

Revised phylogeny of the Physeteridae (Mammalia: Cetacea) in the light of *Placoziphius* VAN BENEDEN, 1869 and *Aulophyseter* KELLOGG, 1927

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Abstract

A recently found Middle Miocene sperm whale skeleton from Stotzing (Burgenland, Austria) represents *Placoziphius duboisii* VAN BENEDEN, 1869, described from the Middle Miocene Crag d'Anvers (Antwerp, Belgium). The high and concave occipital shield, the anteroposteriorly constricted temporal fossa, the massive jugo-lacrimal, the ventrally shifted, small orbits as well as the rudimentary upper teeth lacking enamel are regarded as apomorphic characters of the species, whereas the absence of an elevated lateral wall of the supracranial basin is interpreted as primitive. *Pl. duboisii* is placed into the newly defined subfamily Physeterinae.

Aulophyseter morricei KELLOGG, 1927 and *A. mediatlanticus* (COPE, 1895) are recognized as representatives of a separate evolutionary clade and a new subfamily Aulophyseterinae is introduced for them. Hoplocetinae CABRERA, 1926 are regarded *incertae sedis* because the type genus of this rank is only known from teeth.

Key-words: *Placoziphius*, Physeteridae, Cetacea, phylogeny, systematics, Miocene

Résumé

Un squelette de cachalot récemment trouvé dans des dépôts du Miocène moyen à Stotzing (Burgenland, Autriche) appartient à *Placoziphius duboisii* VAN BENEDEN, 1869, espèce décrite sur base de matériel provenant du Crag d'Anvers (Antwerp, Belgique) d'âge miocène moyen. Le bouclier occipital haut et concave, la fosse temporale rétrécie antéropostérieurement, le jugo-lacrimal massif, les petites orbites déplacées ventralement ainsi que les dents supérieures rudimentaires sans émail sont considérés comme des caractères apomorphiques de l'espèce tandis que le bassin supracranial sans paroi latérale élevée est interprété comme un caractère primitif. *P. duboisii* est placé dans la nouvelle sous-famille des Physeterinae.

Aulophyseter morricei KELLOGG, 1927 et *A. mediatlanticus* (COPE, 1895) sont considérés comme représentant un clade évolutif séparé et placés dans la sous-famille des Aulophyseterinae redéfinie. Les Hoplocetinae CABRERA, 1926 sont regardés comme *incertae sedis* parce que le genre-type de cette sous-famille n'est connu que sur base de dents.

Mots-clefs: *Placoziphius*, Physeteridae, Cetacea, phylogénie, systématique, Miocène

Zusammenfassung

Ein neulich gefundenes Pottwal-Skelett aus Stotzing (Burgenland, Austria; Mittleres Miozän) erwies sich als Angehöriger der Art *Placoziphius duboisii* VAN BENEDEN, 1869, ursprünglich beschrieben aus dem Mittleren Miozän von dem Crag von Antwerpen (Belgien). Das hohe und konkave Supraoccipitale, die anterio-posterior verkürzte Fossa temporalis, das kräftige Jugo-Lacrimal, die kleine und in ventrale Richtung verschobene Orbitalregion sowie die rudimentären Oberkiefer-Zähne ohne Schmelz werden für apomorphische Merkmale angesehen; während das supracraniale Becken ohne herausragende Seitenwand als primitiv interpretiert wird.

Aulophyseter morricei KELLOGG, 1927 und *A. mediatlanticus* (COPE, 1895) sind Vertreter einer gesonderten phylogenetischen Linie, weshalb sie in die hiermit einzuführende Subfamilie Aulophyseterinae eingeordnet werden. Hoplocetinae CABRERA, 1926 wird für *incertae sedis* betrachtet, da die Typus-Gattung dieser Subfamilie nur von Zähnen bekannt ist.

Stichworte: *Placoziphius*, Physeteridae, Cetacea, Phylogenie, Systematik, Miozän

Introduction

A well preserved, albeit incomplete sperm whale skeleton was excavated from the Middle Miocene sands of Stotzing (Burgenland, Austria) in 1998 and the material became available for study in 1999 and 2000. The new find represents VAN BENEDEN's species *Placoziphius duboisii* and exhibits several characters that are not observable in the holotype.

Placoziphius duboisii VAN BENEDEN was described in 1869 as a new species and genus of ziphiid beaked whales (VAN BENEDEN, 1869). Although ABEL (1905a, 1905b) recognized that the species belonged to the sperm whale family, subsequently there were few authors to consider the species within the Physeteridae (KELLOGG, 1928; MCKENNA & BELL, 1997).

In the family Physeteridae *sensu lato* only one sperm whale and two pygmy sperm whale species survive, but physeterids have an extensive paleontological record starting with the Late Oligocene *Ferecetotherium kelloggi* MCHEDLIDZE, 1970 from Azerbaidzhan (BARNES, 1985), and the Early Miocene *Idiorophus patagonicus* (LYDEKKER, 1894) and *Diaphorocetus poucheti* (MORENO, 1892) from Patagonia. Physeterids rapidly diversified

in the Middle and Late Miocene as reflected by the numerous taxa described from Europe, North and South America and Australia (e. g. DU BUS, 1872; BRANDT, 1873; CHAPMAN, 1918; DAL PIAZ, 1916; KELLOGG, 1925; KELLOGG, 1927; BARNES, 1973; PILLERI, 1986; DE MUIZON, 1988). However, many of the taxa were based on isolated teeth, and there is only a handful of fossil species for which well preserved skull material is available.

Phylogenetic relationships between the known sperm whale taxa are poorly understood. The generally accepted systematics of the Physeteridae *sensu stricto* is based on characters of the dentition: the Physeterinae are defined by the loss of enamel and by the reduction of upper teeth (WINGE, 1921; DE MUIZON, 1990); the Hoplocetinae are defined by the presence of enamel and by the upper teeth being rooted in the skull (WINGE, 1921; MCLEOD, 1988). AS DE MUIZON (1990) pointed out, the Hoplocetinae are thus united by plesiomorphic features. Although the Physeterinae are defined by synapomorphies, size reduction of the upper teeth is a tendency that might well be connected with food and prey capturing methods. The benefits of enamel loss in marine mammals is not yet clear, but this feature has also evolved in the unrelated Odobenidae (DEMÉRÉ, 1994). The small enamel cap of the tusks and of the postcanines of the walrus, *Odobenus rosmarus*, is quickly worn away during ontogeny. The teeth of the holotype of a long-snouted dolphin, *Ziphiodelphis abeli*, have lost their enamel-covered crowns by natural wear (DAL PIAZ, 1916; PILLERI, 1985 and DE MUIZON, 1990, p. 314). Consequently, the idea of basing the subfamilies solely on dental characters is hereby rejected.

The main driving force of physeterid evolution (including the pygmy sperm whales) was the development and enlargement of the spermaceti organ, the junk and related structures which affected the whole skull structure. Consequently, true phylogenetic relationships among taxa are best understood by studying evolutionary changes of the supracranial region.

The aim of this paper is to redescribe the Middle Miocene sperm whale, *Placoziphius duboisii* VAN BENEDEEN, 1869 and review some physeterid taxa in an attempt to resolve some of the systematic problems within the Physeteridae. The relationships of physeterids to other odontocete groups is not discussed here.

Abbreviations of Institutions

USNM – United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.; IRScNB – Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium.

Methods and Material

The new specimen of *Placoziphius duboisii* was found and collected by Gerhard Wanzenböck in the sandpit of the Mayer GmbH, Stotzing (Leitha Mt., Burgenland, Austria) in March and May, 1998. The preparation in-

cluded treatment with water soluble glue (Leifa PV/H Holzleim standard by Henkel) and oxylin nitro Mattlack supplied by Reichold-Chemie. The glue was absorbed by the bone substance and ensured stability, the sand was subsequently removed. All preparation was performed by the collector.

Comparative material studied included *Aulophyseter morricei* KELLOGG, 1927 [Shark Tooth Hill Bonebed, California, USNM 11230 holotype]; *Scaldicetus mortezelensis* DU BUS, 1872 [Middle Miocene, Antwerp (Belgium), IRScNB Ct.M. 523 holotype]; *Physeterula dubusii* VAN BENEDEEN, 1877 [Middle Miocene, Antwerp (Belgium), IRScNB Ct.M. 528 cotype]; *Thalassocetus antwerpiensis* ABEL, 1905 [Middle Miocene, Antwerp (Belgium), IRScNB Ct.M. 525 syntype 1, IRScNB Ct.M. 526 syntype 2]; *Orycterocetus crocodilinus* COPE, 1868 [Calvert Formation, Maryland, USNM 14729, USNM 14730, USNM 22926]; *Paracetus mediatlanticus* COPE, 1895 [St. Marys Formation, Maryland, USNM 9463 holotype]; the recent *Kogia breviceps* DE BLAINVILLE, 1838 [USNM 504318]; *K. simus* OWEN, 1866 [USNM 504336]; and *Physeter macrocephalus* LINNAEUS, 1758 [USNM 301634 adult male, USNM 353051 probably adult female, USNM 35315 juvenile]. Comparisons of other species were based on illustrations of the original descriptions.

Age and taphonomy of the Stotzing sperm whale

The geological setting of the site is shown in Fig. 1. The age of the sand is Middle Miocene, Badenian Stage (13–16.4 m.a. according to RÖGL, 1998), probably Middle Badenian (FUCHS & GRILL, 1984 and P. Müller, pers. comm.) which can be correlated with the end of the Langhian of the standard scale (RÖGL, 1998). The specimen was found in a layer of calcareous sand poor in fossils. Fragments of small *Pecten* shells, and one small shark tooth (*Carcharias* sp.) were also found in the layer.

