorsal surface of the rostrum for more than half its length. This faster narrowing of the rostrum in *Physeterula* compared to *Physeter* is a second element indicating a more limited anterior extension of the supracranial basin in the former. Anterior to the antorbital notch, two foramina (32 and 20 mm long respectively) are partly preserved along the suture with the premaxilla. The U-shaped antorbital notch is deep and wide with an anteriorly pointed long preorbital process of the maxilla. As in *Orycterocetus*, the antorbital notch is not lower than the dorsolateral margin of the rostrum, differing on this point from *Aulophyseter* and *Physeter*. Between the antorbital notch and the maxillary crest laterally limiting the supracranial basin is a large dorsal infraorbital foramen (106 mm long). A second oval foramen (maximum diameter 49 mm) is located 68 mm posterior to the large foramen, also lateral to the maxillary crest. In the same area, there are three foramina in *Orycterocetus*, only one major foramen (maxillary incisure) in *Physeter*, located at the top of the elevated maxillary crest, and two foramina both median to the maxillary crest in the

holotype of *Aulophyseter morricei*. In *Physeterula* the maximum lateral extension of the supracranial basin is behind the posterior dorsal infraorbital foramen, as in *O. crocodilinus* USNM 22926 (some intraspecific variation is observed at this level in the latter). Differing from *Orycterocetus* and more similar to *Aulophyseter* and *Physeter*, the posteromedian extremity of the right maxilla does not reach the sagittal plane of the skull.

In lateral view of the supraorbital process, the posterodorsal elevation of the maxilla-frontal suture is less abrupt than in *Aulophyseter* and *Physeter* for most of its length (around 30° from the horizontal plane, close to *Placoziphius*), only curving towards the supraoccipital crest on the posterior third (Fig. 11B).

Frontal. The supraorbital process of the left frontal is nearly complete (Fig. 11D), only lacking a fragment of the posteroventral surface of the postorbital process. The preorbital process is thick and short. The postorbital process is shorter than in *Aulophyseter* and *Orycterocetus*, more similar to *Physeter*.

The frontal part of the posterior wall of the supracranial basin is preserved, whereas the maxillae

and the supraoccipital are nearly completely lost in this area. The two frontals make a high and wide surface slightly anteriorly concave. The maximum vertical distance between the roof of the cerebral cavity and the top of the frontal is 225 mm. The posterodorsal outline of the left temporal fossa indicates a high and pointed roof, as in *Aulophyseter* and *Orycterocetus*. In posterior view, the temporal fossa deeply cuts the lateral margin of the occipital shield (Fig. 12A); the maximum width of the occipital shield is estimated to 490 mm and the minimum width at the level of the temporal fossae is 310 mm.

Vomer-mesethmoid. The anterior portion of the vomer is missing. Anterior to the choanae the vomer is robust, laterally thickened (Fig. 11C). The ossified mesethmoid fills the mesorostral groove on a short distance. As in other physeteroids, the bony nasal tracts are considerably asymmetric: the keel of the mesethmoid separating the two tracts is tilted to the left side (approximately 30° to the vertical) and the left tract is much larger than the right. On the ventral surface of the rostrum the vomer is either not or weakly keeled.

Pterygoid. The pterygoid is robust, particularly at the base of the short posterolaterally pointed hamular process (Fig. 12C). The dorsal plate is not as reduced as in *Eudelphis*.

Squamosal. IRSNB M.528 is significantly larger and more robust than the holotype: the distance between the floor of the temporal fossa and the ventral apex of the paroccipital process of the exoccipital is 205 mm in IRSNB M.528 versus 184 mm in the holotype. In lateral view the zygomatic process of the squamosal is triangular with an elongated, although incomplete, anterior apex (Fig. 11B). The postglenoid process is a thin vertical plate, shorter than in *Eudelphis*, posteriorly limited by a well-defined external auditory meatus. The sternomastoideus fossae are shorter than in *Physeter*, restricted to the proximity of the exoccipital. In ventral view (Fig. 12B), considering the shape of the squamosal the lost alisphenoid was considerably less developed outward and backward than in *Aulophyseter* (see KELLOGG, 1927, pl. 2), more similar to *Orycterocetus* and *Physeter*. The glenoid fossa is a wide and weakly concave surface continuous with the surface of the tympanosquamosal recess. The falciform process of the squamosal is reduced to a tiny bud.

Exoccipital. The exoccipital is thick along its lateral contact with the squamosal. The dorsolateral margin of

the exoccipital posteriorly limiting the temporal fossa overhangs the ventral part of the bone. The jugular notch is wide (Fig. 12A).

Mandible. The more complete right dentary is preserved on a length of 1170 mm (Fig. 13A), but both extremities are missing (condyle and anterior apex). From the curve of the dentary in dorsal view, the length of the unfused narrow symphysis is estimated to 400–500 mm, less than one half of the total length of the mandible, proportionally shorter than in *Zygophyseter* and adult *Physeter* (a very young individual presented by FLOWER, 1869, pl. 56, displays a symphysis less than half the total length of the mandible). Considering the estimated width of the basicranium of this specimen, the mandibular bluntness index (sensu WERTH, 2006) is no more than 0.5, indicating a relatively elongated mandible. The maximum height of the incomplete ramus is 220 mm; the median surface is excavated by a large mandibular foramen, more than 390 mm long. The minimum height of the ramus, located before the symphysis, is 95 mm. At least six mental foramina pierce the lateral surface of the bone. Around 19 deep alveoli are counted on a length of 735 mm, with at least six alveoli more posterior than the symphysis. This count approximately matches the count for the maxillary-premaxillary teeth of *Orycterocetus crocodilinus* (20; KELLOGG, 1965), higher than in *Brygmophyseter* and *Zygophyseter*. The diameter of the alveoli ranges from 27 to 32 mm, with thin or only partial septa. The anterior alveoli are strongly inclined, whereas the posterior alveoli are roughly vertical.

On the right lateral surface of the symphysis, along the alveolus of the fifth anterior dentary tooth is an extra bony growth (Fig. 13E). This thicker area likely corresponds to periosteal new bone formation. As no disruption of the outline of the mandible could be detected ventrally and medially, this 30 mm width oblique protuberance is not the result of a healed fracture. Considering that it follows laterally the curve of the fifth alveolus, the most probable cause is osteomyelitis due to a spread of bacterial infection from the pulp of the adjacent tooth or from periodontal tissue. The adjacent tooth is unfortunately not totally preserved and might even have been relocated in the wrong alveolus. Mandibular osteomyelitis has been described in the Miocene kentriodontid *Hadrodelfhis calvertense* (DAWSON & GOTTFRIED, 2002), but in that case the bony growth is more distant from the alveolar row. Contrary to the above case, no drainage fistula is clearly detected; a mental foramen might be slightly enlarged but its outline is not complete. A dental abscess

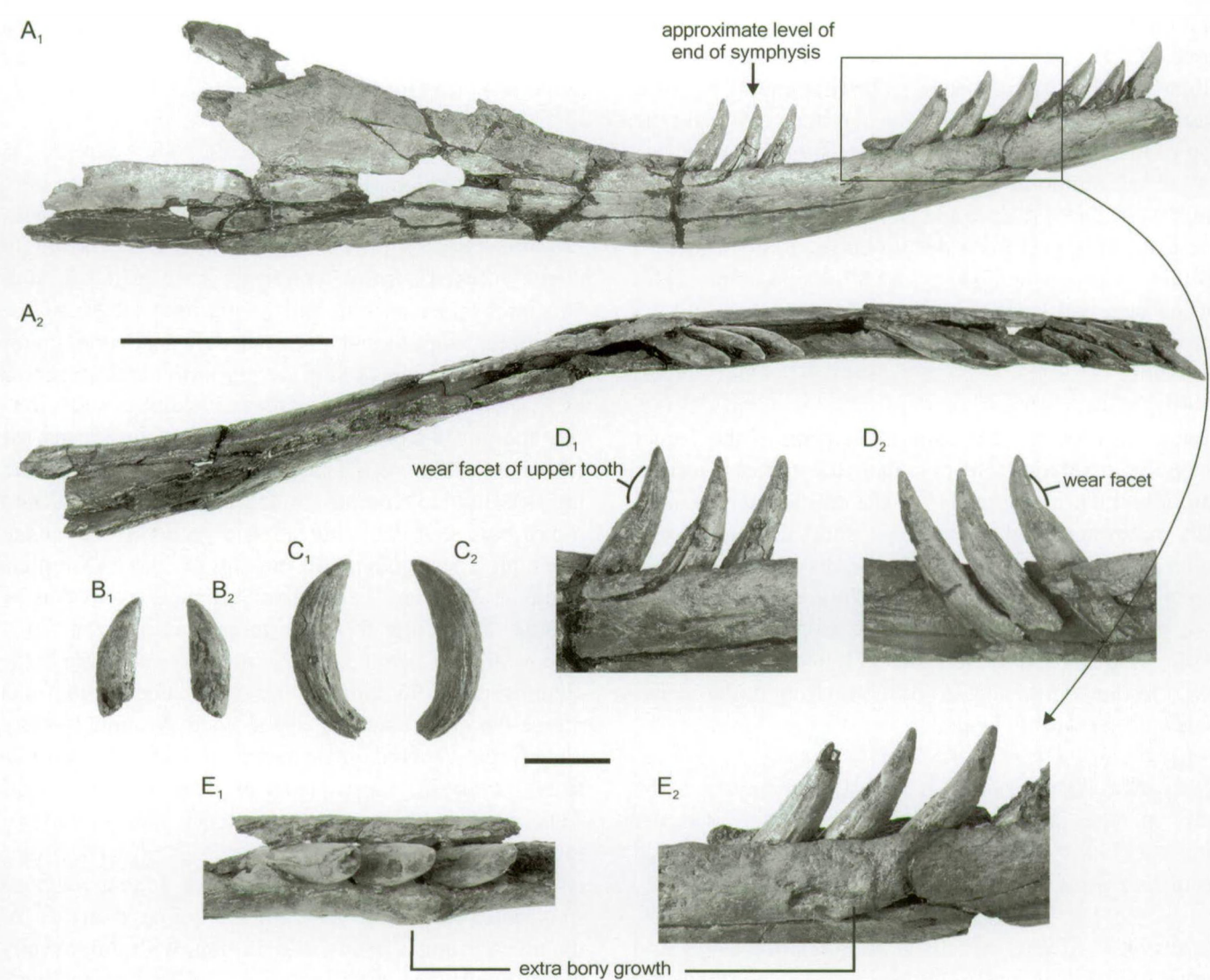


Fig. 13 – Mandible and teeth of *Physeterula dubusi* IRSNB M.527 (holotype), Miocene of Antwerp. **A.** Right dentary in lateral (**A₁**) and dorsal view (**A₂**). **B₁₋₂** and **C₁₋₂**. Detached upper or lower teeth in anterior/posterior views. **D.** Detail of the right dentary with three teeth from the approximate level of the end of the symphysis, in lateral (**D₁**) and medial (**D₂**) view. **E.** Extra bony growth probably due to osteomyelitis on the lateral wall of the right dentary, in dorsal (**E₁**) and lateral view (**E₂**). Scale bar for A equals 200 mm and for B-E equals 50 mm.

is similarly mentioned in the maxillary alveolar groove of the holotype of *Aulophyseter morricei* (KELLOGG, 1927).

