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## The extinct baleen whale fauna from the Miocene-Pliocene of Belgium and the diagnostic cetacean ear bones

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Significant advances of our understanding of the evolutionary history of baleen whales have been gained by the recent focus on the extinct baleen bearing groups. However, a historically important collection from the middle Miocene to Pliocene of Antwerp, Belgium, comprising a third of all described species of early baleen-bearing mysticetes, has proven difficult to include in modern studies. These species are surrounded by taxonomic confusion because they were based on non-comparable composite material. The Belgian species are revised here with a designation of comparable lectotypes. The best-represented comparable element is the periotic bone that surrounds the inner ear. The periotic is shown to have significant diagnostic value, like that of teeth in many extinct mammals. Of the Belgian mysticetes, the genera *Amphicetus* and *Herpetocetus* are retained. *Plesiocetus* is retained and referred to Balaenopteridae, while *Idiocetus* is tentatively referred to Balaenidae. *Burtinopsis*, *Heterocetus*, *Isocetus* and *Mesocetus* are considered *nomen dubia*. Interestingly, all the major extinct mysticete groups known from the west-North Atlantic are represented in the Belgian fauna, although with different relative diversities, while no species seem to fall outside of these families. Diorocetidae, Aglaocetidae and Pelocetidae were thus well established with an east-west North Atlantic distribution by the Middle Miocene, indicating that these families originated in the Oligocene to Early Miocene. Cetotheriidae (*sensu stricto*) is represented by only one species that is probably Pliocene in age, suggesting a later dispersal to the east-North Atlantic region.

**Key words:** Mysticeti; Van Beneden; Miocene; Pliocene; taxonomy; periotic

### Introduction

The origin and evolution of the extant baleen whales and the phylogeny of extinct baleen-bearing species has long been poorly understood (Fordyce & Muizon 2001). The extinct species that could not be shown to belong to extant families were traditionally lumped in the polyphyletic family Cetotheriidae (*sensu lato*) (e.g. Barnes 1985). More recently these extinct mysticetes have received renewed attention, and a better understanding of their phylogeny, biology and diversity is beginning to emerge (Kimura & Ozawa 2002; Bouetel & Muizon 2006; Bisconti 2007; Steeman 2007, 2009). Recent phylogenetic analyses include some or most of the 12 species from Middle to Late Miocene and Pliocene localities described by Remington Kellogg in the middle of the 20th century (Kellogg 1924, 1925, 1931, 1934a, b, 1965, 1968a, b, c, d, 1969; Packard & Kellogg 1934). In contrast, recent studies include none of the 22 species named by P.-J. Van Beneden in the 19th century from Antwerp, Belgium (Van Beneden 1882, 1885, 1886). The reason for this is probably the highly problematic nature of these Belgian species.

During the construction of extensive fortifications of the city of Antwerp from 1860 to 1867 more than 200 m<sup>3</sup> of

fossil marine mammal bones were recovered and brought by the wagonload to the Natural History Museum of Belgium in Brussels (now the Royal Institute of Natural Sciences of Belgium) (Misonne 1958). P.-J. Van Beneden described the material in five beautifully illustrated annals on the extinct marine mammal fauna from Antwerp, of which three volumes were dedicated to the fossil mysticetes (Van Beneden 1882, 1885, 1886). These descriptions became the reference point for studies on fossil mysticetes for almost a century. The species are, however, problematic because the descriptions largely are based on several single isolated elements. Originally, skull fragments, ear bones, vertebrae, limb bones and ribs were sorted and elements from different parts of the body were then combined based on similarity in size, colour and finding place to form composite species. The species were sorted into genera according to size (*Mesocetus* for example refers to medium sized whales) (Smet 1978). It is, however, unlikely that all elements referred to either of these composite species actually came from the same biological species.

To complicate matters further, subsequent authors have used different syntype elements, or a combination of selected syntypes for comparison when assigning new species to Van Beneden's genera, thus spreading the

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taxonomic confusion to several later described species (e.g. Kadic 1907; Cabrera 1926; Pia & Bauml 1937; Roth 1978). The problematic nature of the Belgian species has rendered them useless for modern comparative studies and problematic for diversity studies (Uhen & Pyenson 2007). Aside from a few exceptions (Winge 1909; Abel 1938), there has been no attempt to address the problematic nature of the Belgian species. A revision of these species with establishment of lectotypes is needed to make them accessible to comparative studies and to resolve the taxonomic status of several later described species referred to these genera and thereby gain a better understanding of mysticete evolution.