The whale skeleton was lying in a horizontal plane perpendicular to the wall, with the rostrum facing the working area. Four (cervical or thoracic?) vertebrae were attached to the skull: one pressed into the temporal fossa, three in the occipital shield. A bony mass including some (thoracic?) vertebrae and rib fragments were situated behind the skull (unprepared). This was followed by nine lumbar vertebrae, presumably in anatomical sequence. Three additional vertebrae, destroyed during excavation, were lying dislodged from their anatomical positions (Fig. 1). It is possible that some more vertebrae were preserved but remained undetected during excavation. The vertebrae either lost their processes or the ends of their processes were broken off. Presumed maxillary teeth were found close to the skull; however, neither mandibular teeth nor fragments of the lower jaws were recovered. The caudal region of the skeleton, including the pelvic bones, were missing; likewise, no hyoid nor flipper bones were found.

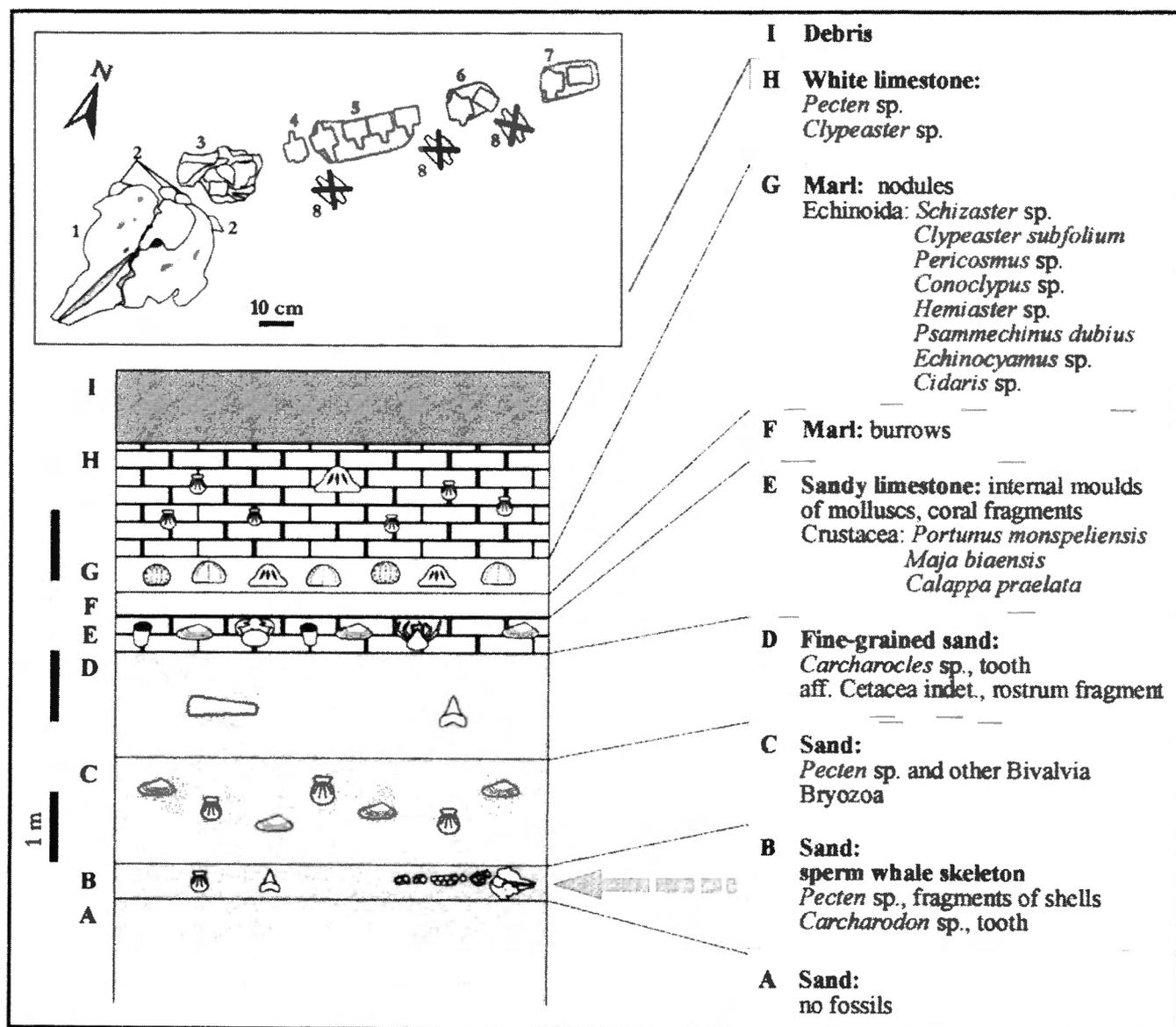


Fig. 1 — Geological setting of the site at Stotzing.

Insertion: Diagram showing main skeletal elements of the Stotzing specimen of *P. duboisii* VAN BENEDEEN, 1869 as they were exposed in the site. 1 — skull; 2 — ?cervical and two thoracic vertebrae appressed to the skull; 3 — bony mass containing vertebral and rib fragments; 4-7 — blocks containing lumbar vertebrae; 8 — vertebrae destroyed during excavation.

Based on field sketches and comments of G. Wanzenböck.

The skull was more or less complete, with the tip of the rostrum missing. The posterior face of the skull underwent serious damage during the taphonomic process. The vertebrae that were pressed into the brain case destroyed most of the occipital shield. Bones surrounding the narial openings, and the maxillary and premaxillary foramina were affected by erosion. An extensive, oblique breakage involved the left side of the rostrum and the right side of the supracranial basin. The left side of the skull was much better preserved than the right side, exhibiting nearly all elements intact. The lateral margin of the proximal part of the rostrum has deep notches on the left side and was eroded on the opposite side, but the distal part remained

almost intact. The ventral surface of the maxilla was eroded, exposing the maxillary canal on both sides of the rostrum base. The exposed part extended farther posteriorly on the right side. Both pterygoid hamuli were twisted towards the right side of the skull.

SCHÄFER (1962) discussed the disintegration stages of drifting marine mammal bodies. Based on his observations it seems likely that the Stotzing specimen underwent extensive decomposition while floating. It probably sank to the bottom after its mandibles, flippers and the caudal region of its vertebral column had already been lost. More anterior parts of the vertebral column plausibly were held together by the slowly decomposing body tissue. Con-

nection with the skull was probably maintained by the strong trachea. At this stage at least one of the tympano-periotic complexes was still retained.

Neither scratches nor other marks indicating scavenger action could be identified on the bones, suggesting either rapid burial or an inhospitable seafloor lacking a rich bottom-dwelling fauna. This latter hypothesis is supported by the lack of invertebrate fossils in the vicinity of the whale skeleton.

Decomposition of the soft tissues progressed on the seafloor. As articulations between the bones were lost, vertebrae could be trundled by water movements. Incomplete condition of the vertebrae and the entire right side of the skull, as well as the overall eroded appearance of the bone surfaces, suggest that the skeleton was exposed for an extended period of time before burial was completed. Breakage of the skull and distortion of the hamular processes are undoubtedly results of forces acting during burial.

Redescription of *Placoziphius duboisii* VAN BENEDEN, 1869

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1867

Superfamily Physeteroidea GRAY, 1821

Family Physeteridae GRAY, 1821

Subfamily Physeterinae GRAY, 1821

Genus *Placoziphius* VAN BENEDEN, 1869

1864 – *Placocetus* genre nouveau – VAN BENEDEN, p. 8.

Emended diagnosis of genus – same as species.

Type species – *Placoziphius duboisii* VAN BENEDEN, 1869

Placoziphius duboisii VAN BENEDEN, 1869

1904 – *Placoziphius duboisi* Van Beneden – TROUËSSART, p. 776.

1905a – *Thalassocetus antwerpiensis* n. spec. – ABEL, p. 70-74, figs. 7-8. (*partim*. 1, IRScNB Ct.M. 525).

Emended diagnosis of species – Medium-sized physeterid having the following set of characters separating it from all known species of the family: occipital shield moderately arched in posterior view, concave in lateral view; supracranial basin without elevated lateral wall; premaxillae not exceeding maxillae in width at any given point; distal portion of rostrum narrow; upper teeth rudimentary, lacking enamel and lodged in the gum.

Holotype – IRScNB Ct.M. 530, fragments of cranium and atlas.

Type locality – Edegem (Antwerp), Belgium.

Age – Burdigalian (Anversian), ?Middle Miocene.

Referred specimens – *Placoziphius duboisii* VAN BENEDEN, 1869 from Stotzing (Burgenland, Austria), housed in the private collection of G. Wanzenböck, Bad Vöslau (Austria); *Thalassocetus antwerpiensis* ABEL, 1905, IRScNB Ct.M. 525 syntype 1, *partim*. 1.

Redescription of the holotype – It is not intended to redescribe the specimen completely. The original description (VAN BENEDEN, 1869) will be supplemented and remarks will be given on some of his conclusions.

The supracranial basin is highly developed. VAN BENEDEN's reconstruction (pl. 1, fig. 3 and pl. 2 in VAN BENEDEN, 1869) is misleading; the cranium is not as high vertically, and the posterior wall of the supracranial basin is not as vertical as the illustrations indicate. The maxilla forms no well-marked lateral wall for the supracranial basin, but the lateral margin of the maxilla is slightly elevated anterior to the antorbital notch.

The rostrum is slightly wider at base than long (length measured from level of antorbital notches to estimated location of tip). The original illustrations (pl. 1, figs. 1-2 in VAN BENEDEN, 1869) suggest that the rostrum tapers gradually from base to tip, but this interpretation is incorrect. The preserved parts of the original lateral margins of the rostrum clearly show that the widest point of the rostrum was situated ca. 5 cm anterior to the level of the antorbital notches, and from this point the rostrum narrowed abruptly toward the distal end.

VAN BENEDEN stated (p. 7; pl. 1, fig. 2 in VAN BENEDEN, 1869) that the left premaxillary foramen is located more anterior than the right one but this is not true. A careful look at the bone revealed that the hole interpreted by him as the left premaxillary foramen is minor damage and only the right premaxillary foramen existed in the living animal (Pl. 1, Fig. 1), as is typical of all physeterids.