Teeth. The mandibular teeth of the holotype have a height ranging from 119 to 135 mm; the lowest teeth are located anteriorly. The section of these regularly curved teeth is roughly circular, with a maximum diameter at mid-height ranging from 24 to 27 mm (Fig. 13D). The pointed crown lacks enamel, similarly to the teeth of *Kogia*, *Orycterocetus*, *Physeter*, and possibly *Aulophyseter morricei* (see comment in KIMURA *et al.*, 2006, contradicting KELLOGG, 1927). The root-crown separation is not clear. The surface of the root is fluted.

The pulp cavity is nearly completely filled, suggesting a relatively old specimen. A part of the teeth referred to *Orycterocetus crocodilinus* and illustrated by KELLOGG (1965, pl. 30) were found isolated; for the comparison, only the teeth associated with skull elements are used. These teeth are lower, more slender, and more strongly curved than most of the teeth of *Physeterula*, except a detached tooth displaying a stronger curvature (Fig. 13C). Note that occasional smaller maxillary teeth of *Physeter* are sometimes more strongly curved than dentary teeth (pers. obs.). The longitudinal grooves on the sides of the teeth of *Orycterocetus* differ from the more numerous grooves giving a fluted aspect to the teeth of *Physeterula*. Actually the teeth of *Orycterocetus*

are more similar to two isolated physeteroid teeth from the Neogene of Antwerp figured by ABEL (1905, figs. 9–10), themselves close to teeth of *Kogia*. The description and illustration of the teeth of *Aulophyseter morricei* in KIMURA *et al.* (2006) are not sufficiently detailed for a comparison. The dentary teeth of *Physeter* are more robust and much larger.

Most of the teeth display an elongated elliptical anterior and/or posterior wear facet (Fig. 13D), supporting the hypothesis of opposite functional maxillary teeth. Apart from one tooth of the left dentary displaying an important apical wear, the apex of the crown of the teeth is barely worn. These elements, combined with the elongated shape of the mandible, suggest that *Physeterula* probably fed by first grasping the moderate size prey between its toothed jaws and then swallowing it by suction.

Post-cranial elements

Atlas. As in *Physeter*, *Placoziphius*, and *Zygophyseter* the atlas is free (Fig. 14F). Only the ventral part is preserved; its maximum anteroposterior length is 61 mm; the distance between the lateral margins of the anterior articular surfaces is estimated to 215 mm. The ventral portion of the neural canal is proportionally wider than in *Physeter*.

Caudal vertebrae. Four caudal vertebrae are preserved with the holotype, displaying the typical articulation facets for the corresponding chevron (one chevron is associated). Considering the development of the partly worn transverse process, the presence of a vertebral arterial canal, and the general size of each vertebra (Table 1), these vertebrae are anteroposteriorly sequenced as shown in Figure 14A–D. By comparison with the

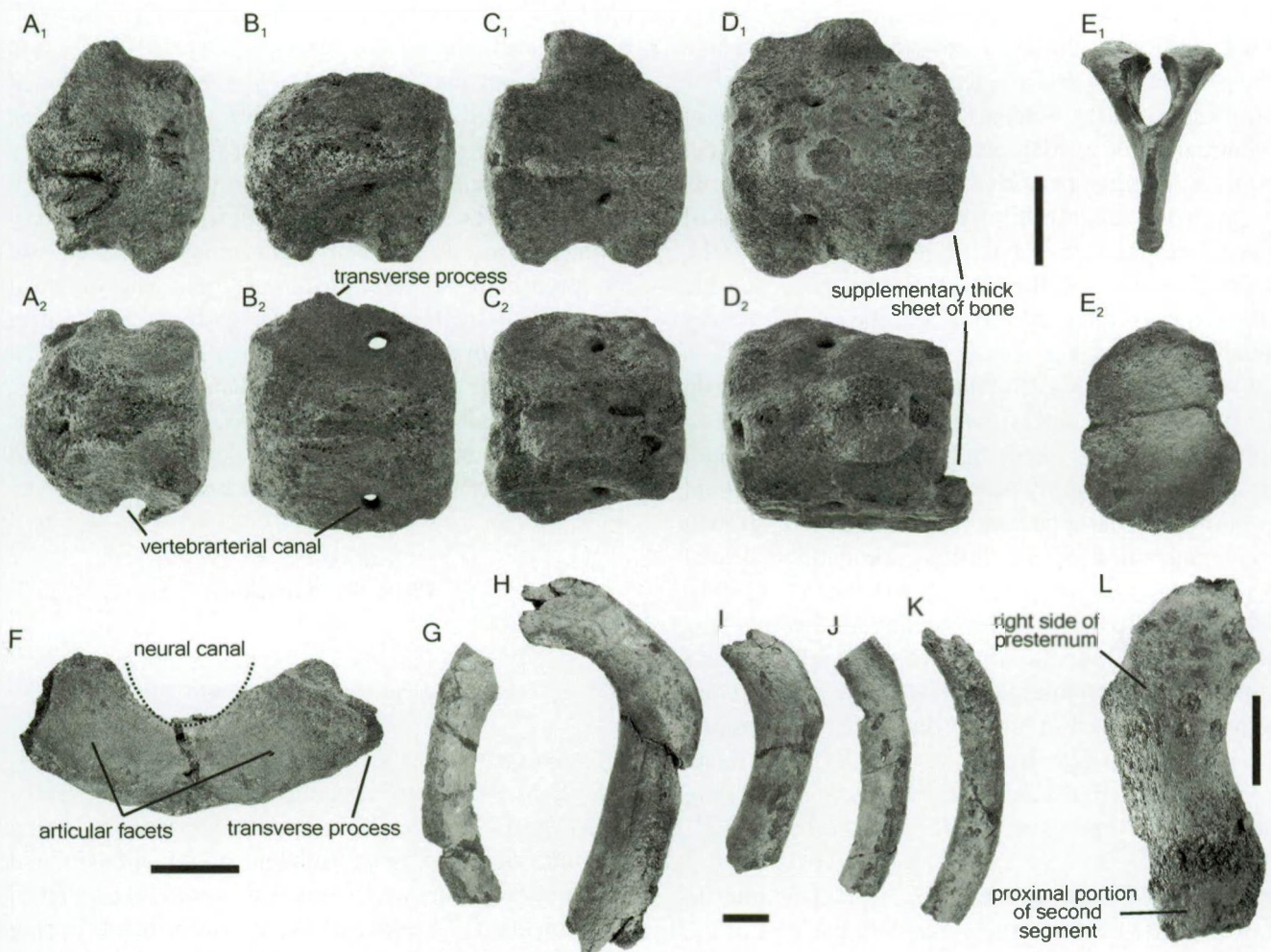


Fig. 14 – Post-cranial elements of *Physeterula dubusi* IRSNB M.527 (holotype), Miocene of Antwerp. **A, B, C, D.** Four caudal vertebrae in left lateral (₁) and dorsal (₂) view. **E.** Chevron in anterior/posterior (E₁) and lateral (E₂) view. **F.** Atlas fragment in anterior view. **G–K.** Rib fragments in anterior view. **L.** Right part of the presternum and ankylosed second segment. All the scale bars equal 50 mm.

	centrum length	centrum width	centrum height
A	+112	130	116
B	131	122	e107
C	129	118	113
D	119	106	106

Table 1 – Measurements (mm) of the caudal vertebrae of *Physeterula dubusi* IRSNB M.527 (holotype), Miocene of Antwerp. The letters identifying the vertebrae correspond to Figure 14. The centrum height does not include the prominent facet for the chevron. ‘e’ indicates estimate, + nearly complete.

vertebral column of *Physeter* (e.g., FLOWER, 1869) and taking account of the slight transverse compression of the centrum of vertebra D, these vertebrae can be positioned at the central torso-caudal tail stock transition sensu BUCHHOLTZ (2001). In *Physeter* all the vertebrae of the torso have a relative length of the centrum < 1 (BUCHHOLTZ, 2001), whereas in this specimen at least the centra of three caudals are longer than high or wide, possibly a primitive condition. This difference suggests that, given the relationship between relative length of the vertebra and axial flexibility (BUCHHOLTZ, 2001), this peculiar area of the column was more flexible in *Physeterula* than in *Physeter*, allowing a wider amplitude of movement.

Interestingly, one vertebra (Fig. 14D) bears on at least one of the lateral surfaces of the centrum a supplementary thick sheet of bone (maximum width 32 mm, height 94 mm) projecting posteriorly behind the epiphysis. The appearance of this bony outgrowth fits characteristics of the diffuse idiopathic skeletal hyperostosis (DISH) listed in KOMPANJE (1999): ‘dripping candle wax’ corresponding to ligamentous calcifications, preservation of the intervertebral disc height, and vertebral foramina not affected. Similar bony outgrowths observed in lumbar vertebrae of mosasaurs and a fossil mysticete lead MULDER (2001) to relate this phenomenon to the axial locomotion, accumulating important strains in this area of the vertebral column.

Chevron. The isolated chevron (Fig. 14E) is similar to one of the last chevrons of *Physeter*, in the area of the 11th-13th caudal vertebrae; its height and width are 111 and 91 mm respectively.

Ribs. The most complete associated rib fragment is the first left rib (Fig. 14H), with a curve more open

than in *Physeter* and *Zygophyseter*. The capitulum, the tuberculum, and the distal end are unfortunately missing. The minimum proximal width of the neck is 71 mm. Other ribs are more fragmentary.

Sternum. The right side of the first segment of the sternum (presternum) ankylosed with the second segment is preserved (Fig. 14L), not significantly differing from *Physeter* except for the much less robust condition and the less prominent anterolateral corner (not complete). The total length of these two fused elements is estimated at 214 mm.

Discussion

Physeterula dubusi is a large sperm whale, with a size close to *Brygmophyseter shigensis*, *Idiorophus patagonicus*, and *Zygophyseter varolai*. The lack of enamel on the teeth places this species in the crown-group *Physeteroidea* as defined by BIANUCCI & LANDINI (2006). The supracranial basin is posteriorly limited by a high wall, as in *Aulophyseter*, *Orycterocetus*, and *Physeter*, but the basin is not as anteriorly developed on the rostrum as in the latter. The right maxilla does not reach the sagittal plane posteromedially, contrary to *Orycterocetus* and similarly to *Aulophyseter* and *Physeter*. The retention of functional maxillary teeth, at least three dorsal infraorbital foramina, and the preorbital process positioned at a higher level along the lateral margin of the rostrum base differ from *Aulophyseter* and *Physeter*. The postorbital process of the frontal is shorter than in *Aulophyseter*, *Diaphorocetus*, and *Orycterocetus*. The mandibular symphysis is shorter and at least some of the caudal vertebrae are proportionally longer than in *Physeter*.