### Institutional abbreviations

**FMNH:** Field Museum of Natural History, Chicago, USA; **IRScNB:** Institute Royal de Sciences Natureles de Belgique, Bruxelles, Belgium; **MLP:** Museo de Ciencias Naturales de La Plata, La Plata, Argentina; **USNM:** United States National Museum of Natural History, Washington DC, USA.

### Methods

To avoid having two or more names for the same biological species, the lectotypes chosen for the Belgian species need to be comparable (based on the same type of element). This element should be diagnostic and well represented among the syntypes of the described species, as well as being figured specimens (ICZN art. 74). The literature offers no consensus on any specific type of element used for comparison in the past. The element that best fits the above-mentioned criteria is the periotic bone. It is made of dense bone and thus preserves well, making it well represented among the syntypes. The diagnostic value has not previously been documented, but ear bones are considered to be useful for identifying cetaceans (Oishi & Hasegawa 1994). Furthermore, the periotic has proved sufficiently diagnostic to be used as a single element in a phylogenetic analysis (Geisler & Luo 1996).

To assess the inter- and intraspecific morphological variation of the cetacean periotic, the variation between three periotics of *Aglaocetus patulus*, between several periotics assigned to *Parietobalaena palmeri* and between several periotics assigned to *Balaenoptera acutorostrata* served as a reference. The terminology used for the periotic morphology follows that of Geisler and Luo (1996).

The material probably came from the Middle Miocene Antwerpen Sands, Berchem Formation, from the Late Miocene Deurne Sands, Diest Formation, or from the Pliocene Kattendijk Sands. The locations of the individual specimens were in most cases noted during collection, while for some specimens it would simply be stated that they came from Antwerp. The stratigraphic level of the specimens is in most cases uncertain. Several layers are present at the localities, and Van Beneden added the strati-

**Table 1.** Revised status of the genera and species described by Van Beneden (1882, 1885, 1886). Type species are in bold.

Original taxa	Revised status
<i>Amphicetus</i>	Retained
<i>Amphicetus editus</i>	Nomen dubium
<b><i>Amphicetus later</i></b>	<b><i>Amphicetus later</i></b>
<i>Amphicetus rotundus</i>	<i>Aglaocetus rotundus</i>
<i>Amphicetus verus</i>	Nomen dubium
<i>Burtinopsis</i>	Nomen dubium
<i>Burtinopsis minutus</i>	Nomen dubium
<b><i>Burtinopsis similis</i></b>	Nomen dubium
<i>Herpetocetus</i>	Retained
<b><i>Herpetocetus scaldiensis</i></b>	<b><i>Herpetocetus scaldiensis</i></b>
<i>Heterocetus</i>	Nomen dubium
<i>Heterocetus affinis</i>	<i>Parietobalaena affinis</i>
<b><i>Heterocetus brevifrons</i></b>	Nomen dubium
<i>Heterocetus guiscardii</i>	Nomen dubium
<i>Heterocetus sprangii</i>	Nomen dubium
<i>Idiocetus</i>	Referred to Balaenidae
<b><i>Idiocetus guicciardinii</i></b>	Pending revision
<i>Idiocetus laxatus</i>	<i>Parietobalaena laxata</i>
<i>Idiocetus longifrons</i>	<i>Aglaocetus (?) longifrons</i>
<i>Idiocetus tsugarensis</i>	Nomen dubium
<i>Isocetus</i>	Nomen dubium
<b><i>Isocetus depauwii</i></b>	Nomen dubium
<i>Mesocetus</i>	Nomen dubium
<i>Mesocetus latifrons</i>	<i>Aglaocetus latifrons</i>
<b><i>Mesocetus longirostris</i></b>	Nomen dubium
<i>Mesocetus pinguis</i>	Nomen dubium
<i>Plesiocetus</i>	Referred to Balaenopteridae
<b><i>Plesiocetus garopii</i></b> ( <i>Balaenoptera musculoides</i> )	Retained, pending diagnosis
<i>Plesiocetus brialmontii</i>	Nomen dubium
<i>Plesiocetus burtinii</i>	<i>Aglaocetus burtinii</i>
<i>Plesiocetus dubius</i>	Nomen dubium
<b><i>Plesiocetus hupschii</i></b>	<b><i>Plesiocetopsis hupschii</i></b> , holotype missing

graphic information in the 1870's based on residual matrix, or colour of the fossils (M. Bosselaers, pers. comm., 2009). It should therefore be noted, that there are considerable uncertainties surrounding the ages presented here.