The exoccipitals are large, projecting ventrolaterally, but they in all probability do not conceal the zygomatic processes in posterior view. None of the tympano-periotic complexes have been preserved. The squamosal exhibits a series of radiating channels on its ventral surface. The preserved fragment of the paroccipital process is formed of a thick bone. The jugular notch is deep. The zygomatic processes are small, triangular, similar in shape to the Stotzing specimen but they are slightly more robust.

The frontal and maxilla are considerably thickened in the region of the supraorbital process, and the whole process slopes laterally. On the ventral aspect of the rostrum the vomer is exposed between the maxillae for about 18 cm long. Palatines and pterygoids are lacking (Pl. 1, Fig. 2).

Teeth are not preserved with the holotype skull. The palatal surface of the rostrum exhibits neither alveoli nor an alveolar groove for maxillary teeth, but shallow and short longitudinal grooves for blood vessels can be seen. If present, maxillary teeth must have been lodged in the gum as in the present sperm whale.

The atlas of the holotype is described by VAN BENEDEN (1869, p. 10). Skull measurements for the holotype and the Stotzing specimen are given in Table 1.

Table 1

Skull measurements of *Placoziphius duboisii* VAN BENEDEEN, 1869 (in cm). (e estimation; + minimum value.)

	Holotype	Stotzing specimen
Total length of skull estimated (supraoccipital to tip of rostrum)	67	67
Total length of skull as preserved (supraoccipital to tip of rostrum)	58+	52
Total length of skull as preserved (transverse crest of supraoccipital to tip of rostrum)	—	52
Length of rostrum as preserved (antorbital notches to extremity)	40	33
Breadth of rostrum at antorbital notches	34e	33
Breadth of rostrum at enlargement in front of antorbital notches	35e	34
Greatest breadth of skull across postorbital processes of frontal	—	43
Greatest breadth of skull across zygomatic processes of squamosals	—	34e
Height of skull (basioccipital to transverse crest of supraoccipital)	—	28
Height of skull (base of exoccipital to transverse crest of supraoccipital)	—	33
Height of skull (hamular process of pterygoid to transverse crest of supraoccipital)	—	22
Length of right premaxilla as preserved, in a straight line	54	51
Breadth of right premaxilla at level of narial openings	ca. 9	8
Greatest breadth of right premaxilla posterior to narial openings	ca. 14,5	15
Greatest anteroposterior diameter of supraorbital process of frontal at extremity (=external measurement)	—	12
Least anteroposterior diameter of supraorbital process of frontal at extremity (=internal measurement)	—	6
Greatest dorsoventral extension of preorbital portion of supraorbital process of frontal	4,8+	10
Least breadth of supraoccipital between temporal fossae	—	25
Distance across skull between outer margins of exoccipitals	34e	34
Distance across basicranium between opposite foramen ovale	—	13,2
Length of vomer exposed on ventral face of rostrum as preserved	18	27
Length of zygomatic process of squamosal	6,5e	6
Inner margin of left premaxilla to inner margin of left antorbital notch	—	16,5

Description of the Stotzing specimen – The skull is more or less complete, exhibiting many important characters of the dorsal and lateral aspects. The tip of the rostrum is missing. The dorsal narial openings are eroded away resulting in that the holes visible in the dorsal view are not the dorsal narial openings themselves, but cross-sections of the narial passages. The lateral wall of the left narial passage is broken inward, resulting in an additional false opening. On the right side of the skull, the posterior maxillary foramen is lost because the dorsal vault of the passage leading to this foramen is missing. In other words, the shallow fissure originating from an anterior

maxillary foramen and being directed posteriorly, is in fact the ventral surface of the tunnel connecting the above mentioned foramen and the posterior maxillary foramen. The difference in size of the maxillary fissures and in the number of foramina between both sides of the skull are due to the fact that part of the maxilla above the passages of the infraorbital system has broken in on the left side.

The posterior face of the skull is poorly preserved. The foramen magnum and the occipital condyles are lacking. Moreover, a major part of the supraoccipital crest is weathered away. The description of characters not involved in cranial asymmetry was mainly based on the

better preserved left side. Vertebrae attached to the occipital region were not removed. Moreover, a bony mass containing some vertebrae and fragments of three ribs could not be freed from the sand.

Due to the special conditions of preservation and preparation of the skull, sutures are indistinct in places. Borders of the bones were determined from fine depressions and differences in the bone surfaces.

SKULL, DORSAL VIEW (Pl. 2, Fig. 1 and Pl. 3, Fig. 1) – Original length of the rostrum is unknown. It was most probably approximately as long as its width at the base. The maxilla broadens in front of the antorbital notch. The widest point of the rostrum is situated ca. 5 cm anterior to the antorbital notch. The extremity of the rostrum (as far preserved) is composed of both maxillae and premaxillae. The mesorostral gutter is open along the whole length of the preserved rostrum. The widest part of the mesorostral gutter is situated 21 cm anterior to the anterior margin of the right narial passage. At this point, width of the mesorostral gutter is 3 cm.

The antorbital notch is deep and directed anteriorly. The anterior portion of the supraorbital process approaches the rostral part of the maxilla, thus the opening of the antorbital notch becomes slightly narrowed. The antorbital process is mediolaterally narrow.

The premaxillae are not wider than the maxillae throughout their lengths. Anteriorly the maxillae and premaxillae seem to be more or less symmetrical in outline. Posteriorly, at the anterior margin of the supracranial basin, the left premaxilla becomes narrower than the right. The left premaxillary foramen is lost. In and posterior to the narial region, there is a striking difference in size and shape between the left and right premaxillae. The ascending process of the right premaxilla extends posteriorly to the supraoccipital crest. Posterior termination of the left one is uncertain, in all probability it does not extend beyond the anterior margins of the nares (see restoration, Pl. 3, Fig. 1). The horizontal expansion of the right premaxilla is greatest posterior to the narial openings. Presence or absence of the nasal is uncertain. Relation of the left maxilla and right premaxilla posterior to the narial openings is not clear. It seems probable that the right premaxilla is in contact with the left maxilla, so that the frontal is completely absent in the supracranial basin. It is also possible that the right premaxilla not only contacts the left maxilla but slides over it.

The left narial passage is wider than the right one, but exact size difference between the narial openings is unknown. The mesethmoid separating the left and right narial passages is oblique, posteriorly it is directed toward the left side of the skull. On its anterior portion the mesethmoid forms an oblique plate between both premaxillae. It does not protrude forward and upward significantly which can be due to erosion of the bone.

There is no facial crest between the nares and the vertex. The supracranial basin is greatly developed. The maxillae are very large and massive bones, forming the major portion of the base of the rostrum and the supracranial basin. The ascending processes of the maxillae are

expanded backward to such an extent that they reach (and partially form) the supraoccipital crest. The maxillae do not form a supraorbital crest, thus, the supracranial basin does not have an elevated lateral wall.

All foramina are large. The posterior maxillary foramina are located close to the supraoccipital crest. The anterior maxillary foramina are represented on each side by a separate foramen located at the level of, or slightly posterior to, the posterior margin of the nares, as well as by a fissure in which a pair of passages from the infraorbital system opens. This maxillary fissure is located at the level of the anterior margin of the nares and at the level of the antorbital notches. The illustration shows the foramina restored (Pl. 3, Fig. 1).

VENTRAL VIEW (Pl. 2, Fig. 2 and Pl. 3, Fig. 2) – The greatest width is measured between the preorbital processes. The zygomatic processes of the squamosals do not flare laterally from the braincase. There is no trace of glenoid fossa on the squamosals.

On each side of the ventral aspect of the rostrum a continuous groove can be seen. These grooves correspond to the maxillary canals exposed due to erosion of the bone and do not necessarily indicate the presence of an alveolar groove. The ventral or palatal surface of the rostrum is formed largely by the maxillae. They are separated by a strip of the vomer, the exact extent of which is not clear. Restoration of the exposed vomer in Pl. 3, Fig. 2 is a composite from the holotype and the Stotzing specimen. Lateral to the vomer, the maxilla is hollowed out, forming a large concave area in front of the anterior infraorbital foramen. The infraorbital system opens with well separated foramina on each side. The anterior orifice seems to be entirely enclosed in the maxilla. Boundaries of the posterior infraorbital foramen are unknown. From the anterior infraorbital foramen a canal extends upward through the maxilla and opens on the dorsal face of the skull in the anterior maxillary foramen. The canal leading upward from the posterior infraorbital foramen diverges and opens in all maxillary foramina of the dorsal surface of the skull.

Form and extent of the fused jugo-lacrimal is unknown. A postero-dorsal process of the jugo-lacrimal is lacking. The optic canal is wide throughout its length and opens slightly distally. Exact location and form of the palatine and pterygoid is not known. In all probability the pterygoid is not expanded laterally since the alisphenoid does not seem to be overridden by this bone. The hamular processes are relatively large (for a sperm whale) and broad, triangular in shape and completely conceal the narial passages from a ventral view. Both hamular processes project backward beyond the level of the furrow for the optic nerve. The internal edges of the hamular processes are in contact at their anterior ends only and in their present state diverge posteriorly.

The alisphenoid appears to be large and laterally expanded but again, exact boundaries are unclear. Morphology of the optic canal and the alisphenoid of the Stotzing specimen look similar to the same structures of *Idiophyster merriami*. There is no groove originating from the foramen ovale.

The paroccipital processes, if identified correctly, are relatively small. The jugular notch is not distinguishable on either of the exoccipitals.

LATERAL VIEW (Pl. 4, Fig. 1) – The occipital shield is vertical and slightly concave when viewed from the side. The supraoccipital crest is elevated and robust. The supracranial basin is moderately deep. The vertical distance between the highest point of the supraoccipital shield and the lowest point of the exoccipital is much larger than the horizontal distance between the former point and the antorbital notch.

The temporal fossa is vertically expanded i.e. antero-posteriorly constricted. The zygomatic process of the squamosal is an elongated, slender bone, triangular in shape and projects anteriorly to the midline of the orbit. The zygomatic process does not come in contact with the postorbital projection of the supraorbital process of the frontal. The orbit is relatively small and set ventrally relative to the level of the mouth. The supraorbital process is extremely thick, its dorsoventral expansion measuring 70 mm and the whole process sloping laterally. The jugo-lacrimal forms a large, thick and distinct process (= preorbital process) projecting posteroventrally but not reaching posteriorly to contact the zygomatic process of the squamosal.