Physeteridae indet.
Fig. 15

1877 — *Physeterula dubusii* (part) VAN BENEDEN, p. 852.

Referred specimen

IRSNB M.1937, third specimen of *Physeterula dubusi* sensu VAN BENEDEN (1877), fragmentary skull including rostrum fragments, most of the supracranial basin, and supraorbital processes. It was discovered December 3, 1863 in the 3^{ème} section of the inner fortification ring around Antwerp (MOURLON, 1878; Fig. 1).

Horizon

MOURLON (1878) provided a brief description of the sediment and a list of bivalves discovered with the

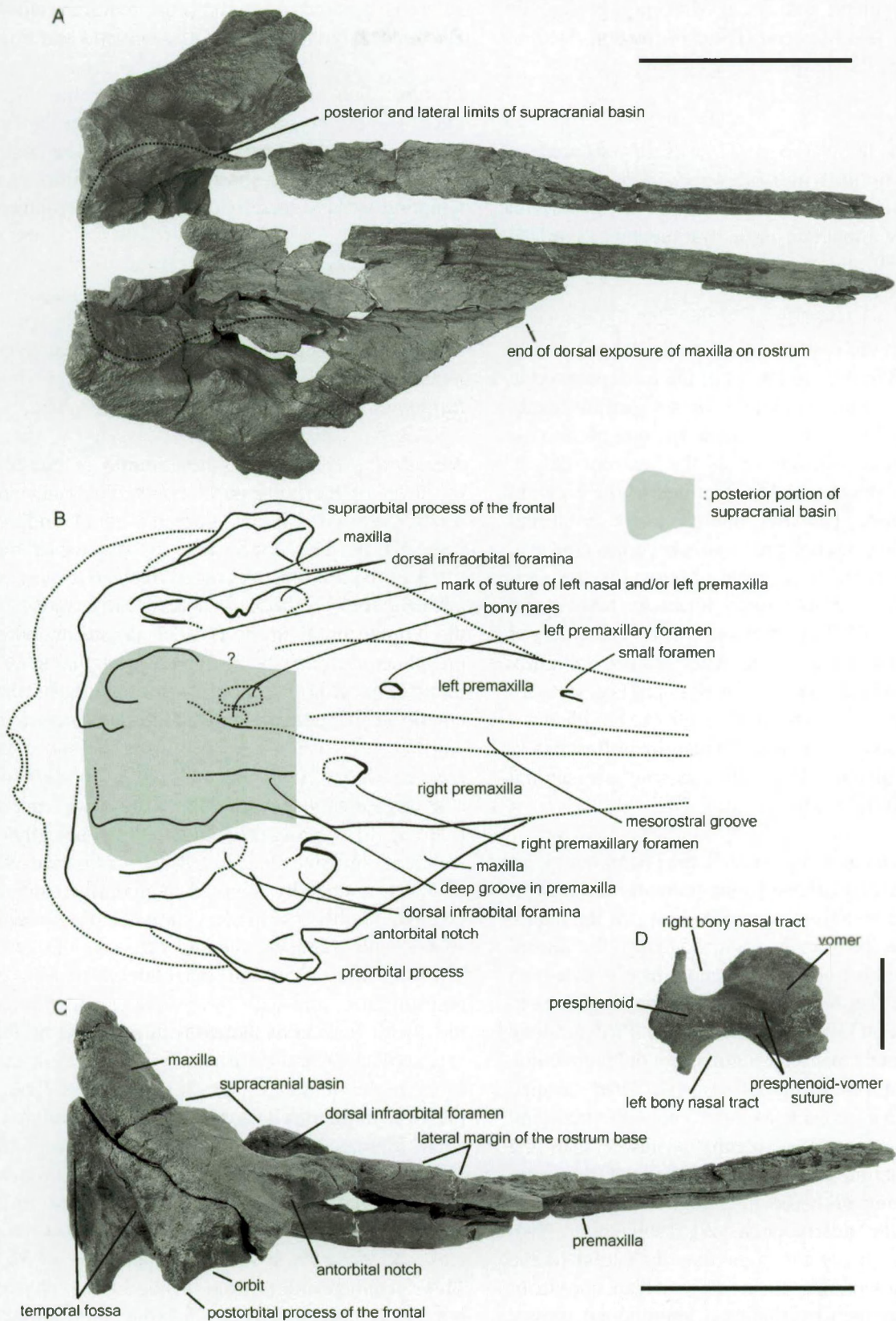


Fig. 15 – Skull IRSNB M.1937, *Physeteridae* indet., Miocene of Antwerp. **A.** Dorsal view. **B.** Schematic reconstruction of the dorsal view. The shaded area corresponds to the posterior portion of the supracranial basin. The relative position of the right and left side elements is approximate in A-B. The basicranium is completely lacking, reconstructed based on other *physeteroids*. **C.** Right lateral view. **D.** Area of the bony nasal tracts in ventral view, displaying the asymmetry of the tracts and the presphenoid uncovered by the vomer. Scale bar for A-C equals 200 mm and for D equals 50 mm.

skull; these elements indicate a Miocene age for this skull, possibly late Miocene (Diest Formation, Deurne Sands Member; R. Marquet, pers. comm., 2007).

Description

The specimen IRSNB M.1937 was not figured in the brief descriptions of *Physeterula dubusi* by VAN BENEDEN (1877) and ABEL (1905). The postorbital width of this moderate size fragmentary skull is estimated at 470 mm, close to *Diaphorocetus poucheti* and *Orycterocetus crocodilinus*.

Premaxilla. On the rostrum, the premaxillae are poorly preserved. The preserved length of the right premaxilla provides a minimum estimation for the rostrum length of 530 mm. The dorsal surface of the premaxilla is sloping medially for most of the rostrum length, suggesting a supracranial basin limited to the cranium and rostrum base. 120 mm anterior to the antorbital notch, the surface of each premaxilla becomes concave, progressively more excavated backwards. A left premaxillary foramen is present (diameter 8 mm), not as reduced as in most other physeteroids. The enlarged right premaxillary foramen (diameter 22 mm) is slightly anterior to the level of the antorbital notch (Fig. 15A-B). Lateral to the right bony naris, the right premaxilla has a V section and an elevated median margin, unfortunately incomplete, probably originally crossing the sagittal plane of the skull.

Maxilla. From the antorbital notch, the lateral margin of the rostrum base is oriented longitudinally for a short distance before an abrupt narrowing towards the lateral margin of the premaxilla. Consequently the dorsal surface of the rostrum was predominantly occupied by the premaxillae on more than half its length, as in *Aulophyseter* and *Physeterula*. Only a tiny foramen pierces the maxilla along the suture with the premaxilla, differing on that point from *Physeterula*. The U-shaped antorbital notch is as wide as long. The wide preorbital process of the maxilla is distinctly lower than the dorsolateral margin of the rostrum base at the same level, a condition observed in *Aulophyseter*, *Physeter*, and possibly the poorly preserved *Idiophyseter*. Two large foramina pierce the right maxilla lateral to the wall of the supracranial basin. The median margin of the anterior foramen overhangs a longitudinal groove anteriorly directed. The posterior foramen is followed backwards by a wide sulcus nearly reaching the occipital crest, a feature absent in *Physeterula*. A small foramen on the median wall of this posterior foramen is directed posteroventrally. In lateral view the maxilla-frontal

suture is sigmoid above the orbit, more erected than in *Physeterula* but less than in *Aulophyseter* and *Physeter*.

Frontal. The supraorbital process of the frontal is thick, leaving no space for a projection of the lacrimal between frontal and maxilla (Fig. 15C). The postorbital process is robust and shorter than in *Aulophyseter*. The temporal fossa is dorsally pointed and anteroposteriorly compressed.

Supraoccipital. Combined with the shape of the underlying frontal and maxilla, the preserved fragments of supraoccipital indicate an erected and slightly concave occipital shield roughly similar to *Aulophyseter*, *Orycterocetus*, and *Physeterula*.

Mesethmoid/Vomer. The mesethmoid is preserved at the level of the bony nasal tracts. The right and left tracts have a minimum diameter of 24 and 53 mm respectively. The dorsal keel of the mesethmoid is tilted to the left side. As noted in *Aprixokogia*, *Kogia*, and *Physeter* (WHITMORE & KALTENBACH, 2008) the vomer of IRSNB M.1937 does not cover the presphenoid ventrally at the level of the bony nasal tracts (Fig. 15D), supporting the hypothesis that this condition characterizes at least the stem-physeteroids.

Discussion

The fragmentary specimen IRSNB M.1937, previously referred to *Physeterula dubusi* but actually much smaller (skull size close to *Orycterocetus crocodilinus*) displays a dorsally pointed temporal fossa and an erected slightly concave supraoccipital shield. It shares with *Aulophyseter* and *Physeter* the preorbital process lower than the dorsolateral margin of the rostrum base, and with *Aulophyseter* and *Physeterula* the dorsal surface of the rostrum occupied by the sole premaxillae on more than half its length. In addition to the higher temporal fossa it differs from *Physeter* in the more numerous dorsal infraorbital foramina. Only a small foramen is present along the maxilla-premaxilla suture at the rostrum base, differing from *Physeterula*. The postorbital process is much shortened compared to *Aulophyseter*, *Diaphorocetus*, and *Orycterocetus*, closer to *Physeterula* and some specimens of *Physeter*. This specimen differs from all the known physeterids, but it is too fragmentary to allow the definition of a new taxon. It is provisionally referred to *Physeteridae* indet.

Family Kogiidae
Genus *Thalassocetus* ABEL, 1905

Type species: *T. antwerpiensis* ABEL, 1905

Diagnosis. The diagnosis is the same as for the only included species.

***Thalassocetus antwerpiensis* ABEL, 1905**
Figs 16-18

1905 — *Thalassocetus antwerpiensis* (part) ABEL, p. 70, fig. 7.

2002 — *Placoziphius duboisii* (part) KAZÁR, p. 154.

2006 — *Thalassocetus antwerpiensis* BIANUCCI & LANDINI, p. 125.

Lectotype

IRSNB M.525 (old number 3248).

Type locality

Antwerp, no exact locality.

Type horizon

The dark colour and the preservation state of the bones of the lectotype suggest an origin in one of the members of the Berchem Formation, lower to middle Miocene (LOUWYE, 2001, 2005), possibly the Antwerpen Sands.