In cases where species described by Van Beneden are referred to by a later described genus, a diagnosis of the periotic of the type species of this genus is provided. The original description of the genus should be consulted for a full diagnosis of the remaining material. A description and illustrations of the original syntype material may be found in Van Beneden (1882, 1885, 1886). An overview of the revised status of the original species is presented in Table 1 and a list of museum numbers of type specimens of the revised species is presented in Table 2. A complete list of syntypes illustrated by Van Beneden (1882, 1885, 1886) can be found in Supplementary Data.

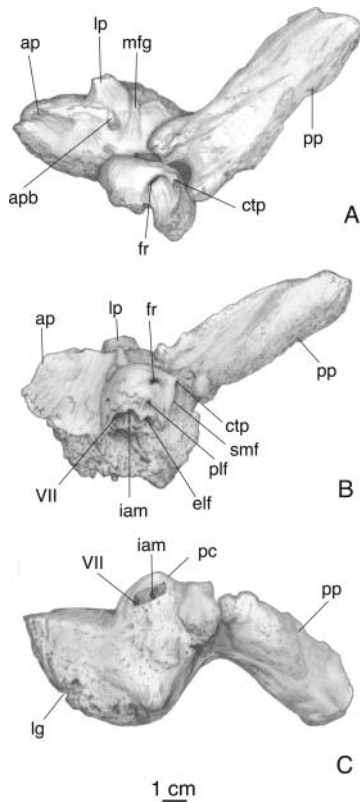
### Systematic palaeontology

Order Cetacea Brisson, 1762  
Pelagiceti Uhen, 2008

**Table 2.** Museum numbers of type specimens of the extinct mysticete species following revision.

Classification	Lectotype, IRScNB CtM/Reg	Referred specimens, IRScNB CtM/Reg
Balaenopteroidea		
Aglaoetidae		
<i>Aglaoetus burtinii</i>	676/1409	652/880
<i>Aglaoetus latifrons</i>	567/198	(612a-b/155)
<i>Aglaoetus (?) longifrons</i>	719 a-c/769	
<i>Aglaoetus rotundus</i>	594/37	
Balaenopteridae		
<i>Plesiocetus garopii</i>	Non assigned	
Diorocetidae		
<i>Amphicetus later</i>	575/313	548 a-b/1539, 622/296
<i>Plesiocetopsis hupschii</i>	Holotype missing	
Pelocetidae		
<i>Parietobalaena affinis</i>	605 a-b/301	
<i>Parietobalaena laxata</i>	727/61	
Cetotherioidea		
Cetotheriidae		
Herpetocetinae		
<i>Herpetocetus scaldiensis</i>	379 a-b/14	378 a-b/137, 380/406, 381/404, 382/405, 388/355