Though there is no distinct posterolateral wall of the supracranial basin, the dorsal surface of the maxilla is deflected upward in its posterior region. Anterior to the antorbital notch the maxilla is slightly elevated, contributing to the formation of the anterolateral demarcation of the supracranial basin. The distal part of the rostrum is flat. The lateral aspect of the rostrum as far as preserved is formed entirely by the maxilla.

POSTERIOR VIEW – From the slope of the preserved part on the left side it seems very likely that the supraoccipital crest was not highly arched (Pl. 4, Fig. 2). One can estimate that in the occipital view the skull is higher than wide (height measured between highest point of restored supraoccipital crest and basioccipital; width measured between both temporal fossae) and the ratio is ca. 4:3. The exoccipitals are large, projecting ventrolaterally. They conceal the zygomatic processes when viewed from behind. In the same view it is apparent that the supraorbital process of the frontal projects laterally far beyond the zygomatic process of the squamosal. The occipital shield is only moderately excavated laterally by the temporal fossae.

TYMPANO-PERITIC COMPLEX – Because the tympano-periotic complex has not been removed from the skull, only a very brief description of these elements can be given. The tympano-periotic complex is relatively small as is typical for all physeterids. The bulla is rectangular in ventral view; the sigmoid process is moderately large and has a vertically oriented lateral lip (Pl. 1, Fig. 3).

Around the tympano-periotic bones the squamosal exhibits a series of radiating channels (Pl. 1, Fig. 3). As FRASER & PURVES (1960) pointed out, in recent *Physeter* (and *Kogia*) the mastoid or posterior process of the periotic is not interdigitated with the pars mastoidea of the

Table 2

Measurements of the preserved vertebrae of the Stotzing specimen of *Placoziphius duboisii* VAN BENEDEEN, 1869 (in mm).

Vertebrae, in sequence as they were found	Length of centrum	Greatest width of vertebral epiphysis	Greatest height of vertebral epiphysis
Vert. thorac.	41	81	49
Vert. thorac.	ca. 55	63	52
Vert. lumb.	86	73	58
Vert. lumb.	93	77	56
Vert. lumb.	91	78	54
Vert. lumb.	95	78	55
Vert. lumb.	100	84	63
Vert. lumb.	108	77	62
Vert. lumb.	108	71	73
Vert. lumb.	96	81	66
Vert. lumb.	83	67	58

squamosal but freely movable between the bones adjacent to it. On the other hand, the same authors stated that two plates of laminated bone can be observed extending from the posterior and outer end of the tympanic. They interpret these plates as the tympanic and periotic elements of the mastoid process. The laminated bone surface observed on the squamosal of the holotype and Stotzing specimen of *Placoziphius duboisii* probably corresponds to the same structure.

TEETH – Seven teeth or tooth fragments were associated with the skull. The two complete teeth measure 43 mm (Pl. 1, Fig. 4d) and 33 mm (Pl. 1, Fig. 4b) in length; relatively small compared to the measurements of the skull. Their small size and slender appearance suggest that they represent some of the upper teeth. This is further supported by the fact that the lower jaws were not found.

It appears that the preserved teeth vary in length, thickness and shape (Pl. 1, Fig. 4). The long axis of the two complete teeth (Pl. 1, Fig. 4b, 4d) is weakly curved from end to end. The preserved parts of the fragments (Pl. 1, Fig. 4a, 4e, 4f, 4g) are more noticeably curved. Only two of the teeth (Pl. 1, Fig. 4e, 4f) are slightly gibbous near the presumed middle and taper to the extremity.

Distinction between the apical portion which could be regarded as the crown and the root is difficult. Among the preserved teeth, there is only one (Pl. 1, Fig. 4b) where the crown is clearly recognizable. Here, the crown is small (comprising about one-third of the total length)

conical, slightly oval in cross section ($7,1 \times 7,4$ mm), its base is obliquely connected to the root. No trace of enamel could be discovered on any of the teeth.

In general appearance the surface of all preserved teeth is strongly corroded. The cement appears as a thick, spongy layer vertically fluted or ridged, but the neck is not bulbous. The fluting can be observed on the presumed crown to a limited extent. Small bumps are also present on all teeth. The dentine is formed in concentric layers and represents a dense substance. The pulp cavity is almost completely closed in each of the teeth, leaving only a narrow hole on the root apices.

VERTEBRAE (Pl. 4, Figs. 3, 4, Table 2) – Total count of the vertebral column is unknown. The two preserved thoracic vertebrae are relatively small and anteroposteriorly short. The dorsal margins of both the anterior and posterior epiphyses are horizontal. The lumbar vertebrae have moderately broad transverse processes.

Description of referred specimen Thalassocetus antwerpiensis, partim. 1 – The supracranial basin is well-developed; the occipital shield is vertically oriented and concave as in the Stotzing sperm whale; the right premaxillary foramen is large; the supraoccipital crest is elevated; the ascending process of the right premaxilla extends posteriorly to reach the supraoccipital crest; the supracranial basin has no well-defined elevated lateral wall posterior to the antorbital notch; the maxilla slopes laterally on the supraorbital region; the exoccipital is large; the zygomatic process is delicate and triangular, its morphology being identical to that of the Stotzing specimen of *Placoziphius duboisii*; the laminated structure of the squamosal is well-marked.

There are two differences between the *partim. 1* of *Thalassocetus antwerpiensis* and both the holotype and the Stotzing specimen of *Placoziphius duboisii*: the skull of the *partim. 1* is significantly smaller, and the supraorbital region does not seem to be extremely thickened in the latter. However, the main part of the orbital region is missing in the *partim. 1* skull of *Thalassocetus antwerpiensis* and thus, this difference should not be overweighted. The size difference might represent sexual dimorphism, as is known for the present-day *Physeter macrocephalus*. In conclusion, the *partim. 1* of *Thalassocetus antwerpiensis* ABEL 1905; should be included in the species *Placoziphius duboisii* VAN BENEDEEN, 1869.

Relationships of *Placoziphius duboisii* VAN BENEDEEN, 1869

DE MUIZON (1990, fig. 5) defined the *Physeteridae sensu stricto* with four synapomorphies: lack of facial crest; marked enlargement of the posterior extremity of the right premaxilla that widens transversally and passes to the left side of the skull; great reduction and loss of the postero-dorsal process of jugo-lacrimal; enlargement of posterior process of petiotic that forms a right angle with the anterior process. Out of these, the first three can be studied in *Placoziphius duboisii* and all of them match the

above diagnosis. As a consequence, *Pl. duboisii* is obviously a member of the *Physeteridae*.

Scaldicetus shigensis and *Sc. mortezelensis* can easily be distinguished from *Placoziphius duboisii* by the unique form of their large upper teeth bearing a small cap of wrinkled enamel; by their sloping occipital shields and anteroposteriorly elongated temporal fossae (Fig. 2). Also, the rostrum of both species of *Scaldicetus* continuously tapers toward its tip. *Diaphorocetus poucheti* and *Aulophyseter rionegrensis* have relatively longer braincases than *Placoziphius duboisii* and sloping occipital shields. Differences are, moreover, the separate alveoli for the upper teeth and the ascending processes of the maxillae that do not reach the occipital shield in *Diaphorocetus poucheti*. *Idiorophus patagonicus* has large, slender upper teeth rooted in separate alveoli and a much more robust rostrum than *Placoziphius duboisii*. *Aulophyseter morricei* and *Paracetus mediatlanticus* clearly differ from *Placoziphius duboisii* in their larger skull sizes and broad premaxillae.

The holotype skull of *Physeterula dubusii* VAN BENEDEEN, 1877 differs from *Placoziphius duboisii* in having a straight or slightly convex occipital shield if viewed laterally. Based on the length of the mandibles it seems that the holotype of *Ph. dubusii* had a significantly longer rostrum than *Pl. duboisii*. *Idiophyseter merriami* KELLOGG, 1925 differs from *Pl. duboisii* in having a slightly convex occipital shield; circular temporal fossae and separate alveoli for the upper teeth. *Thalassocetus antwerpiensis (partim. 2, fig. 8* in ABEL, 1905a) can be separated from *Pl. duboisii* by its more slender and elongated postorbital process and its horizontally flattened supraorbital process. The recent *Physeter macrocephalus* LINNAEUS, 1758 is characterized by a much larger skull size than any other known odontocete. It differs further from *Pl. duboisii* in having a straight, vertical occipital shield (Fig. 2); in having a different rostrum shape and relatively smaller hamular processes; the greatly developed supracranial basin being bounded laterally by a highly elevated maxillary crest as well as the sigmoid process of the tympanic bulla being large but not twisted.

Based on cranial material, *Orycterocetus crocodilinus* appears to stand closest to *Pl. duboisii* among the known taxa. This has been concluded from the high and in lateral view strongly concave occipital shields, anteroposteriorly constricted temporal fossae of both species (Fig. 2c, d) as well as from their rostrum morphology. The narrow distal part of the rostrum is not restricted to these species: *Idiorophus patagonicus* and *Diaphorocetus poucheti* also show this feature. In the latter species, however, the rostrum tapers from its widest point toward the narrow portion in an almost straight line, whereas in *Orycterocetus crocodilinus* and *Placoziphius duboisii* there is a slight or marked concavity in the lateral margin of the corresponding rostral part.