Diagnosis

Thalassocetus antwerpiensis is a small physeteroid species with a skull size close to *Kogia breviceps*. It differs from all the other kogiids in the nodular

postglenoid process of the squamosal, and the thin supraorbital area of the skull, from *Kogia* and *Scaphokogia* in the U-shaped short antorbital notch, from *Aprixokogia*, *Kogia*, and *Praekogia* in the right antorbital notch being distinctly outside the supracranial basin and in larger dorsal infraorbital foramina, from *Aprixokogia* and *Praekogia* in the temporal fossa being anteroposteriorly compressed, and from *Kogia* and *Praekogia* in the absence of a wide notch in the squamosal for the enlarged posterior process of the tympanic bulla.

Comments

The status of the second specimen referred to *T. antwerpiensis* by ABEL (1905) (IRSNB M.526) was only briefly commented in KAZÁR (2002). This right portion of the cranium including the frontal and maxillary parts of the orbit and temporal fossa has a size close to IRSNB M.525. The postorbital process of the frontal is indeed more slender, excavated on its posterolateral surface; the lateral maxillary crest limiting the supracranial basin might be lower; and the elevation of the maxilla towards the posterior wall of the supracranial basin is less abrupt. Nevertheless, the differences between these two specimens are clearly less important than the differences between any of them and the holotype of *P. duboisii*. Considering the fragmentary state of IRSNB M.526 it is nevertheless more careful to refer it to Kogiidae aff. *Thalassocetus*.

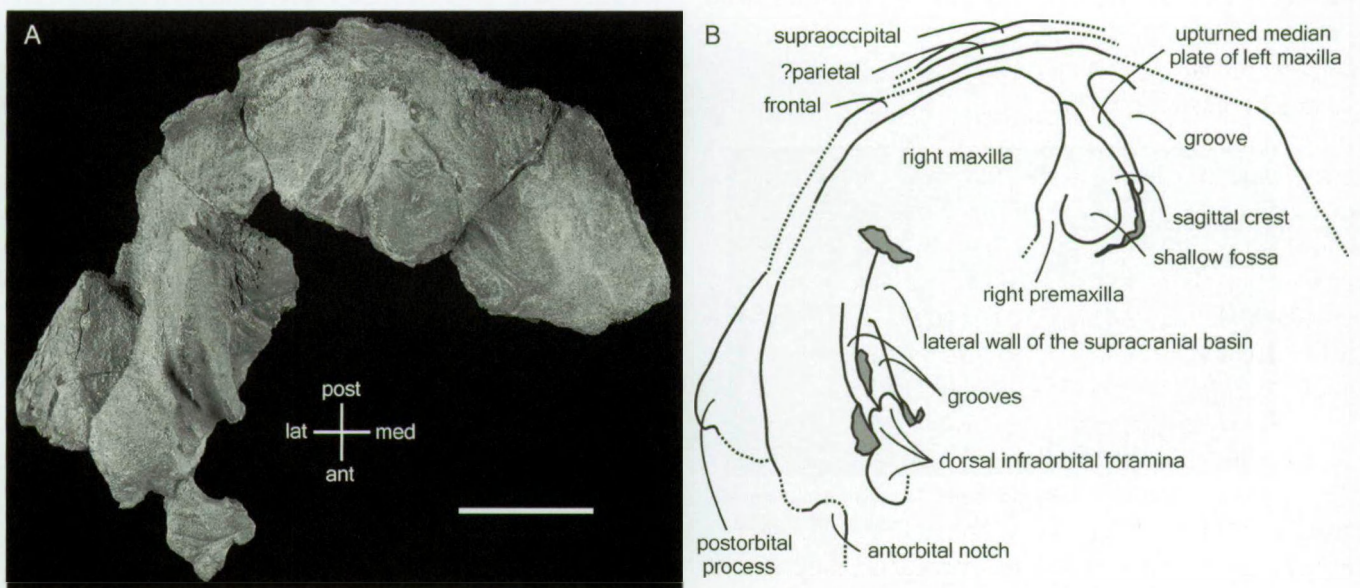


Fig. 16 — Skull of *Thalassocetus antwerpiensis* IRSNB M.525 (lectotype), Miocene of Antwerp. **A.** Anterodorsal view. **B.** Corresponding line drawing. Scale bar equals 50 mm.

Description of the lectotype of *Thalassocetus antwerpiensis*

ABEL (1905) provided a brief description of *Thalassocetus antwerpiensis*; concerning the specimen identified here as the lectotype only the fragmentary supracranial basin was illustrated in anterodorsal view. The only informative elements are the right side and the posterior wall of the supracranial basin from the antorbital notch to the supraoccipital crest (lacking portions of the maxilla), a part of the left supraorbital process, the right squamosal, and the right exoccipital. The postorbital width of this small skull is roughly estimated at 280-290 mm, larger than the holotypes of *Praekogia cedrosensis* and *Scaphokogia cochlearis*, in the size interval of *Kogia breviceps* (sample of three specimens in ROSS, 1984), and significantly smaller than all the other physeteroids from Antwerp studied here. Because the premaxilla is not preserved on the rostrum the description starts with the maxilla.

Maxilla. The right antorbital notch is widely open anterolaterally (Fig. 16). Even if the preorbital process of the maxilla is incomplete, it did not limit laterally a slit-like notch, contrary to *Kogia* and *Scaphokogia*. Medial to the antorbital notch the maxilla is pierced by a major infraorbital foramen, larger than in *Aprixokogia*, *Kogia*, and *Praekogia*. At least two septae, only partly preserved, indicate a more or less complete subdivision of this foramen in three branches. The two smaller posterior branches extend posteriorly as grooves along the maxillary crest laterally limiting the supracranial basin: the first branch on the outer wall of the crest, the second branch on the inner wall. This condition, with

only one of the dorsal infraorbital foramina opening inside the supracranial basin is roughly similar to *Orycterocetus crocodilinus* (e.g., USNM 14730). The maxillary crest laterally limiting the basin occupies a more median position compared to the right antorbital notch than in *Aprixokogia*, *Kogia*, and *Praekogia*. In the two last genera the notch enters the supracranial basin. On the preorbital process the outer margin of the maxilla is thin in lateral view, contrasting with other kogiids.

Premaxilla. The right premaxilla is only preserved on the posterior wall of the supracranial basin, for a large part located on the left side of the skull beyond the sagittal plane. As previously suggested by ABEL (1905) and BIANUCCI & LANDINI (2006), this area strongly reminds the sagittal crest of *Aprixokogia*, *Kogia*, and *Praekogia* (the sagittal crest of *Scaphokogia* is probably secondarily modified by the enlargement of the supracranial basin; MUIZON, 1988). The premaxilla is posteriorly pointed. Its transverse section is triangular; the medial face is applied along the curved median margin of the left maxilla, forming together a crest overhanging the maxilla (Figs. 16-17A). The surface of the premaxilla is slightly concave at its widest preserved level. In *Kogia* this depression (Fig. 17B) corresponds to the seat of the nasofrontal sac and adjoining small spermaceti organ (SCHENKKAN & PURVES, 1973; CRANFORD *et al.*, 1996; Fig. 20B-C). If the hypothesized homology with the sagittal crest of *Aprixokogia*, *Kogia*, and *Praekogia* is correct, a similar soft anatomy structure might have been present in *Thalassocetus*. In *Physeter*, the enlarged spermaceti organ occupies most of the supracranial basin and the

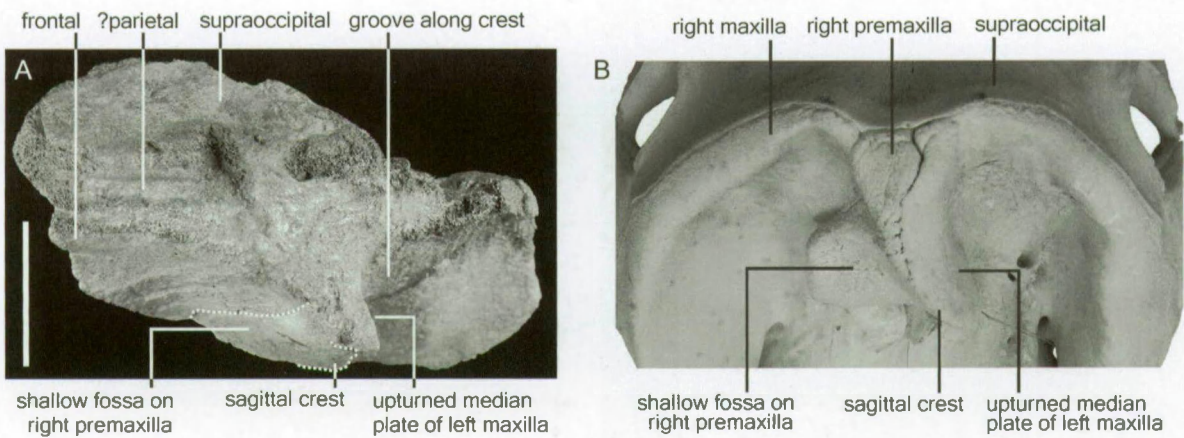


Fig. 17 – A. Vertex of the skull of *Thalassocetus antwerpiensis* IRSNB M.525 (lectotype), Miocene of Antwerp, in dorsal view. Scale bar equals 30 mm. B. Vertex of the skull of Recent *Kogia breviceps* ZMA 14.817, in dorsal view. Note the similarities at the level of the sagittal crest.