**Neoceti** Fordyce & Muizon, 2001Suborder **Mysticeti** Gray, 1864a *sensu* Scammon & Cope, 1869Infraorder **Chaemysticeti** Mitchell, 1989Superfamily **Balaenopteroidea** (Gray 1968) *sensu* Steeman, 2007Family **Aglaoetidae** Steeman, 2007Genus ***Aglaoetus*** Kellogg, 1934b**Type species.** *Aglaoetus moreni* Lydekker, 1894 *sensu* Kellogg, 1934b.**Referred species.** *A. burtinii* (Van Beneden, 1859); *A. latifrons* (Van Beneden, 1886); *A. (?) longifrons* (Van Beneden, 1886); *A. patulus* Kellogg, 1968c; *A. rotundus* (Van Beneden, 1886).**Diagnosis.** The periotic of *Aglaoetus* differs from that of all other stem-balaenopterid mysticetes except *Isanacetus* Kimura & Ozawa, 2002 by following characters: periotic body thick with small anterior process; malleolar fossa broad with shallow groove across anterior aspect; furrow on lateral side extending dorsally from anterior side of lateral projection of anterior process; stylomastoid fossa broad and extends onto pars cochlearis; fenestra rotunda small and laterally elongate.The following characters on the *Aglaoetus* periotic differ from that of *Isanacetus*: anterior process with long anterior edge and laterally constricted base; lateral projection of anterior process more developed; lateral surface furrowed or strongly irregular; caudal tympanic process more developed.**Remarks.** The holotype (Lydekker 1894: pl. 1; see below) of the type species, housed at Museo de Ciencias Naturales de La Plata, Argentina, was temporarily unavailable for study at the time this research was conducted. The referred specimen (MLP 5–14) does not include a well preserved periotic. Comparisons with the species described by Van Beneden are therefore based on the holotype of *A. patulus*, which is considered to be a well-established member of the genus (Kellogg 1968c).***Aglaoetus moreni*** (Lydekker, 1894) *sensu* Kellogg, 1934b1894 *Cetotherium moreni* Lydekker: p. 2, fig. 1.1926 *Plesiocetus moreni* (Lydekker); Cabrera: p. 369.**Holotype.** MLP 5-1, partial skeleton.**Referred specimens.** MLP 5-14, partial skull; FMNH p. 13407, skull and mandibles (Kellogg 1934b).**Locality and age.** Chubut region, Patagonia, Argentina. Early Miocene.**Remarks.** The holotype was temporarily unavailable for research at the time of this study. See Kellogg (1934b) for diagnosis.***Aglaoetus patulus*** Kellogg, 1968c  
(Fig. 1)**Holotype.** USNM 23690, skull, left periotic, tympanics, atlas, two cervical, two dorsal and eight lumbar vertebrae, rib fragments.**Referred specimens.** USNM 23049, right squamosal, right periotic, ten lumbar and five caudal vertebrae, five chevrons, right scapula fragments, two metacarpals, two phalanges, rib fragments (Kellogg 1968c); USNM 13472, partial skull, both periotics, right bulla (Kellogg 1968c).**Diagnosis.** Periotic body almost triangular in lateral outline, lateral projection of anterior process well-defined, dorsally prolonged groove on lateral side of periotic body weakly developed, caudal tympanic process well-developed with extension ventral to fenestra rotunda (pronounced in holotype).**Locality and age.** Stratford Bluffs, Zone 14, Calvert Formation, Maryland, U.S.A. Serravalian.



**Figure 1.** Left periotic of *Aglaocetus patulus* Kellogg, 1968 (holotype, USNM 23690). **A**, ventral view; **B**, medial view; **C**, dorsal view. Abbreviations: ap, anterior process; apb, anterior pedicle for the bulla; ctp, caudal tympanic process; elf, endolymphatic foramen; fr, fenestra rotunda; iam, internal auditory meatus; lg, lateral groove; lp, lateral projection of the anterior process; mfg, malleolar fossa groove; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

**Remarks.** A diagnosis of the remaining material can be found in Kellogg (1968c).

*Aglaocetus burtinii* (Van Beneden, 1859)  
(Figs 2–3)

- 1859 *Plesiocetus burtinii* Van Beneden: p. 141.  
 1872 *Cetotherium burtinii* (Van Beneden); Van Beneden: p. 18.  
 1873 *Cetotherium (Plesiocetopsis) burtinii* (Van Beneden); Brandt: p. 146.  
 1874 *Heterocetus burtinii* (Van Beneden); Vanden Broeck: p. 198.  
 1880 *Plesiocetus burtini* (Van Beneden); Van Beneden: p. 19.  
 1887 *Cetotherium burtini* (Van Beneden); Lydekker: p. 44.

**Lectotype.** IRScNB CtM 677 / Reg 1409, right periotic.

**Referred specimens.** IRScNB CtM 652 / Reg 880, right periotic.

**Diagnosis.** Like the periotic of *A. patulus* with the following exceptions: body more massive; anterior process more developed and more lateromedially constricted; lateral projection of anterior process well developed but less well defined; groove in malleolar fossa more developed; groove on lateral side of body only present ventrally; ventral edge of caudal tympanic process levelled with that of promontorium.

**Locality and age.** Originally described as “Anvers, 3<sup>e</sup> section, fossé du ravelin, face gauche de l’ancien fort n°1”. This fort is now destroyed, but was located at the boundary of the communes of Deurne and Borgerhout, eastern suburbs of Antwerp at the approximate geographic coordinates N51°12'55"E4°27' (O. Lambert pers. comm., 2009). Possibly from the late Miocene Deurne Sands, Diest Formation.