A number of differences confirm that *O. crocodilinus* and *Pl. duboisii* belong to different genera. *Pl. duboisii* is more progressive in that its upper teeth were no longer

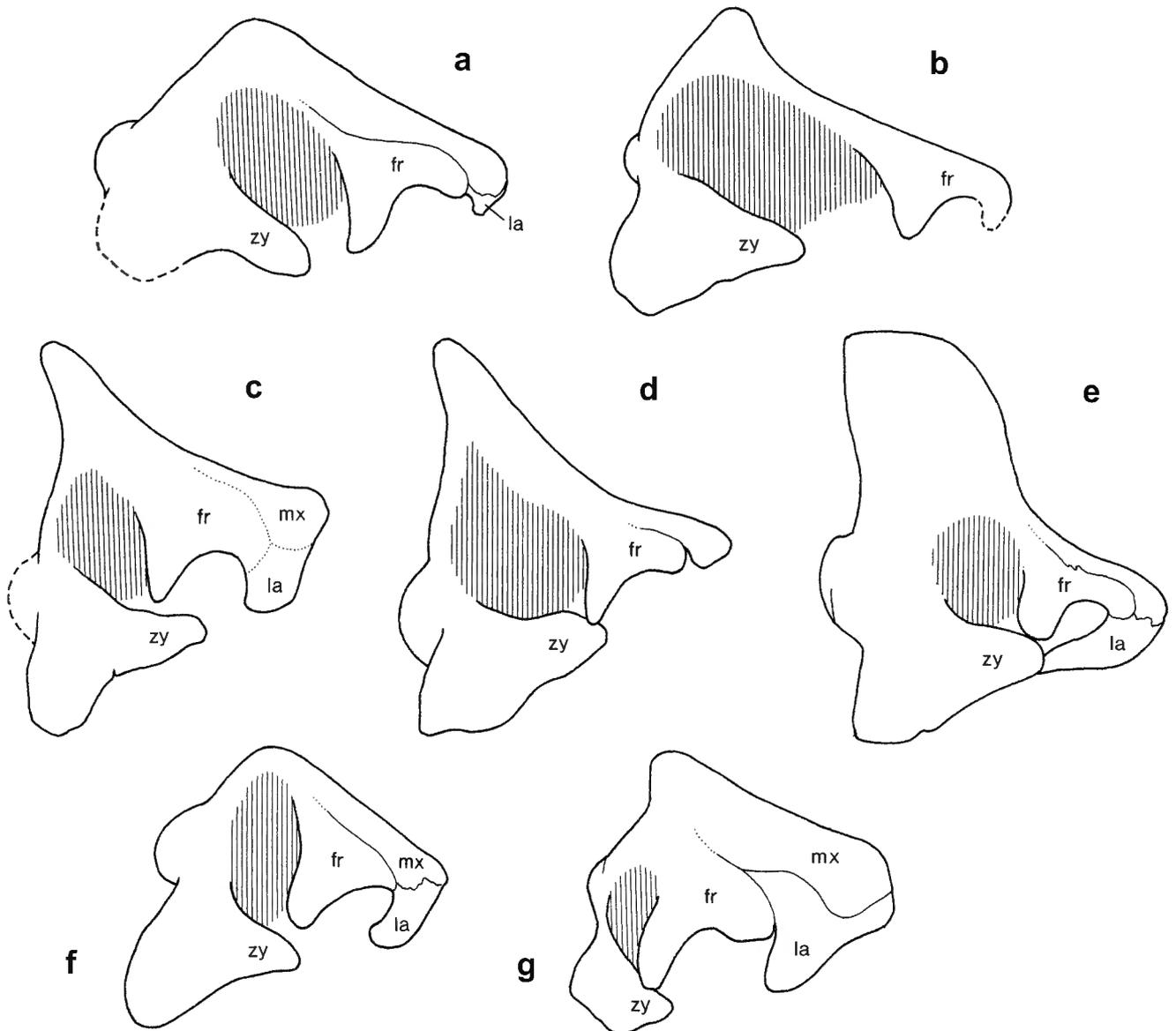


Fig. 2 — Zygomatic process of the squamosal (zy), temporal fossa (shaded) and orbital region (la – jugo-lacrimal; fr – frontal; mx – maxilla) in some physeterid species: a – *Diaphorocetus poucheti* (redrawn from pl. 10 in MORENO, 1892 and modified according to fig. 10 in CABRERA, 1926); b – *Scaldicetus shigensis* (drawing based on left side of skull, fig. 6b in HIROTA & BARNES, 1994); c – *Placoziphius duboisii* (based on left side of skull of the Stotzing specimen); d – *Orycterocetus crocodilinus* (drawing based on pl. 24 in KELLOGG, 1965); e – *Physeter macrocephalus*; f – *Aulophyseter morricei* (drawing based on fig. 1, pl. 5 in KELLOGG, 1927); g – *Kogia breviceps*. Not to scale.

rooted in the skull, whereas *O. crocodilinus* retained separate alveoli for the maxillary teeth. On the other hand, *O. crocodilinus* is more advanced in the marked size difference between the nares, and in having a more elevated occipital shield, a single orifice for the infraorbital foramina on each side, and an elevated lateral wall of the supracranial basin formed by the maxilla that continues anteriorly on the rostrum as a maxillary ridge or crest.

The phylogenetic value of the following differences is not fully understood: the pterygoid hamuli are smaller and more slender, the optic canal is narrower, the orbit is relatively larger and is not sheltered by the jugo-lacrimal

anteriorly, and the exoccipitals are extremely excavated laterally in *O. crocodilinus*. The right premaxillary foramen is located slightly anterior to the antorbital notch in *O. crocodilinus*, whereas it is at the level of the antorbital notch in *Pl. duboisii*. The base of the rostrum is wider and the broad part of the rostrum extends further anteriorly in *Pl. duboisii*, and might have housed a wider spermaceti organ. In *O. crocodilinus*, the maxillary ridges anterior to the antorbital notch probably delineate the lateral margin of the spermaceti organ or the junk. This suggests that *O. crocodilinus* possessed a rather narrow and elongate spermaceti case. The supraorbital region is also different: in *O. crocodilinus*, the supraorbital region of the frontal is

not much exposed under the maxilla. The jugo-lacrimal and the overlying maxilla of the preorbital process is separated by a notch from the supraorbital region of the frontal. In *Pl. duboisii*, this notch is absent, and the whole supraorbital process together with the jugo-lacrimal is extended ventrolaterally, resulting in the ventral shift of the orbit.

Ferecetrotherium kelloggi can not be compared to *Placoziphius duboisii* because the Caucasus species is known only from mandibles and poorly preserved skull fragments, whereas all specimens of *Pl. duboisii* lack mandibles. However, their markedly different age makes it most unlikely that *F. kelloggi* would be a synonym of *Pl. duboisii*. All other named taxa of the *Physeteridae sensu stricto* are either regarded as synonyms or they are represented by non-cranial elements (or both).

Besides the holotype, the *partim*. 1 and the Stotzing specimens, *Placoziphius duboisii* has two other reported occurrences. A rostrum fragment from Hemiksem (Antwerp, Belgium) is illustrated in VAN BENEDEN & GERVAIS (1880, pl. XXVII, fig. 11a) and CAPELLINI (1893) reports a partial skull from the Pliocene of North Italy. The former lacks diagnostically important features and its taxonomic assignment to *Pl. duboisii* or to any other species is questionable. The latter was described by PILLERI (1987) as the holotype of *Hyperoodon pusillus* but BIANUCCI (1997) recognized that the specimen is a pygmy sperm whale. BIANUCCI & LANDINI (1999) described it as *Kogia pusilla*.

Systematic palaeontology

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1867

Superfamily *Physeteroidea* GRAY, 1821

Family *Physeteridae* GRAY, 1821

Subfamily *Physeterinae* GRAY, 1821

Emended diagnosis of subfamily – Anteroposterior expansion of the spermaceti organ leading to an elevated and vertical occipital shield (exact shape of which can vary); mesorostral gutter open along entire length of rostrum; temporal fossae anteroposteriorly constricted; they are either circular or have the form of an idealized water-drop; lack of enamel on tooth crowns.

Included taxa – *Physeter macrocephalus* LINNAEUS, 1758; *Placoziphius duboisii* VAN BENEDEN, 1869; *Physeterula dubusii* VAN BENEDEN, 1877; *Orycterocetus crocodilinus* COPE, 1895; *Idiophyseter merriami* KELLOGG, 1925.

Although the holotype of *Physeterula dubusii* is incomplete and lacks some of the diagnostically important characters, the vertical occipital shield and the lack of enamel on the teeth indicate that this species should be included in the *Physeterinae*. Likewise, *Idiophyseter merriami* is known from a skull fragment, but as KELLOGG (1925) noted, there are marked similarities to *Physeter*.

Indeed, the slightly convex occipital shield and the small, circular temporal fossa of *I. merriami* resemble the morphology of young *Physeter* skulls and indicate phylogenetic affinities to members of the *Physeterinae*.

Subfamily *Aulophyseterinae* new rank

Diagnosis of subfamily – Both premaxillae extremely broad throughout their lengths; mesorostral gutter closed in anterior part of rostrum; temporal fossae anteroposteriorly constricted and have the form of a lance.

Aulophyseter KELLOGG, 1927

Emended diagnosis of genus – A genus of the subfamily *Aulophyseterinae* having the following set of characters: total skull length extending 100 cm; premaxillae dominating dorsal surface of anterior part of rostrum; supraoccipital shield low; mesethmoid forming a protruding plate between premaxillae (termed mesethmoid crest); vomer exposed as a long strip (longer than 50% of rostrum length) on the palatal surface; palatine not covered by pterygoid; having separate infraorbital foramina.

Type species – *A. morricei* KELLOGG, 1927

Aulophyseter morricei KELLOGG, 1927

Emended diagnosis of species – A species of the genus *Aulophyseter* having right premaxillary foramen situated in level of antorbital notch and of anterior end of mesethmoid crest; ratio of rostrum width at base: length of maxilla exposed on dorsum of rostrum measured from antorbital notch being ca. 1: 0,7; and having a common alveolar groove for upper teeth.

Holotype – USNM 11230

Type locality – Shark Tooth Hills, Kern County, California, USA.

Age – Uppermost horizon of the Temblor Formation, Middle Miocene.