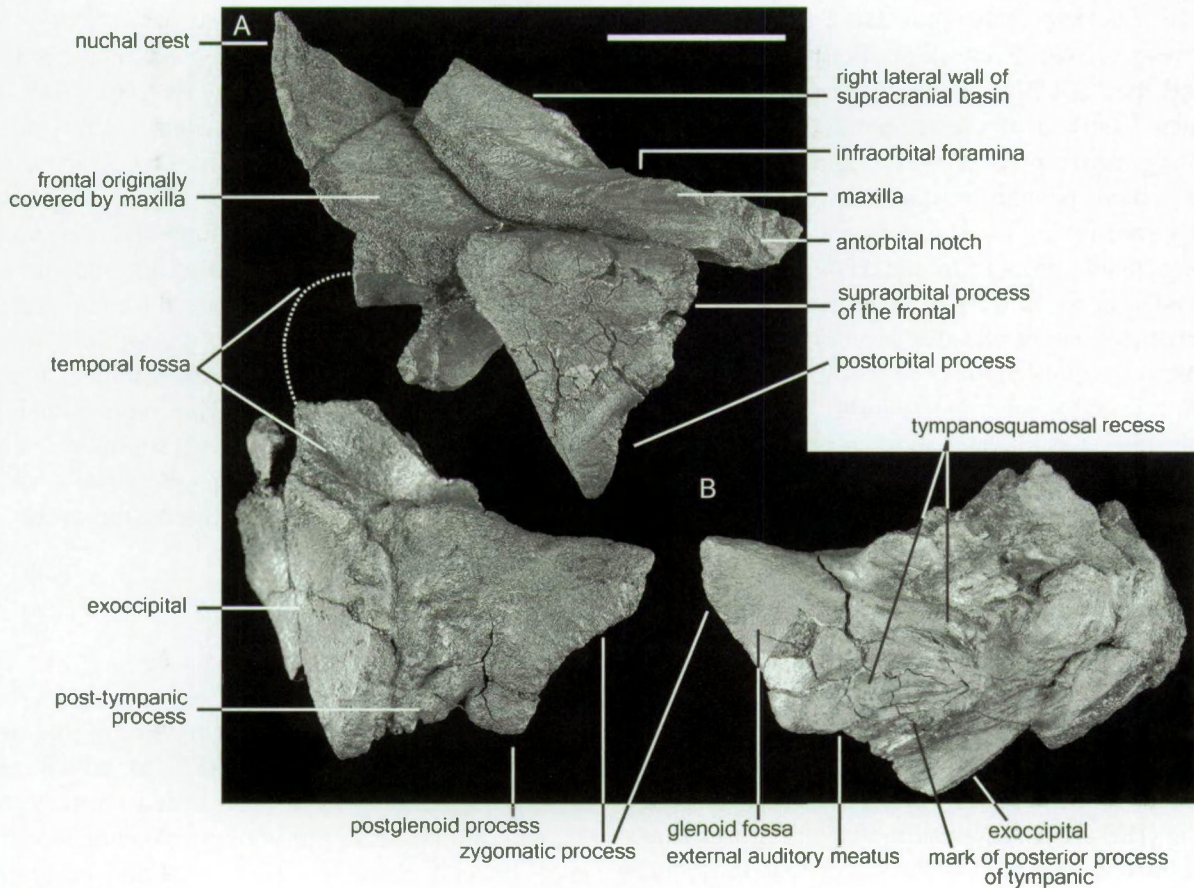


Fig. 18 – Skull of *Thalassocetus antwerpiensis* IRSNB M.525 (lectotype), Miocene of Antwerp. **A.** Supraorbital area and squamosal/exoccipital in right lateral view. The relative position of the two elements is approximate. **B.** Right squamosal/exoccipital in anteroventral view. Scale bar for A-B equals 50 mm.

right premaxilla is flat and much wider than in *Kogia* (see discussion below; Fig. 20A).

In non-kogiid physeteroids, the left nasal is located median to the left maxilla, posterior to the left bony naris. Because this area is occupied by the right premaxilla in *Thalassocetus*, the left nasal is probably absent in the latter, as in *Aprixokogia*, *Kogia*, *Praekogia*, and *Scaphokogia*.

Frontal. The geometric relationship between the supraorbital process of the frontal and the overlying maxilla might be inaccurate; the past reconstruction of the skull fragment from several elements lead to slight mistakes and the orbit might be artificially too anterolaterally directed, also modifying somewhat the shape of the temporal fossa. The preorbital process of the frontal is not complete. The postorbital process is long (73 mm) and pointed, roughly vertically oriented (Fig. 18A). In lateral view the frontal-maxilla suture is much less erected than proposed by ABEL (1905), with an angle no more than 20-25° to the horizontal

plane for most of its length. Where it gets close to the supraoccipital crest the suture curves to a nearly vertical orientation. The preserved dorsal and anterior outlines of the temporal fossa suggest a fossa anteroposteriorly compressed, longitudinally shorter than in *Aprixokogia* and *Praekogia*. On the posterior wall of the supracranial basin, most of the covering of the frontals by the maxillae is missing. In anterodorsal view, the outline of the frontals on the cranium is posteromedially pointed, more than in *Aprixokogia*, *Kogia*, and *Praekogia*.

Parietal. On the supraoccipital crest, between the frontal and the supraoccipital is a narrow strip of bone (Figs 16-17A) that probably corresponds to the parietal, reaching the top of the crest as suggested by ABEL (1905), medially longer than in *Idiophyseter* (see comment in KELLOGG, 1927). The dorsomedian area of the supraoccipital is slightly concave and nearly vertical at its dorsal end. The general slope of the supraoccipital shield was probably around 60-70°, as in *Kogia* (the slope is steeper in some individuals of the latter).

Squamosal. The zygomatic process of the squamosal is short (Fig. 18A). Even if no bony contact with the dorsal part of the cranium is preserved, the reconstructed outline of the temporal fossa indicates that the zygomatic process was originally overhung to some extent by the postorbital process of the frontal, as seen in *Kogia*. The distance from the apex of the zygomatic process to the ventral end of the postglenoid process is 64 mm. The dorsal margin of the zygomatic process elevates posteriorly and bears a low hump at mid-length. The postglenoid process is nodulous, not as anteroposteriorly flattened as in most other physeteroids, and short, reaching the same ventral level as the post-tympanic process. The distance between the postglenoid process and the exoccipital is not as important as in *Kogia* and *Praekogia*, leaving no space for an enlarged posterior process of the tympanic bulla as in the two latter, more similar to *Aprixokogia* on this point. However, individual variation has been proposed at this level in the latter, based on isolated squamosals (WHITMORE & KALTENBACH, 2008). The glenoid fossa is narrow, surrounded anteromedially and posteromedially by a developed tympanosquamosal recess (Fig. 18B). The remains of falciform process are broken at the base, probably less reduced than in *Kogia*, *Physeter*, and *Physeterula*. Along the narrow external auditory meatus, the ventral surface of the post-tympanic process is grooved, indicating the surface of contact with, or elements of, the posterior process of the tympanic bulla, elongated but narrow.

Discussion

The temporal fossa of the small *Thalassocetus antwerpiensis* is anteroposteriorly compressed, as in physeteroids more derived than *Brygmophyseter* and *Zygophyseter* (BIANUCCI & LANDINI, 2006). The postglenoid process of the squamosal is nodular rather than anteroposteriorly flattened, differing from other physeteroids.

As previously mentioned (ABEL, 1905; BIANUCCI & LANDINI, 2006), *Thalassocetus* shares with members of the family Kogiidae a sagittal crest between the bony nares and the supraoccipital. The polarity of the character discussed here is still somewhat controversial: either the development of a sagittal crest is plesiomorphic, present in some basal physeteroids (not only kogiids) and subsequently lost in derived physeterids, in relation with the increased development of the spermaceti organ (MUIZON, 1991), or the presence of a crest is a synapomorphy of the kogiids (BIANUCCI & LANDINI, 2006). As until now no basal physeteroid has shown a crest obviously homologous to the kogiid sagittal crest,

the second hypothesis is preferred.

Among the other morphological areas providing characters defining the kogiids (MUIZON, 1988, 1991; BIANUCCI & LANDINI, 1999, 2006), only the right antorbital notch is preserved in *Thalassocetus*; it is clearly not slit-like, contrary to *Kogia*, *Scaphokogia*, and possibly *Praekogia*. Furthermore, the notch is located outside the supracranial basin and the dorsal infraorbital foramina are large, differing from the Kogiinae MUIZON, 1991 (= *Aprixokogia* + *Kogia* + *Praekogia*). The supraorbital area is thinner in lateral view than in other kogiids. The supracranial basin is not as deep and as extended posteriorly as in the monogeneric subfamily Scaphokogiinae MUIZON, 1988. This genus might represent the most basal member of the kogiid lineage.

Phylogeny

The phylogenetic analysis is based on the matrix of BIANUCCI & LANDINI (2006), to which several characters and taxa have been added (Appendices 1-2), with a total of 36 morphological characters and 16 taxa. Several characters were modified according to recently published data and additional observations. Two outgroups are chosen a priori, the archaeocete *Zygorhiza* and the stem-odontocete *Agorophius*. All the characters are treated as unordered.

The cladistic analysis (Paup 4.0b10; heuristic search; character-state optimisation acctran) produced seven most parsimonious trees (tree length 69 steps; CI 0.72; RI 0.76). The consensus tree is shown in Figure 19, on a stratigraphic framework. Besides the addition/removal of some taxa this tree differs from the consensus tree of BIANUCCI & LANDINI (2006) in the more crownward position of *Diaphorocetus* (depending on the interpretation of the damaged supraoccipital shield), the more stemward position of *Orycterocetus* and *Placoziphius*, and the nested position of *Aulophyseter* among the Physeteridae (based on the new information published by KIMURA *et al.*, 2006). Keeping in mind the low resolution at the level of *Diaphorocetus*, *Orycterocetus*, and *Placoziphius*, a new definition and content of the families Kogiidae and Physeteridae is proposed here. The Kogiidae group all the physeteroids more closely related to *Kogia* than to *Physeter*. The main characters defining the clade are: small size; development of a sagittal crest; loss of the two nasals; maxillae, premaxillae, and vomer reaching the tip of the rostrum; and posterior process of the periotic not ventrally oriented (the two last synapomorphies are