**Remarks.** The referred specimen was originally assigned to *Plesiocetus dubius* (Van Beneden 1885). The large foramina of the specimen, compared to those of the lectotype could indicate that the ossification process was not complete (the specimen was perhaps sub-adult).

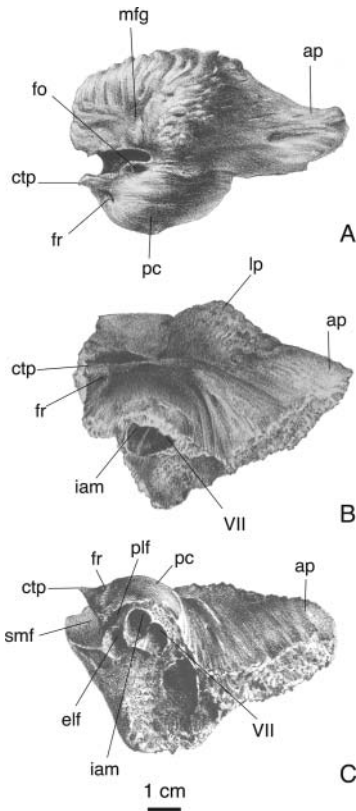
A specimen (IRScNB CtM 661/Reg 1239) referred to *P. hupschii* by Van Beneden (1885: pl. 21, figs 2, 6–7) (not the holotype of *P. hupschii*) includes a periotic that is now missing, but judging by the illustration it does closely resemble that of *P. burtinii* and should probably be referred to the same species if recovered. This specimen also includes skull fragments. Kellogg (1968b) considered the periotic referred to *P. hupschii* to be balaenopterine. There is a superficial resemblance between these periotics and that of *Megaptera* because of the larger size and the triangular shape of the body viewed medially. However, as in other species of *Aglaocetus* the body is thick, with a deep groove running anterolaterally across a well-defined malleolar fossa and a furrowed lateral surface. Furthermore, the pars cochlearis is not extended dorsally, the foramina for the auditory meatus and the facial nerve are visible in medial view and, although the caudal tympanic process is large, the tip does not point dorsally like in balaenopterid periotics.

*Aglaocetus latifrons* (Van Beneden 1880)  
(Fig. 4)

- 1880 *Mesocetus latifrons* Van Beneden: p. 23.  
 1931 *Plesiocetus latifrons* (Van Beneden); Van Deinse: p. 133.

**Lectotype.** IRScNB CtM 567/Reg 198, left periotic.

**Diagnosis.** Periotic differs from that of *Aglaocetus patulus* in the following features: body extends less dorsally; furrows on lateral surface less pronounced; more pronounced groove running dorsally from anterior aspect of lateral projection of anterior process; caudal tympanic

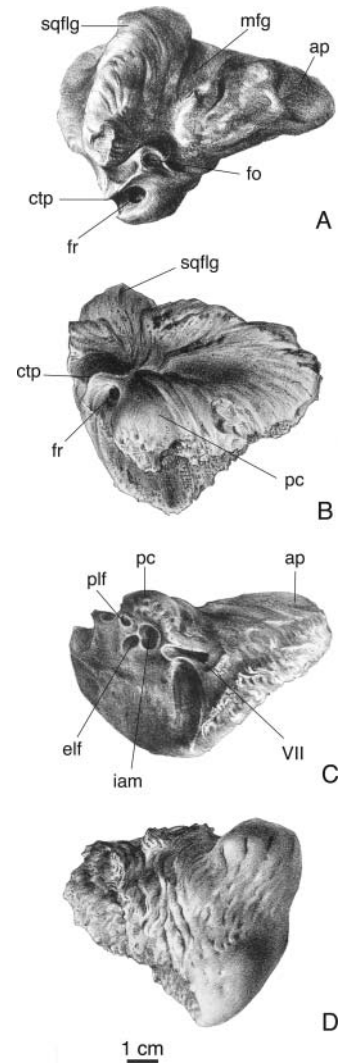


**Figure 2.** Right periotic of *Aglaocetus burtinii* (Van Beneden, 1859) (lectotype, IRScNB CtM 677/Reg 1409). **A**, ventral view; **B**, medial view; **C**, dorsomedial view. From Van Beneden (1885). Abbreviations: ap, anterior process; ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; lp, lateral projection of the anterior process; mfg, mallear fossa groove; pc, pars cochlearis; plf, perilymphatic foramen; smf, stylomastoid fossa; VII, facial nerve canal.

process more developed with ventral edge levelled with that of promontorium; lateral projection of anterior process well defined but not laterally extended, dorsal foramina extended into funnel-like extension with smooth dorsal surface.