Aulophyseter mediatlanticus (COPE, 1895)

- *1895 – *Paracetus mediatlanticus* sp. nov. – COPE, p. 135.
- 1902 – *Hypocetus mediatlanticus* (Cope) – HAY, p. 596.
- 1904 – *Diaphorocetus mediatlanticus* Cope – TROUESSART, p. 772.
- 1904 – *Hypocetus mediatlanticus* (Cope) – CASE, p. 30, pl. 17, figs. 6a, 6b.
- 1915 – *Diaphorocetus mediatlanticus* (Cope) – SELLARDS, p. 103, fig. 32.
- 1921 – *Diaphorocetus mediatlanticus* (Cope) – ALLEN, p. 154.
- 1925 – *Orycterocetus mediatlanticus* (Cope) – KELLOGG, p. 11.
- 1926 – “*Paracetus*” *mediatlantiens* Cope – CABRERA, p. 409.

Emended diagnosis of species – A species of the genus *Aulophyseter* having right premaxillary foramen situated ca. 3 cm posterior to antorbital notch and ca. 5 cm posterior to anterior end of mesethmoid crest; ratio of rostrum width at base: length of maxilla exposed on dorsum of rostrum measured from antorbital notch being ca. 1: 1; and having separate alveoli for upper teeth.

Holotype – USNM 9463

Type locality – Drum Point, Chesapeake Bay, Maryland, USA.

Age – St. Marys Formation, Middle Miocene.

Aulophyseter mediatlanticus was described by COPE as a new species of the genus *Paracetus* in 1895. The genus *Paracetus* at that time included another species, "*Paracetus*" *poucheti* and the two forms were related on the basis of their well-developed upper dentitions (COPE, 1895). The name *Paracetus* was proposed by LYDEKKER (1894) replacing *Mesocetus* MORENO, 1892, a name preoccupied by the mysticete taxon *Mesocetus* VAN BENEDEEN, 1880. By mistake, LYDEKKER (1894) used the name *Hypocetus* for the same purpose earlier in his own paper. A few months earlier in the same year, AMEGHINO (1894) also replaced *Mesocetus* MORENO non VAN BENEDEEN, and proposed the name *Diaphorocetus* which should, therefore, have priority over *Paracetus* and *Hypocetus*. Still, COPE (1895) adopted the name *Paracetus* for his newly described species. TROUËSSART (1904), SELLARDS (1915) and ALLEN (1921) used the correct generic name for the species.

KELLOGG (1925) tentatively placed COPE's species into the genus *Orycterocetus* LEIDY, 1853, because he recognized marked similarities between "*Diaphorocetus*" *mediatlanticus* and the teeth-bearing rostrum fragment known as *Orycterocetus quadratidens* LEIDY, 1853. Surprisingly, in his thoughtful paper KELLOGG (1965) re-describing *O. crocodilinus* COPE, 1868, no reference is made to "*O.*" *mediatlanticus*.

There is little doubt that "*O.*" *mediatlanticus* (COPE, 1895) and *O. crocodilinus* COPE, 1868 belong to different evolutionary lineages within the family. In the holotype of "*O.*" *mediatlanticus* the medial margin of the premaxillae are eroded away (see also p. 7 in KELLOGG, 1927) and thus the widely open mesorostral gutter was probably not the original condition. Presuming that the premaxillae were appressed to each other in the midline of the rostrum, these bones were similarly broad as in *Aulophyseter morricei*. Another important character shared by both species is that the lateral border of the well-developed supracranial basin does not form an elevated maxillary ridge. Similarity of the skull size in these two species is also striking. Differences between both holotype skulls do not justify generic difference and hence, I hereby include "*Orycterocetus*" *mediatlanticus* (COPE, 1895) into the genus *Aulophyseter* KELLOGG, 1925.

Re-investigation of the holotype of *Orycterocetus quadratidens* LEIDY, 1853 was beyond the scope of the present study. KELLOGG (1965, p. 48) stated that "no characters of generic importance can be defined to distinguish these teeth [of *O. quadratidens*] from *Orycterocetus crocodilinus*". Close relationship of both species is further supported by a specimen from the Calvert Formation that has teeth of both morphologies (BOHASKA, 1998, p. 183).

Another large-sized form was described by GONDAR (1975) from the Upper Miocene of Argentina as *Aulophyseter rionegrensis*. However, this sperm whale does not seem to be closely related to *A. morricei* and *A. mediatlanticus*. The slender anterior part of its rostrum, posteriorly broad but anteriorly narrow premaxillae, anteroposteriorly wide temporal fossae, laterally flaring zygomatic processes as well as the distinct alveoli for maxillary teeth of *A. rionegrensis* indicate a closer relationship with *Diaphorocetus poucheti*. I suggest that the systematic position of *A. rionegrensis* needs reconsideration.

Phylogeny and classification of sperm whales

Regardless of problems in classification, two main types of sperm whales survived into present days. One of these, the pygmy sperm whales (Kogiinae) have developed a greatly enlarged melon and a small spermaceti organ situated between the frontal sac and the right nasal passage (HEYNING, 1989). As RAVEN & GREGORY (1933) pointed out, these structures expanded laterally and thus, a brevirostral skull is linked with a wide supracranial basin. The posterior wall of the supracranial basin is not very high, but the lateral borderings of the melon are extremely massive structures formed by the maxillae. The elevated lateral wall of the supracranial basin always is positioned lateral to the antorbital notches, and it protrudes anterolaterally so that the antorbital notches become constricted and are narrow slits. As a consequence of these modifications, the orbits are shifted posteroventrally (Fig. 2). Although the Late Miocene *Scaphokogia* DE MUIZON, 1988 is not brevirostral (DE MUIZON, 1988), the sagittal crest formed by both premaxillae and other synapomorphies (DE MUIZON, 1990; LUO & MARSH, 1996) clearly define the highly specialized group of pygmy sperm whales.

The other type, representatives of the Physeterinae, developed a large spermaceti organ that has expanded anteroposteriorly. In concordance with this, a more or less long rostrum as well as the tendency to increase skull size can be observed within this lineage. The mechanical stress on the posterior wall of the supracranial basin also increased, and in the more advanced forms the occipital shield elevated as a vertical wall to lean against the huge spermaceti organ. The spermaceti organ and the junk are bordered laterally by an elevated maxillary wall, which always is situated medial to the antorbital notch. Sometimes a maxillary ridge and, in larger forms, a mesethmoid plate is found. The orbit is sheltered anteriorly by

the robust and posteroventrally elongated jugo-lacrimal bone. In large, old (male) specimens of the recent *Physeter*, a complete bony ring formed by the jugo-lacrimal and the postorbital process of the frontal, which is fused to the anterior tip of the zygomatic process of the squamosal, sometimes completely surrounds the orbit (Fig. 2).

The fossil record indicates that during the evolutionary history of physeterids, at least two more lineages evolved. One of these is represented by the Aulophyseterinae new rank, with records from the Middle Miocene. The low and anteriorly sloping occipital shield, and the lack of elevated lateral wall for the supracranial basin of *Aulophyseter morricei*, are probably not primitive character states in this species because they are not linked with a large temporal fossa and a robust zygomatic process (Fig. 2). On the contrary, the temporal fossa of *A. morricei* is strongly constricted anteroposteriorly and the small, triangular zygomatic process of the squamosal is not flaring laterally. Some (unknown) adaptations of *Aulophyseter* led to the closure of the mesorostral gutter and the extreme broadening of the premaxillae in this genus, while the low posterior and lateral walls of the supracranial basin were retained.

Although the genus *Scaldicetus* bears many primitive features (e.g. the low skull profile with anteriorly sloping occipital shield, large and anteroposteriorly elongated temporal fossae, strong and laterally flaring zygomatic processes, functional upper dentition, teeth retaining enamel on crowns) some of its characters indicate that *Scaldicetus* might well represent a different lineage specializing into different direction than the rest of the family. Size difference between the bony nares is unknown in *Sc. mortezelensis* and the poor illustrations of the original description of *Sc. shigensis* do not allow any conclusions in this respect, but HIROTA & BARNES (1994) state that the right naris is considerably larger than the left one. Also, the sigmoid process of the tympanic has a ventrally elongated lateral lip according to HIROTA & BARNES (1994). It should also be kept in mind that records of *Scaldicetus* range from the Early Miocene through the Early Pliocene (DAL PIAZ, 1916; FORDYCE, 1984; CIGALAFULGOSI & PILLERI, 1985; PILLERI et al., 1989) or possibly as far as the Pleistocene (MCKENNA & BELL, 1997).

A hypothetical phylogenetic tree of the Physeteridae is presented in Fig. 3. *Idiorophus patagonicus*, *Ferecototherium kelloggi* and *Thalassocetus antwerpiensis* (partim. 2) were not considered because they are too poorly known to be included, nor were used taxa based on teeth, periotics or non-cranial elements. The Early Miocene *Diaphorocetus* seems to represent a primitive form of sperm whale and might be an ancestor of some of the more progressive physeterids. The subfamily Hoplocetinae is regarded *incertae sedis*, because the type species of its type genus, *Hoplocetus* GERVAIS, 1848 was based on two teeth.