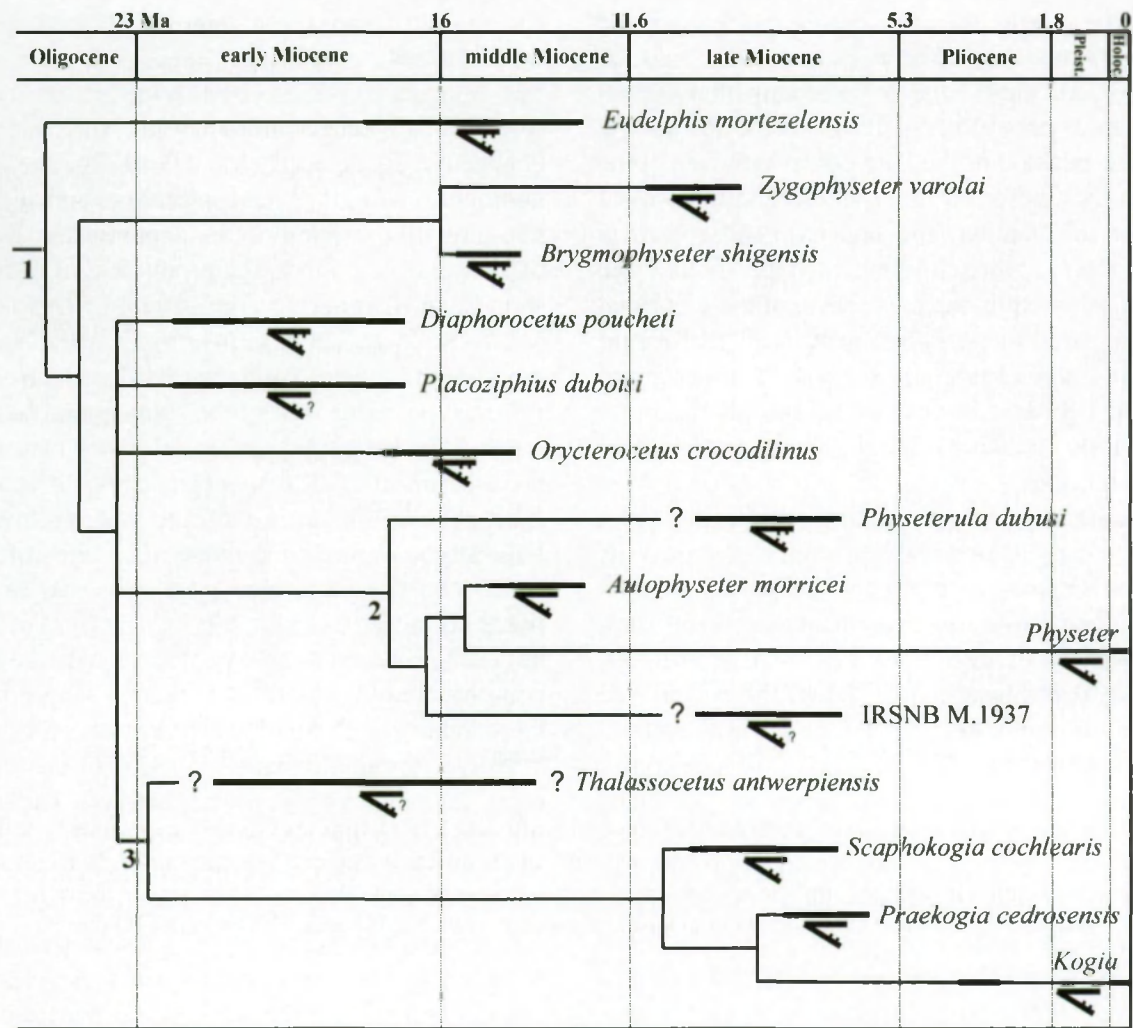


Fig. 19 – Consensus tree of the phylogenetic analysis, presented on a stratigraphic frame. The length of the branches is therefore not proportional to the number of steps towards a given taxon. Tree length 69 steps; CI 0.72; RI 0.76. 1 Physeteroidea; 2 Physeteridae; 3 Kogiidae. The thick bars indicate the stratigraphic record of the species; question marks associated to the bars indicate stronger uncertainty on dates. Data from areas other than the North Sea are taken from BARNES, 1973; BIANUCCI & LANDINI, 1999, 2006; COZZUOL, 1996; HIROTA & BARNES, 1995; KELLOGG, 1927, 1965; MUIZON, 1988. The schematic jaws illustrate the presence/absence of functional maxillary teeth in the different taxa as proposed by the parsimony analysis; question marks associated to the jaws indicate equivocal states.

unknown in *Thalassocetus*). The narrower posterior portion of the right premaxilla possibly constitutes another synapomorphy of the Kogiidae.

The Physeteridae group all the physeteroids more closely related to *Physeter* than to *Kogia*. This clade is only poorly defined, with the dorsal exposure of the maxilla on the rostrum limited to the posterior portion (reversion in *Physeter*). In this family there is also a trend in the increase of size, but a similar trend characterizes the clade *Brygmophyseter* + *Zygophyseter*. With better preserved specimens of *Diaphorocetus* and *Placoziphius* changes in the content and definition of

the Physeteridae can be expected.

Focusing on the Miocene North Sea species, *Eudelphis* is the most stemward physeteroid in the proposed consensus tree, possessing a distinct supracranial basin, asymmetric bony nares, a widened and posteriorly longer right premaxilla, and a triangular zygomatic process of the squamosal in lateral view, but retaining a large left premaxillary foramen and a long postglenoid process of the squamosal. This basal position is further supported by the rather conservative general morphology of the premaxillae at the rostrum base. The branch of *Eudelphis* is followed by a clade

grouping the Mediterranean *Zygophyseter* and the Pacific *Brygmophyseter*. The position of *Placoziphius* is not resolved, partly due to its fragmentary state. Nevertheless it provisionally falls outside the family Physeteridae because of the long dorsal exposure of the maxilla on the rostrum. *Physeterula* is the most basal member of this family. The undetermined specimen IRSNB M.1937 is more closely related to *Aulophyseter* and *Physeter*, based on the lower level of the preorbital process compared to the lateral margin of the rostrum base. Finally the cladogram suggests a sister-group relationship between *Thalassocetus* and all the other known kogiids (see above for the synapomorphies of the Kogiidae).

Considering the stratigraphic frame of the cladogram (Fig. 19) the early Miocene age of several physeteroids points to an Oligocene origin for the superfamily, as proposed by the discovery of fragmentary remains from this epoch (MCHEDLIDZE, 1970; FORDYCE & MUIZON, 2001). Several lineages branch before the appearance of the crown-Physeteroidea (including the last common ancestor of *Kogia* and *Physeter*, and all its descent), including the branch towards *Eudelphis* and the clade *Brygmophyseter* + *Zygophyseter*. The oldest Kogiidae is probably *Thalassocetus*, but new material found in situ would better support this hypothesis. It should be noted that a fossil species of *Kogia*, *K. pusilla*, has been described in the middle Pliocene of Italy (BIANUCCI & LANDINI, 1999), partly filling the gap between *Praekogia* and *Kogia*. The oldest Physeteridae, but not the most stemward, is *Aulophyseter*, dated from the middle Miocene. Therefore the first Physeteridae should have appeared during the early Miocene or before. A long ghost lineage separates *Physeter* from its sister-group *Aulophyseter*, although postcranial remains from the Pliocene of Piedmont, Italy, have been referred to *Physeter* (PARONA, 1930). Because the divergence between the well defined Kogiidae and *Placoziphius*/*Diaphorocetus* is not later than very early in the Miocene, the origin of the crown-Physeteroidea must probably be sought in Oligocene levels. A more precise dating of the different cladogeneses will depend on the improvement of stratigraphic information and a better resolved phylogeny.

Functional anatomy and palaeoecology

In the evolutionary history of the sperm whales, two features deserve special attention and are commented here: the spermaceti organ and the oral apparatus.

Evolution of the spermaceti organ and associated structures

The spermaceti organ is a fat-filled cavity of the forehead of Recent physeteroids surrounded by a connective tissue wall (MEAD, 1975). The proposed homology with the right posterior dorsal bursa of non-physeteroid odontocetes supports the hypothesis of a similar function in the production of echolocative sounds (see CRANFORD *et al.*, 1996; CRANFORD, 1999; MADSEN *et al.*, 2002). In *Physeter* the spermaceti organ is the most voluminous head structure, running from the posterior wall of the supracranial basin to the level of the blowhole, farther anteriorly than the tip of the rostrum of adult males (Fig. 20A). It is separated from the dorsal surface of the rostrum by another large structure, the junk, made of a series of lens-like concavoconvex lipid elements limited by connective tissue columns (CLARKE, 1978). The junk of *Physeter* has been proposed to be homologous with the melon of non-physeteroid odontocetes, much likely involved in the conduction of echolocative sounds (CRANFORD *et al.*, 1996; for an alternative function of the spermaceti organ and junk in *Physeter*, namely a battering ram for male-male fights, see CARRIER *et al.*, 2002). As commented above, the spermaceti organ is considerably smaller in *Kogia*, occupying a reduced volume of the supracranial basin close to the dish-like pedestal of the right premaxilla (part of the sagittal crest). Most of the anterior part of the forehead of *Kogia* is instead filled by the melon (CRANFORD *et al.*, 1996, fig. 8; Fig. 20B-C).

The asymmetry of the bony nares and surrounding bony elements is already much pronounced in the oldest, most stemward physeteroids (e.g. *Eudelphis*), more than in any other odontocete. It is therefore pertinent to propose a similar (even if to a lower degree) asymmetry for the forehead soft anatomy, including the nasal passages, air sacs, and sound production structures (phonic lips). This condition supports the existence of a spermaceti organ in all known physeteroids. Considering the size of the spermaceti organ in the two Recent physeteroid genera *Kogia* and *Physeter*, the size and anterior extent of the supracranial basin in fossil physeteroids, and the size of the posterior dorsal bursae in other odontocetes (see CRANFORD *et al.*, 1996), it is more parsimonious to propose a relatively small spermaceti organ in basal physeteroids, considerably shorter anteriorly than in *Physeter* (BIANUCCI & LANDINI, 2006), but also less voluminous, not occupying the whole supracranial basin. In that case, the primary function of the supracranial basin would not be to contain the spermaceti organ, but rather to act as a parabolic structure reflecting the sounds produced in an

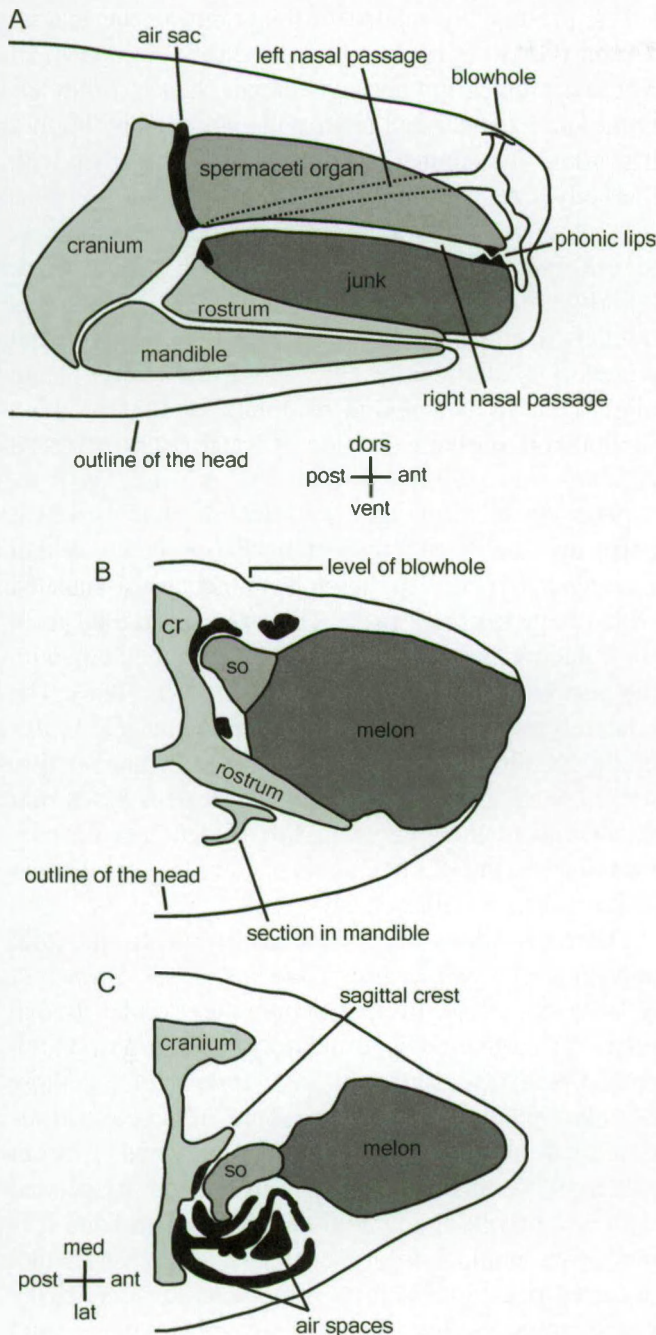


Fig. 20 – Soft anatomy of the forehead in the extant *Physeter* and *Kogia*. **A.** Schematic parasagittal section of the head of *Physeter* (modified from CRANFORD, 1999). **B-C.** Tomography reconstructions of the head of *Kogia* (modified from CRANFORD *et al.*, 1996). cr cranium; so spermaceti organ. **B.** Vertical (parasagittal) section. **C.** Horizontal (frontal) section. The hypothetical homologies between cephalic structures are highlighted with similar shading. Note the enlarged spermaceti organ, the longer rostrum, and the anteriorly shifted blowhole in *Physeter*. Drawings are not at the same scale.