**Locality and age.** Originally described as “Anvers, 3<sup>e</sup> section, face gauche de l’ancien fortin”. This is probably fort n°1 that was located at the boundary of the communes of Deurne and Borgerhout, eastern suburbs of Antwerp at the approximate geographic coordinates N51°12'55"E4°27' (O. Lambert pers. comm., 2009). Possibly from the late early to middle Miocene, Antwerpen Sands Member, Berchem Formation.

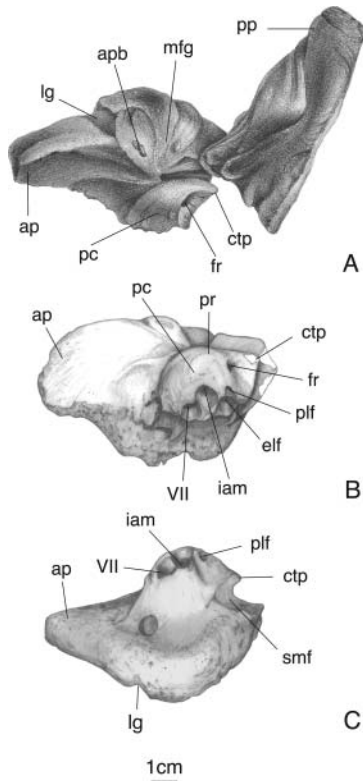
**Remarks.** The lectotype was originally described as *Mesocetus latifrons* (Van Beneden, 1886). A specimen consisting of a left periotic and a skull fragment was described as *Heterocetus brevifrons* (IRScNB CtM 612a-b/Reg 155, same locality as lectotype, but possibly from the



**Figure 3.** Right periotic of *Aglaocetus burtinii* (Van Beneden, 1859) (referred specimen, IRScNB CtM 652/Reg 880). **A**, ventral view; **B**, medial view; **C**, dorsal view; **D**, lateral view. From Van Beneden (1885). Abbreviations: ap, anterior process; ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; mfg, mallear fossa groove; pc, pars cochlearis; plf, perilymphatic foramen; sqflg, squamosal flange of the posterior process; VII, facial nerve canal.

late Miocene Deurne Sands, Diest Formation). The periotic cannot currently be located in the collection and the skull fragment is missing a part shown in the original drawings (Van Beneden 1886, pl. 26, fig. 1). However, based on the original illustrations the periotic is similar to that of the here established lectotype of *A. latifrons*. The skull fragment is not diagnostic, but the preserved fragments are generally consistent with the morphology of *Aglaocetus patulus*. The specimen is therefore tentatively referred to *A. latifrons*.

*Aglaocetus* (?) *longifrons* (Van Beneden, 1880)  
(Figs 5–6)



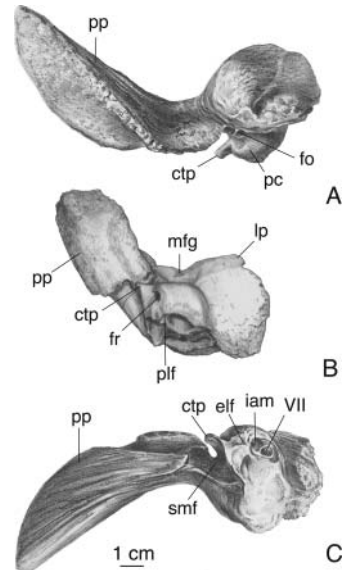
**Figure 4.** Left periotic of *Aglaocetus latifrons* (Van Beneden 1880) (IRScNB CtM 567/Reg 198). **A**, ventral view; **B**, medial view; **C**, dorsal view. Posterior process not included in B and C. A from Van Beneden (1886). Abbreviations: ap, anterior process; apb, anterior pedicle for the bulla; ctp, caudal tympanic process; elf, endolymphatic foramen; fr, fenestra rotunda; iam, internal auditory meatus; lg, lateral groove; mfg, malleolar fossa groove; pc, pars cochlearis; pr, promontorium; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

1880 *Idiocetus longifrons* Van Beneden: p. 24.

1931 *Plesiocetus longifrons* (Van Beneden); Van Deinsse: p. 143.