The proposed classification of the Physeteridae is as follows:

Class Mammalia LINNAEUS, 1758

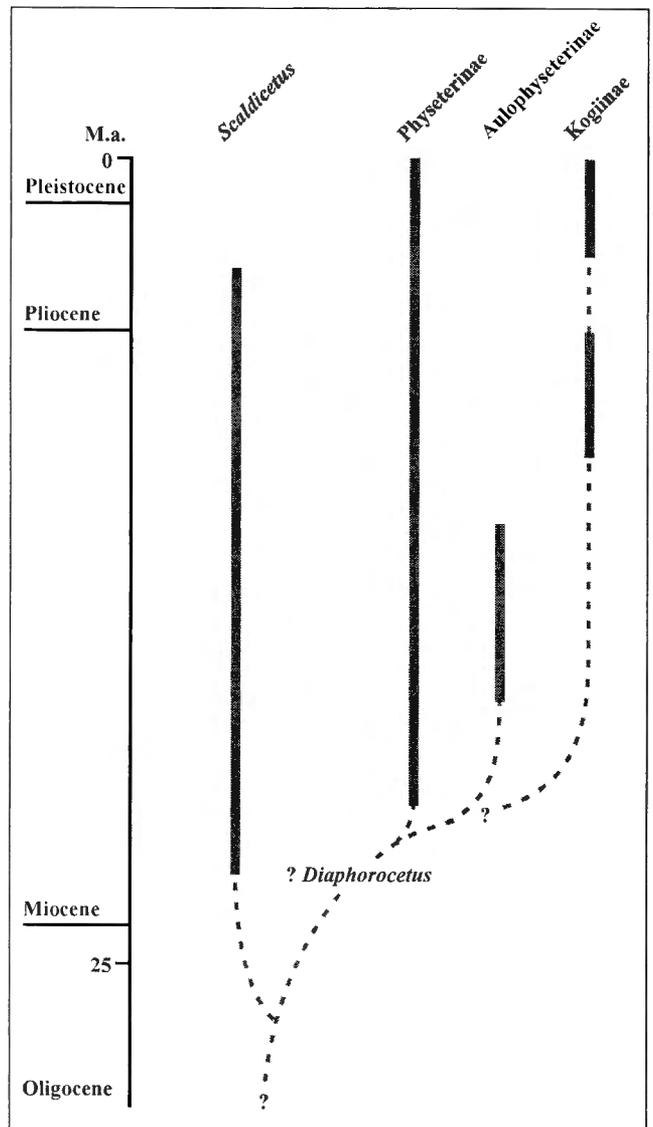


Fig. 3 — Hypothetical phylogenetic tree of the family Physeteridae. For definition of the family see DE MUIZON (1990, fig. 5, definition of Physeteroidea). The genus *Scaldicetus* is regarded as a separate evolutionary stock based on its retained plesiomorphic features linked with apomorphies. The primitive *Diaphorocetus poucheti* could be a common ancestor of some of the later forms. For diagnosis of the Physeterinae see systematic part of the present paper. The Aulophyseterinae are characterized with broad premaxillae, antero-posteriorly constricted temporal fossae and with the retainment of a low posterior wall for the supracranial basin. In all probability the Kogiinae have diverged last. Synapomorphies of this subfamily include the loss of both nasals, the transformation of the antorbital notch into a narrow slit, the formation of a horizontal plate on the posterior process of the periotic (see also DE MUIZON, 1990).

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1867

Superfamily Physeteroidea GRAY, 1821

Family Physeteridae GRAY, 1821
Subfamily Physeterinae GRAY, 1821
Physeter LINNAEUS, 1758

P. macrocephalus LINNAEUS, 1758
Orycterocetus LEIDY, 1853
O. quadratidens LEIDY, 1853
O. crocodilinus COPE, 1868
Placoziphius VAN BENEDEEN, 1869
Pl. duboisii VAN BENEDEEN, 1869
Physeterula VAN BENEDEEN, 1877
Ph. dubusii VAN BENEDEEN, 1877
Idiophyseter KELLOGG, 1925
I. merriami KELLOGG, 1925

Subfamily Aulophyseterinae new rank
Aulophyseter KELLOGG, 1927
A. morricei KELLOGG, 1927
A. mediatlanticus (COPE, 1895)

Subfamily Kogiinae GILL, 1871
Kogia GRAY, 1846
K. breviceps DE BLAINVILLE, 1838
K. simus OWEN, 1866
K. pusilla (PILLERI, 1987)
Praekogia BARNES, 1973
Pr. cedrosensis BARNES, 1973
Scaphokogia DE MUIZON, 1988
S. cochlearis DE MUIZON, 1988

incertae sedis:

Hoplocetus GERVAIS, 1848
H. crassidens (VAN BENEDEEN & GERVAIS, 1880)
H. perpenguis PILLERI & PILLERI, 1982
H. minor (PORTIS, 1885)
Paleophoca VAN BENEDEEN, 1859
Pa. nystii VAN BENEDEEN, 1859
Scaldicetus DU BUS, 1867
Sc. caretii (DU BUS, 1867)
Sc. mortezelensis DU BUS, 1872
Sc. grandis (DU BUS, 1872)
Sc. leccense (GERVAIS, 1872)
Sc. macgeei CHAPMAN, 1912
Sc. bolzanensis DAL PIAZ, 1916
Sc. lodgei CHAPMAN, 1918
Sc. inflatus CIGALA-FULGOSI & PILLERI, 1985
Sc. crispus CIGALA-FULGOSI & PILLERI, 1985
Sc. shigensis HIROTA & BARNES, 1994
Physetodon MCCOY, 1879
Phy. baileyi MCCOY, 1879
Priscophyseter PORTIS, 1885
Pri. typus PORTIS, 1885
Diaphorocetus AMEGHINO, 1894
D. poucheti (MORENO, 1892)
"Aulophyseter" rionegrensis GONDAR, 1975
Thalassocetus ABEL, 1905
T. antwerpiensis ABEL, 1905
Prophyseter ABEL, 1905
Pro. dolloi ABEL, 1905
Scaptodon CHAPMAN, 1918
Sca. lodderi CHAPMAN, 1918
Idiorophus KELLOGG, 1925
Id. patagonicus (LYDEKKER, 1894)
Kogiopsis KELLOGG, 1929
Ko. floridana KELLOGG, 1929
Ferecetotherium MCHEDLIDZE, 1970

F. kelloggi MCHEDLIDZE, 1970
Preaulophyseter CAVIGLIA & JORGE, 1980
Pre. gualichensis CAVIGLIA & JORGE, 1980
Miokogia PILLERI, 1986
M. elongatus (PROBST, 1886)
Helvicetus PILLERI, 1986
He. rugosus PILLERI, 1986

Conclusions

1. A new specimen of *Placoziphius duboisii* VAN BENEDEEN, 1869 from the Middle Miocene of Austria is described and a third specimen ("*Thalassocetus antwerpiensis*" ABEL, 1905, *partim*. 1) is shown to belong to the same species.
2. Definition of the subfamily Physeterinae GRAY, 1821 is supplemented by cranial characters. The present classification of the Physeterinae is basically identical with that of MCKENNA & BELL (1997) with the exception that *Thalassocetus antwerpiensis* ABEL, 1905 and genera without known skull are not included in the subfamily.
3. *Paracetus mediatlanticus* COPE, 1895 is placed into the genus *Aulophyseter* KELLOGG, 1927.
4. The subfamily Aulophyseterinae is introduced for large-sized sperm whales with extremely broad premaxillae, low supraoccipital shield and lance-like temporal fossae. The new subfamily represents a highly specialized subgroup within the Physeteridae.
5. Hoplocetinae CABRERA, 1926 is regarded *incertae sedis*, because its type genus was based on teeth only. Systematic position of *Scaldicetus* DU BUS, 1867, *Diaphorocetus* AMEGHINO, 1894, *Thalassocetus antwerpiensis* ABEL, 1905 and *Idiorophus patagonicus* (LYDEKKER, 1894) remain unresolved.

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Abbreviations of anatomical terms

aif – anterior infraorbital foramen; *afmx* – anterior maxillary foramen; *ant* – antorbital notch; *apr* – antorbital (or preorbital) process; *exo* – exoccipital; *fo* – foramen ovale;

me – mesethmoid; *mg* – mesorostral gutter; *mx* – maxilla; *oc* – optic canal; *of* – optic foramen; *pfmx* – posterior maxillary foramen; *pif* – posterior infraorbital foramen; *pmx* – premaxilla; *pmxf* – premaxillary foramen; *ppr* –

postorbital process of frontal; *pth* – pterygoid hamulus; *soc* – supraoccipital crest; *spr* – supraorbital process of frontal; *tf* – temporal fossa; *tp* – tympano-periotic complex; *vo* – vomer; *zy* – zygomatic process of squamosal.

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Explanation of Plates

PLATE 1

- Fig. 1 — *Placoziphius duboisii* VAN BENEDEN, 1869, holotype, IRScNB Ct.M. 530 (1718), dorsal view of skull. Scale bar equals 10 cm.
- Fig. 2 — *Placoziphius duboisii* VAN BENEDEN, 1869, holotype, IRScNB Ct.M. 530 (1718), ventral view of rostrum. Scale bar equals 10 cm.
- Fig. 3 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, tympano-periotic complex *in situ*. Natural size.
- Fig. 4 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, maxillary teeth. Natural size.

PLATE 2

- Figs. 1, 2 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, skull, dorsal and ventral view. Scale bar equals 10 cm.

PLATE 3

- Figs. 1, 2 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, partial restoration of skull, dorsal and ventral view. Scale bar equals 10 cm.

PLATE 4

- Fig. 1 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, skull, lateral view. Scale bar equals 10 cm throughout the plate.
- Fig. 2 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, skull, posterior view.
- Fig. 3 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, thoracic vertebrae, anterior view.
- Fig. 4 — *Placoziphius duboisii* VAN BENEDEN, 1869, Stotzing specimen, lumbar vertebrae in presumed anatomical sequence, dorsal view. Cau – caudal; cra – cranial.