anterodorsal direction. Further supporting the primary role of the supracranial basin as a parabolic structure, the fact that the skull is projected ventrally to the body axis in both *Kogia* and *Physeter* (CRANFORD, 1999) suggests a trend towards a more efficient anterior focus of the echolocative sounds. As is the case in *Kogia*, the most voluminous structure in the supracranial basin of the stem-physeteroids would have been the melon. And the blowhole was probably located roughly vertical to the bony nares, as in the latter (for an alternative hypothesis with a larger spermaceti organ and a somewhat anteriorly shifted blowhole in stem-physeteroids see BIANUCCI & LANDINI, 2006). Besides the development of a small spermaceti organ, the most basal physeteroids possibly retained some forehead structures inherited from more ‘classical’ odontocetes, for example the premaxillary sacs and the nasals plugs (see above, the conservative morphology of the premaxillae around the premaxillary foramina in *Eudelphis* and possibly *Diaphorocetus*).

In the family Physeteridae there is a trend towards an anterior development of the supracranial basin, occupying the posterior portion of the rostrum. But in no fossil physeterid the basin reaches the development seen in *Physeter*; in the latter the dorsal surface of the rostrum is concave and considerably widened along its whole length. So the spermaceti organ of known fossil physeterids was probably not as anteriorly long and voluminous as in *Physeter*. However, it should be noted that the rather fragmentarily known middle Miocene *Idiophyseter* possibly possessed an anteriorly extended supracranial basin (see KELLOGG, 1925). At some unknown time of the evolution of the physeterids, the blowhole and the underlying right side sound production structures shifted to a more anterior location, leading to a longer nose. Such a feature might have been selected for the production of lower frequency sound and/or for acoustic display, as suggested by CRANFORD (1999). Interestingly the rostrum of *Physeter* is proportionally longer than in related physeteroids (e.g. *Aulophyseter*), suggesting that a longer rostrum (edentulous, as discussed below) has been selected in the former to support the longer spermaceti organ and junk, leading to an increased distance between the sound production area and the posterior wall of the supracranial basin. It should be noted that the trend towards a larger body size is not unique to physeterids (*Aulophyseter*, *Physeter*, and *Physeterula*), as some stem-physeteroids are also large (e.g., *Brygmophyseter* and *Zygophyseter*), even if not as large as *Physeter*. Additionally KELLOGG (1925) refers anterior fragments of a rostrum, mandible, and teeth from the late Miocene of California to a huge enamel-bearing physeteroid, providing an estimation of

the skull length of 12-15 feet (3.7-4.6 m).

Besides the trend towards a reduction of the body size, in the Kogiidae the spermaceti organ remains small and, except in *Scaphokogia*, it lies on a bony shelf (sagittal crest) somewhat isolating it from the floor of the supracranial basin. This modification is accompanied by the loss of the left nasal. As proposed by MUIZON (1988) the size and the smooth surface of the supracranial basin in *Scaphokogia* suggests an important development of the spermaceti organ, progressively filling the basin and reducing the sagittal crest. However, contrary to the lineage towards *Physeter* the enlarged supracranial basin is limited to the cranium by an abrupt step in *Scaphokogia*, not extending on the rostrum base. There is therefore no clue for an anterior shift of the narial passages and blowhole in kogiids.

Evolution of the feeding apparatus

Both the large *Physeter* and the considerably smaller *Kogia* lack functional upper teeth; in these two genera only vestigial teeth sometimes erupt on the maxilla (CALDWELL & CALDWELL, 1989; RICE, 1989). Furthermore the crown of the lower teeth does not bear enamel any more, the temporal fossa is relatively reduced, and in *Physeter* a common anomaly of the mandible leading to a strong lateral curvature does not lead to the death of the individual (RICE, 1989). Together with behavioural and anatomical observations (WERTH, 2004; BLOODWORTH & MARSHALL, 2005) all these elements support the idea that Recent physeteroids mostly rely on suction for catching and swallowing their prey (mostly squid). In *Kogia*, the strongly shortened rostrum and mandible (amblygnathy, *K. breviceps* and *K. sima* are the two odontocete species with the highest bluntness index; WERTH, 2004) reduce the length of the oral opening and correlate well with other suction feeding clues, whereas *Physeter* retains long jaws and sucks the prey directly into the oropharyngeal opening (WERTH, 2004).

Freed from their feeding role the robust lower teeth of *Physeter* could be used for combat, as seen in other odontocete lineages, e.g. the ziphiids (WERTH, 2006); tooth scars inflicted by other large males are frequent on the head of *Physeter* males (KATO, 1984; RICE, 1989), suggesting that beside vocalization fights might be occasionally determinant for breeding success (CARRIER *et al.*, 2002; WHITEHEAD, 2003). Differing from *Physeter macrocephalus*, with adult males several meters larger than females, no obvious size dimorphism is detected in *Kogia breviceps* and *K. sima* (ROSS, 1984; CALDWELL & CALDWELL, 1989). Parallel rows of scars have been observed in *Kogia* too, but on both

sexes, presumably related to fights during the mating season (GASKIN, 1972). However, the lower teeth of *Kogia* are much thinner and sharper than in *Physeter*, borne on a slender and short underslung mandible not best fitted for combat. These elements, together with the body size, the prominent dorsal fin, and the 'false gill' white coloration between the flipper and the eye, give *Kogia* the appearance of a bottom feeding shark (CALDWELL & CALDWELL, 1989; WERTH, 2006). This mimicry could have been selected to repel potential predators. Additionally, the elongated lower teeth might be used by *Kogia* to retain the food after having suctioned it, during expulsion of water (BLOODWORTH & MARSHALL, 2005).

The most stemward physeteroids retain robust upper and lower teeth (especially *Brygmophyseter* and *Zygophyeter*) (Fig. 19), bearing enamel, and associated with a large temporal fossa. These taxa used their teeth for catching large preys, possibly cutting them with the posterior teeth (BIANUCCI & LANDINI, 2006). The relatively more slender teeth of the smaller *Eudelphis* probably allowed the capture of somewhat smaller preys. Among the physeterids, at least *Physeterula* retains functional upper teeth, but its teeth lack enamel, meaning that the loss of enamel occurred before the loss of functional maxillary teeth.

There is little information available on the oral apparatus of fossil kogiids (BARNES, 1973; BIANUCCI & LANDINI, 1999). In *Aprixokogia* the alveolar groove retains at least seven large and deep alveoli (WHITMORE & KALTENBACH, 2008) and in *Scaphokogia* a shallow alveolar groove containing some relict alveoli is described along the moderately shortened rostrum (MUIZON, 1988). No teeth were found associated with any fossil kogiid. With the elements in hand it is more parsimonious to propose that the loss of enamel occurred one time in the evolutionary history of the physeteroids, before the node grouping kogiids and physeterids (as in the tree of BIANUCCI & LANDINI, 2006, but differing from MUIZON, 1991). The temporal fossa of *Thalassocetus* and *Praekogia* is reduced, indicating a jaw musculature less voluminous than in stem-physeteroids, closer to the Recent *Kogia*.

The presence of functional upper teeth in at least one physeterid suggests that the reduction of the dentition occurred in parallel in both lineages: kogiids and physeterids, possibly related to a similar diet change (major food items of *Physeter* are cephalopods, but the diet of *Kogia* is somewhat more varied; RICE, 1989; CALDWELL & CALDWELL, 1989). This convergence supports the idea of an independent improvement of the suction feeding function in multiple odontocete

lineages, progressively replacing the grasping function of the jaws by a more efficient suction apparatus (WERTH, 2006).

Conclusions

1. Based on the cranial material of the Antwerp area, the systematic revision of the sperm whale species from the Miocene of the southern margin of the North Sea lead to the detailed redescription of four species: the stem-physeteroids *Eudelphis mortezelensis* and *Placoziphius duboisi*, the physeterid *Physeterula dubusi*, and the kogiid *Thalassocetus antwerpiensis*, the identification of the eastern North American species *Orycterocetus crocodilinus* in the North Sea, and the description of a new undetermined physeterid.

2. The precision of the stratigraphic information associated to several specimens has been improved. All the specimens originate from Miocene levels. *Placoziphius duboisi* is dated from early Miocene, *Eudelphis mortezelensis* from latest early to middle Miocene, and *Orycterocetus crocodilinus* from the middle Miocene. The incertitude is higher for *Thalassocetus antwerpiensis* (much likely early to middle Miocene), *Physeterula dubusi*, and the new undetermined physeterid (probably late Miocene). The fossil record in the North Sea further stresses the relatively high physeteroid diversity during the Miocene, compared to the two relict Recent genera *Kogia* and *Physeter*. The Pliocene gap in the fossil record of the physeteroids is likely partly due to changes in deposition conditions; indeed isolated physeteroid teeth, often bearing enamel, are not rare in Pliocene shallow marine deposits.

3. The cladistic analysis produced a consensus tree with *Eudelphis* as the most stemward physeteroid known by cranial material. *Eudelphis* displays a distinct supracranial basin and a strong asymmetry of the bony nares and premaxillae, but it retains enamel on teeth and its morphology is conservative in several areas of the skull (rostrum shape, maxillary alveoli, premaxillary foramina, falciform process of the squamosal...). The family Physeteridae is defined as the clade grouping all the physeteroids more closely related to *Physeter* than to *Kogia*. It includes among others the large *Physeterula*, retaining functional upper teeth, and the moderate size IRSNB M.1937. *Placoziphius* is provisionally placed outside the family Physeteridae, together with *Orycterocetus*. Displaying a sagittal crest the small

Thalassocetus is confirmed as a kogiid, sister-group to all the other members of the family.