**Lectotype.** IRScNB CtM 719 a-c /769, skull fragment, right periotic, right tympanic.

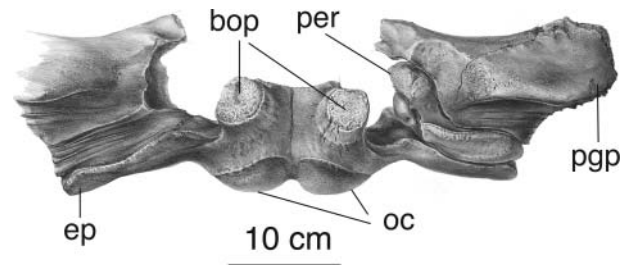
**Diagnosis.** Basioccipital process massive with flat, circular ventral surface; lateral extension of exoccipital posteriorly levelled with occipital condyle with posterior extents of postglenoid process further anteriorly. Periotic resembles that of *A. latifrons* with the following exceptions: anterior process insignificant; groove across malleolar fossa shallow; lateral projection of anterior process less pronounced; body barely extending dorsal to pars cochlearis; lateral side of periotic without furrowed; irregular surface. Dorsal surface of pars cochlearis smooth but dorsal foramina not extended into funnel.



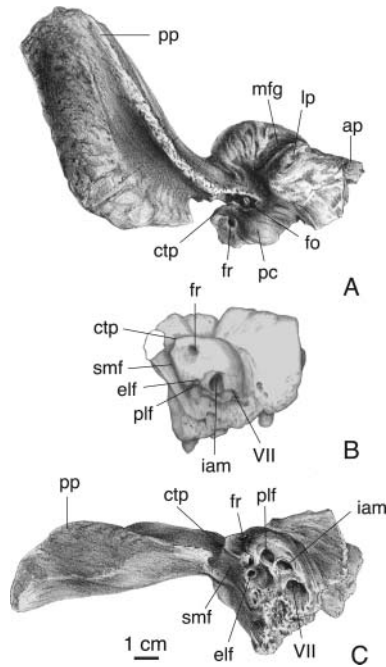
**Figure 5.** Right periotic of *Aglaocetus (?) longifrons* (Van Beneden, 1880) (IRScNB CtM 719 c/769). **A**, ventral view; **B**, medial view; **C**, dorsal view. A and C from Van Beneden (1886). Abbreviations: ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; lp, lateral projection of the anterior process; mfg, malleolar fossa groove; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

**Locality and age.** Original label: “Anvers, 3<sup>e</sup> section”, which is the portion of the old inner fortification ring corresponding to the eastern part of the ring road around Antwerp (O. Lambert pers. comm., 2009). Likely from the late early to middle Miocene Antwerpen Sands Member, Berchem Formation.

**Remarks.** A poorly preserved bulla is included in the lectotype specimen, but it probably does not belong to the periotic and is therefore here disregarded. Because of the different shape of the periotic body, the lack of the furrowed or irregular surface of the lateral side and the short



**Figure 6.** Skull fragment of *Aglaocetus (?) longifrons* (Van Beneden, 1880) (IRScNB CtM 719 a/769). From Van Beneden (1886). Abbreviations: bop, basioccipital process; ep, exoccipital process; oc, occipital condyles; per, periotic; pgp, postglenoid process.



**Figure 7.** Right periotic of *Aglaocetus rotundus* (Van Beneden, 1880) (IRScNB CtM 594/Reg 37). **A**, ventral view; **B**, medial view; **C**, dorsomedial view. Posterior process not included in B. Illustrations A and C from Van Beneden (1886). Abbreviations: ap, anterior process; ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; lp, lateral projection of the anterior process; mfg, malleolar fossa groove; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

anterior process, the species is only tentatively referred to *Aglaocetus*.

*Aglaocetus rotundus* (Van Beneden 1880)  
(Fig. 7)

1880 *Amphicetus rotundus* Van Beneden: p. 21.

**Lectotype.** IRScNB CtM 594/Reg 37, right periotic.

**Diagnosis.** Periotic similar to that of *A. patulus* with the following exceptions: body thicker; anterior process short and ends abruptly with almost flat, smooth anterior surface; lateral projection of anterior process not extending laterally from body; caudal tympanic process more developed with ventral surface levelled with that of promontorium; fenestra ovalis large and visible in ventral view.