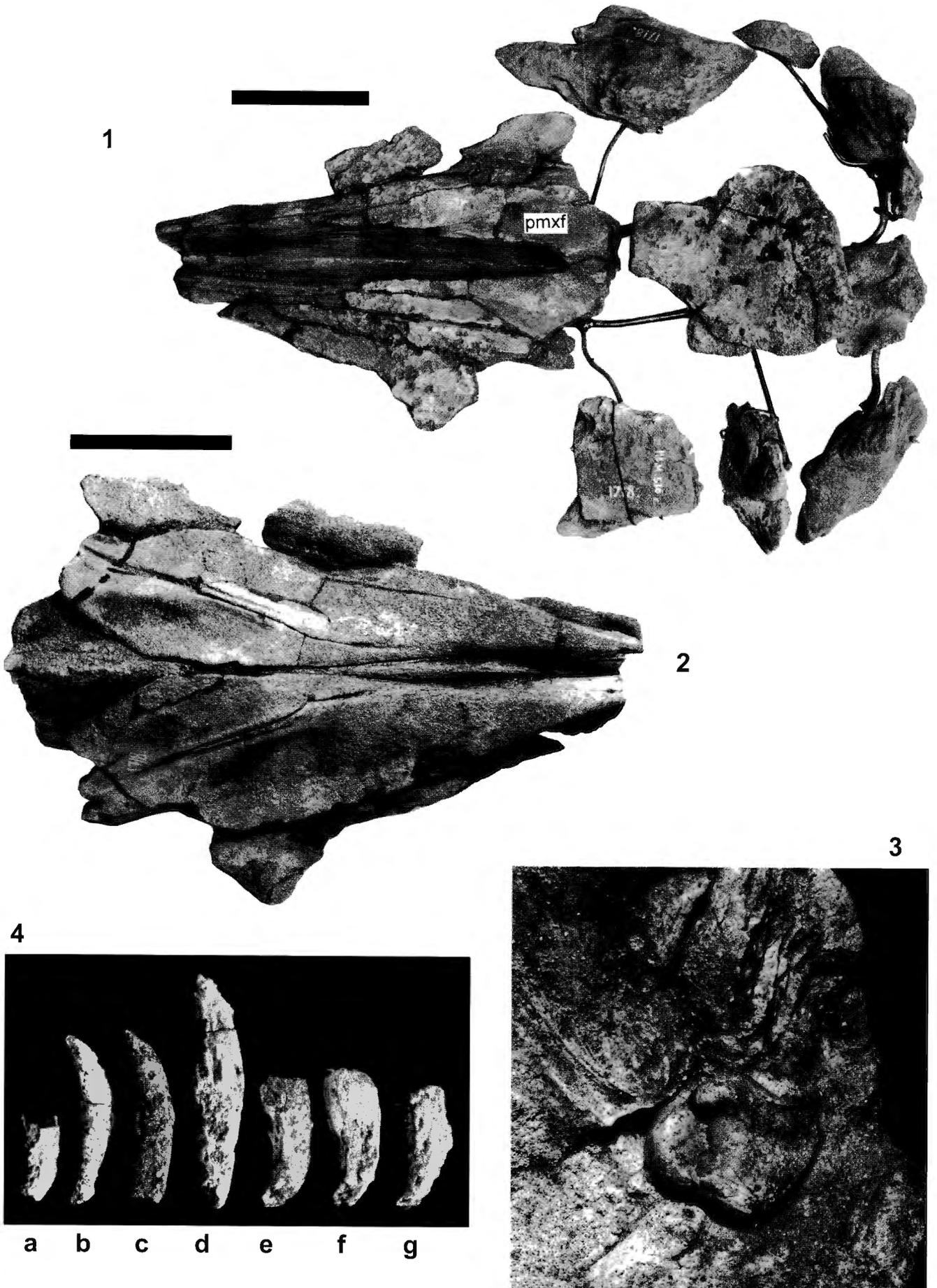
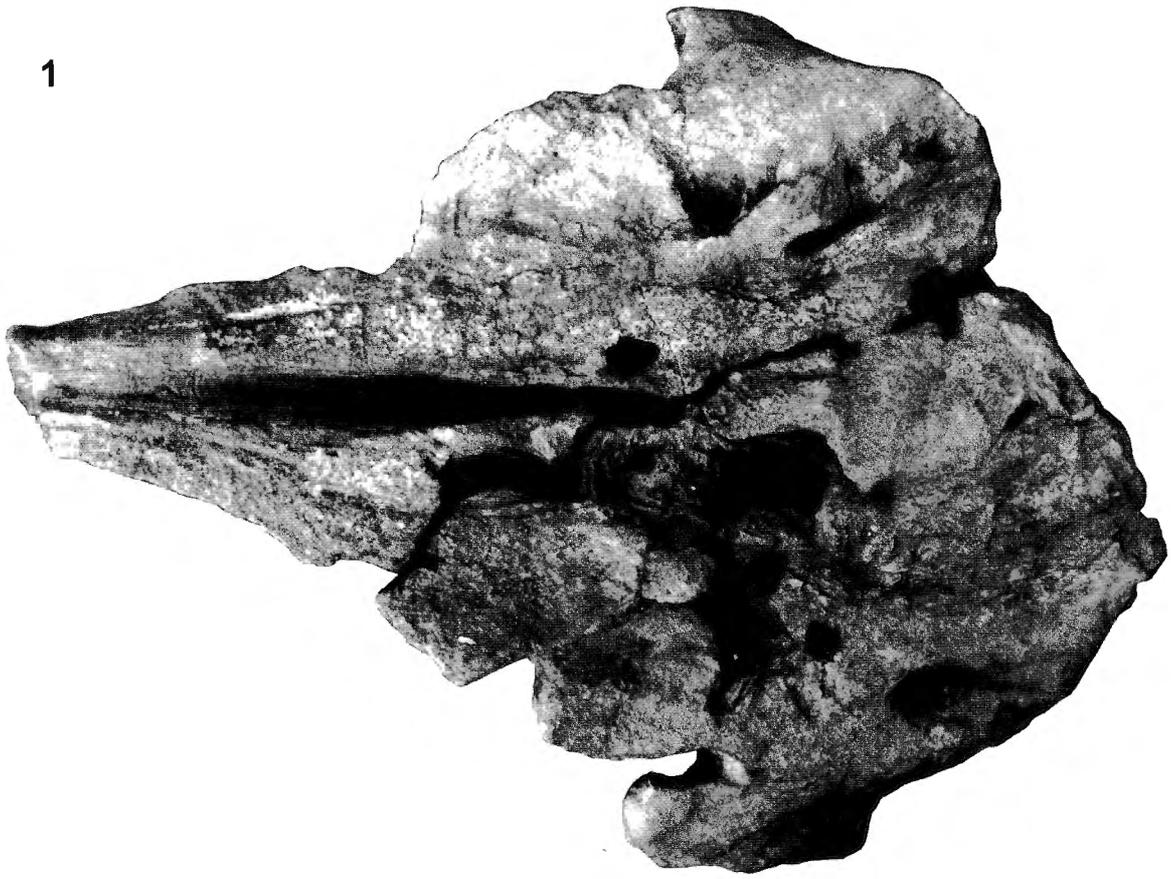


PLATE 1

1



2



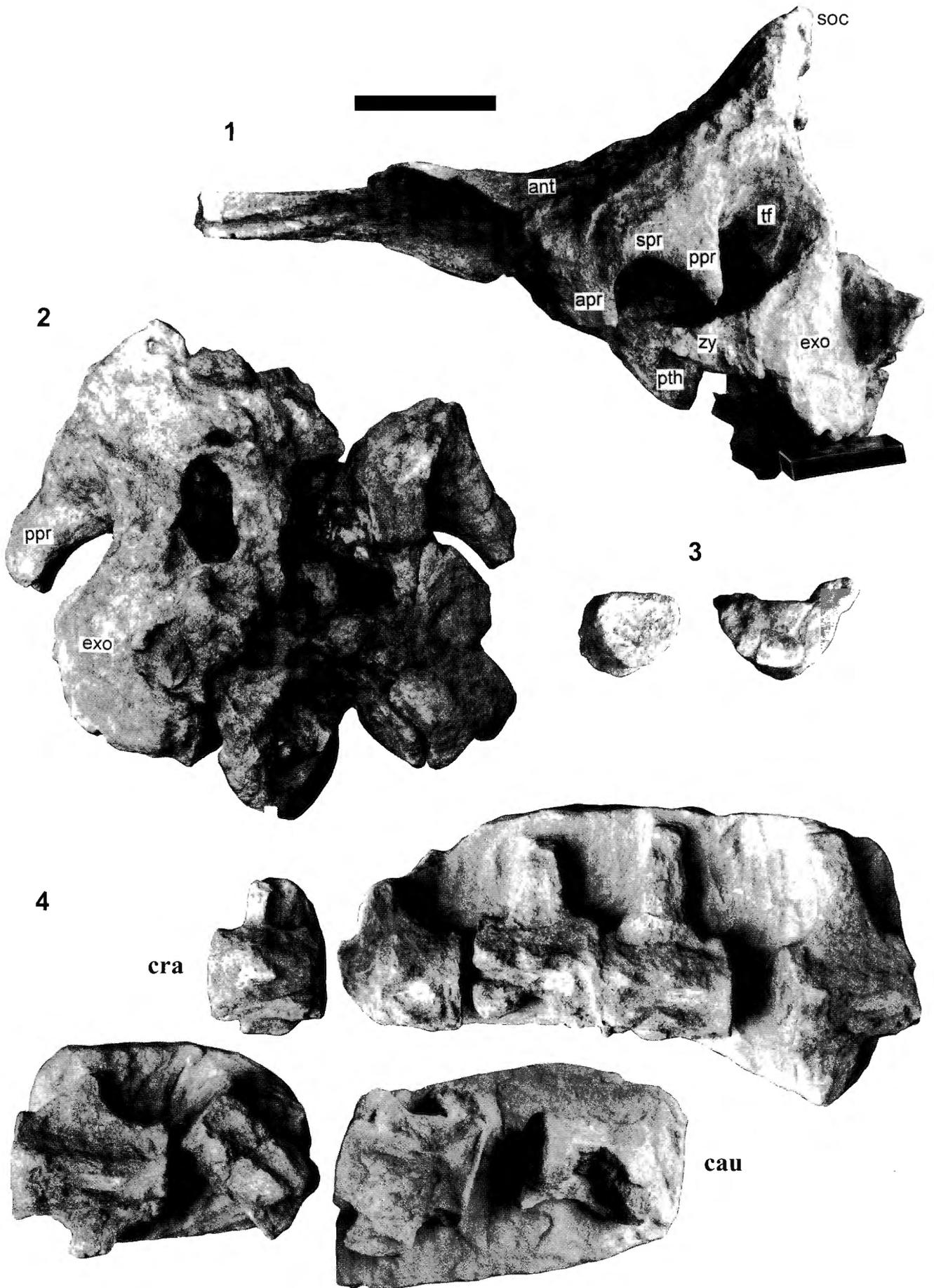


PLATE 4