4. Based on the anatomy of the different taxa and on the framework of the proposed phylogeny, the evolutionary history of the supracranial basin and the oral apparatus are commented. Already developed on the cranium of *Eudelphis* the supracranial basin probably originates during the Oligocene. Parsimony suggests that the basin contained a relatively small spermaceti organ in early physeteroids, leading to the proposal that the basin mostly acted as a parabolic structure for reflection and anterior focusing of the echolocative sounds. In the physeterid clade the spermaceti organ became considerably enlarged towards *Physeter*, eventually growing anteriorly on the dorsal surface of the rostrum to produce the enormous nose of *Physeter*. A strong sexual dimorphism observed in this area for *Physeter* might indicate a function in acoustic sexual display. In kogiids the spermaceti organ remained small, being more distinctly separated from the bottom of the supracranial basin by the development of the sagittal crest.

All the stem-physeteroids for which this area is known bear functional upper teeth with enamel on the crown. The enamel is probably lost before the clade Kogiidae + Physeteridae. A reduction of the upper teeth associated to the decreasing size of the temporal fossa is a trend observed in parallel in both lineages of crown-physeteroids: the small kogiids and the larger physeterids, likely associated to a major change in diet. The lower teeth are secondarily used as weapons in *Physeter*, whereas in *Kogia* they keep a function in food processing.

5. Even if fragmentary the cranial physeteroid material of the North Sea taken as a whole proved to be a useful source of information for investigating different aspects of the evolutionary history of the sperm whales during the Miocene. Besides the promising current anatomical, ecological, and experimental works on Recent sperm whales, new fossils from different times will be crucial to better understand the origin and development of the various adaptations (deep diving, echolocation, food processing, sexual dimorphism...) of the Recent members of this fascinating cetacean group.

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Appendix 1

Data-matrix of 36 characters for two outgroups *Zygorhiza* and *Agorophius*, and 14 analysed taxa. All characters with multiple states are treated as unordered. 0 primitive state; 1, 2, 3 derived states; a variable between 0 and 1; b variable between 1 and 2; ? missing character; - irrelevant character.

	5	10	15	20	25	30	36
<i>Zygorhiza</i>	0000-	00--0	02000	00000	00002	-0---	--0000
<i>Agorophius</i>	?01?0	00000	00?00	????0	?0?00	000-0	000?00
<i>Eudelphis</i>	1110?	1?01?	????1	????0	00?0?	?100?	??1100
<i>Zygophyseter</i>	21b01	11111	0?101	22?10	10100	2121?	000110
<i>Brygmophyseter</i>	211?1	1111?	01?01	????0	101??	?120?	?01?10
<i>Diaphorocetus</i>	011?1	1111?	0?111	?????	00??1	21?0?	001??0
<i>Placoziphius</i>	01101	11111	0???1	?????	????1	1??0?	001210
<i>Orycterocetus</i>	01101	11111	02?21	22011	00?00	11101	001210
<i>Physeterula</i>	211?1	111??	02??1	????1	00??2	?1200	?0?210
<i>Aulophyseter</i>	21102	11111	02121	220?1	01??2	21200	a11?10
<i>Physeter</i>	22102	11111	02121	22011	01a11	21300	011210
IRSNB M.1937	?11?1	??01?	?2?2?	?????	????2	1120?	01????
<i>Thalassocetus</i>	3?1?1	10??2	11?21	?????	?????	??101	?01?20
<i>Scaphokogia</i>	31211	10102	1?1??	221??	?1?10	2100?	11????
<i>Praekogia</i>	?12?1	10??2	11?01	?????	???1?	??011	1?1201
<i>Kogia</i>	31212	10102	1b121	22111	01a11	b1011	101201

Appendix 2

List of characters used in the cladistic analysis. The 23 first characters are taken from BIANUCCI & LANDINI, 2006 (modified where noted).

- 1. Size of skull (expressed as condylobasal length) (BIANUCCI & LANDINI, 2006): 0, 50-90 cm; 1, 90-120 cm; 2, >120 cm; 3, <50 cm.
- 2. Supracranial basin of the skull (BIANUCCI & LANDINI, 2006): 0, absent; 1, present; 2, extended onto the whole dorsal surface of the rostrum.

- 3. Antorbital notch (modified from BIANUCCI & LANDINI, 2006): 0, absent; 1, present; 2, transformed into a very narrow slit.
- 4. Maxillae, premaxillae and vomer, all reaching the tip of the rostrum which is not formed only by the premaxillae (BIANUCCI & LANDINI, 2006): 0, no; 1, yes.
- 5. Frontal-maxilla suture, with skull in lateral view (modified from BIANUCCI & LANDINI, 2006): 0, forming an angle < 15° from the axis of the rostrum; 1, 15-35°; 2, > 35°. It should be noted that this character varies with age in *Physeter* (see KELLOGG, 1925).
- 6. Right premaxilla (BIANUCCI & LANDINI, 2006): 0,

- posteriorly extended as the left premaxilla; **1**, more posteriorly extended than the left premaxilla.
7. Right premaxilla (modified from BIANUCCI & LANDINI, 2006): **0**, not widened posteriorly; **1**, posterior extremity of the right premaxilla laterally widened, occupying at least one third of the width of the supracranial basin.
 8. Left premaxillary foramen very small or absent (BIANUCCI & LANDINI, 2006): **0**, no; **1**, yes.
 9. Increase in size of the right premaxillary foramen (BIANUCCI & LANDINI, 2006): **0**, no; **1**, yes.
 10. Lack of nasals (BIANUCCI & LANDINI, 2006): **0**, both nasals present; **1**, one nasal absent; **2**, both nasals absent.
 11. Presence of a sagittal crest (BIANUCCI & LANDINI, 2006): **0**, absent; **1**, present as a shelf covered by the pointed right premaxilla.
 12. Occipital shield (BIANUCCI & LANDINI, 2007): **0**, convex and forming an angle of about 40° from the axis of the rostrum; **1**, as state 0 with an angle of about 60°; **2**, flat or concave forming an angle of about 90°. Most of the dorsal elements of the supracranial basin are damaged in *Diaphorocetus poucheti*; therefore the supraoccipital shield might have been originally more erected. For *Aulophyseter morricei*, a second specimen displays a supraoccipital shield more elevated than in the holotype; the latter might have undergone some abrasion (KIMURA *et al.*, 2006).
 13. Fusion of lacrimal and jugal (BIANUCCI & LANDINI, 2006): **0**, no; **1**, yes.
 14. Temporal fossa (BIANUCCI & LANDINI, 2006): **0**, anteroposteriorly elongated (width/height > 1); **1**, not anteroposteriorly elongated (width/height = 1); **2**, anteroposteriorly compressed (width/height < 1).
 15. Zygomatic process of squamosal in lateral view (BIANUCCI & LANDINI, 2006): **0**, 'L'-shaped with dorsal margin ventrally bending in its posterior portion; **1**, triangular, with dorsal margin dorsally bending in its posterior portion.
 16. Anterior bullar facet of the periotic (BIANUCCI & LANDINI, 2006): **0**, very anteroposteriorly elongated; **1**, reduced; **2**, absent or very small.
 17. Accessory ossicle of the tympanic bulla (BIANUCCI & LANDINI, 2006): **0**, absent; **1**, present; **2**, present and partially fused with the anterior process.
 18. Posterior extension of the posterior process of the periotic parallel to the general plane of the bone and not ventrally orientated (BIANUCCI & LANDINI, 2006): **0**, no; **1**, yes.
 19. Involucrum of the tympanic bulla with an evident central concavity, visible in ventral and medial views, due to the marked pachyostosis of its anterior and posterior portion (BIANUCCI & LANDINI, 2006): **0**, no; **1**, yes.
 20. Loss of dental enamel (BIANUCCI AND LANDINI, 2006): **0**, no; **1**, yes. KIMURA *et al.* (2006) suggest that enamel is absent in *Aulophyseter morricei*, contradicting KELLOGG (1927).
 21. Size of teeth (greatest diameter of root expressed as percentage of the condylobasal length of skull) (BIANUCCI & LANDINI, 2006): **0**, < 3%; **1**, > 3%. Considering the strong heterodonty in *Zygorhiza* this character is restricted to single-rooted teeth.
 22. Upper tooth row (BIANUCCI & LANDINI, 2006): **0**, deep alveoli; **1** alveoli shallow or absent.
 23. Ventral position of the mandibular condyle (BIANUCCI & LANDINI, 2006): **0**, no; **1**, yes.
 24. Long axis of the skull (CRANFORD, 1999): **0**, roughly parallel to the long axis of the body (perpendicular to the surface of the occipital condyles); **1**, projected ventrally.
 25. Dorsal exposure of the maxilla on the rostrum (modified from KAZÁR, 2002): **0**, exposed on most of the length of the rostrum, narrower than the premaxilla at some levels; **1**, wider than the premaxilla all along; **2**, exposure limited to less than half the rostrum length.
 26. Anteroposterior level of right premaxillary foramen: **0**, distinctly anterior to antorbital notch; **1**, slightly anterior to antorbital notch; **2**, same level or posterior to antorbital notch.
 27. Asymmetry of the bony nares: **0**, absent or reduced; **1**, strong, left bony naris significantly larger than right naris.
 28. Number and size of dorsal infraorbital foramina, in the area of the right antorbital notch and posteriorly: **0**, small to moderate size foramina, at least three-four; **1**, three large foramina; **2**, two large foramina; **3**, one large foramen (maxillary incisure).
 29. Transverse level of right maxillary crest laterally limiting the supracranial basin: **0**, median to the antorbital notch; **1**, at the level of the antorbital notch or lateral.
 30. Right maxilla reaching or crossing the sagittal plane of the skull on the posterior wall of the supracranial basin: **0**, no; **1**, yes.
 31. Projection of lacrimal-jugal between frontal and maxilla on preorbital process (seen in lateral view): **0**, short or absent; **1**, long.
 32. Preorbital process considerably lower than the elevated dorsolateral margin of the rostrum base: **0**, no; **1**, yes.
 33. Zygomatic process of the squamosal: **0**, elongated, length more than two times higher than height at mid-length; **1**, more robust and/or shorter, length no more than two times higher than height at mid-length.
 34. Falciform process of the squamosal: **0**, contacting the corresponding pterygoid; **1**, forming a thin isolated plate; **2**, reduced to a simple peg or absent.
 35. Postglenoid process of the squamosal: **0**, significantly ventrally longer than post-tympanic process; **1**, roughly same ventral extent as post-tympanic process.
 36. In lateral view of the skull, wide notch posterior to the postglenoid process of the squamosal for the enlarged posterior process of the tympanic: **0**, no; **1**, yes.