**Locality and age.** “Anvers, 3<sup>e</sup> section, front 6, fossé du ravelin”. The third section of the old inner fortification ring corresponds to the eastern part of the ring road around Antwerp. The front 6 is a part of the section at the boundary of the communes of Deurne and Borgerhout, in the area of

the Stenenbrug (O. Lambert pers. comm., 2009). Possibly from the late Miocene Deurne Sands, Diest Formation.

**Remarks.** The lectotype also included an incompletely preserved thoracic vertebra, but because it is not certain that it belongs to the same individual as the periotic, it is excluded from the lectotype.

Family **Balaenopteridae** Gray, 1864b  
Genus ***Plesiocetus*** Van Beneden, 1859

**Type species.** *Plesiocetus garopii* Van Beneden, 1859, designated by Kellogg (1931).

**Remarks.** The name *Plesiocetus* first appears in a note on the three species *P. hupschii*, *P. burtinii* and *P. garopii* (Van Beneden 1859). Van Beneden (1872) then referred *P. burtinii* and *P. hupschii* to *Cetotherium*, leaving only *P. garopii* in the genus. Subsequently Van Beneden (1880) gave *P. garopii* the new binomen *Balaenoptera musculoïdes*, but at the same time, he returned *P. burtinii* and *P. hupschii* to the genus *Plesiocetus*, creating a new species, *P. brialmontii* and referring to *Plesiocetus* the species *Cetotherium dubium*, which he created in 1872. Winge (1909) considered the type of the genus to be *P. hupschii*, the first species Van Beneden (1859) mentioned. However, Kellogg (1931) interpreted the removal of all species but *P. garopii* from the genus by Van Beneden in 1872 to be the establishment of this species as the type of the genus. At the same time, Kellogg (1931) elevated the subgenus *Plesiocetopsis* Brandt, 1873 to genus level and made *P. hupschii* the type. Deméré *et al.* (2005) followed the interpretation of Kellogg (1931). To support continuity, this interpretation is followed here (contrary to Steeman 2007, who followed Winge 1909). The syntypes Van Beneden (1882) described and illustrated as *Balaenoptera musculoïdes*, the synonym he created for *P. garopii*, are clearly balaenopterids (Van Beneden 1880; Deméré *et al.* 2005). The specimen illustrated by Van Beneden & Gervais (1880) is not a balaenopterid, but a stem-balaenopterid according to the tympanic morphology.

*Plesiocetus* has to a wide extent been used to accommodate species representing an overall form but spanning a great variation. Species have been included in, and removed from, the genus without substantial argument and regard to previous actions and often in journals that are not easily accessible. Listing all referred species and synonyms would be extensive and more confusing than informative (information can be found in the Paleobiology Database (Uhen & Pyenson 2005) and Ichishima (1997)). A separate, detailed revision of this material is needed, but is beyond the scope of this study. Also, because this study is focused on the species not belonging to Recent families, a formal diagnosis of *Plesiocetus* will not be provided here.

*Plesiocetus garopii* Van Beneden, 1859

- 1859 *Plesiocetus garopii* Van Beneden: p. 141.  
 1880 *Plesiocetus goropii* Van Beneden; Van Beneden: p. 15.  
 1880 *Balaenoptera musculoides* Van Beneden; Van Beneden: p. 15.  
 1887 *Balaenoptera goropi* Lydekker: p. 36.  
 1904 *Balaenoptera goropii* Lydekker; Trouessart: p. 782.

**Remarks.** The type series consists of several syntypes, including a periotic and tympanic (IRScNB CtM 752 / Reg. 936) but also a mandible (IRScNB CtM 690 / Reg. 11). Since mandibular morphology has been used to diagnose extinct balaenopterids, both may be possibly suitable lectotypes. It is, however, beyond the scope of this study to revise the species belonging to Recent families, and a formal diagnosis will therefore not be provided here.

***Plesiocetus brialmontii*** Van Beneden 1880

- 1887 *Cetotherium brialmonti* (Van Beneden); Lydekker: p. 42.

**Remarks.** Among the 16 syntypes none are sufficiently diagnostic to support the species and it is therefore considered a *nomen dubium*.

***Plesiocetus dubius*** Van Beneden, 1872

- 1872 *Cetotherium dubium* Van Beneden: p. 18.  
 1873 *Cetotherium (Plesiocetopsis) dubium* Van Beneden; Brandt: p. 146.  
 1874 *Heterocetus dubius* (Van Beneden); Vanden Broeck: p. 198.

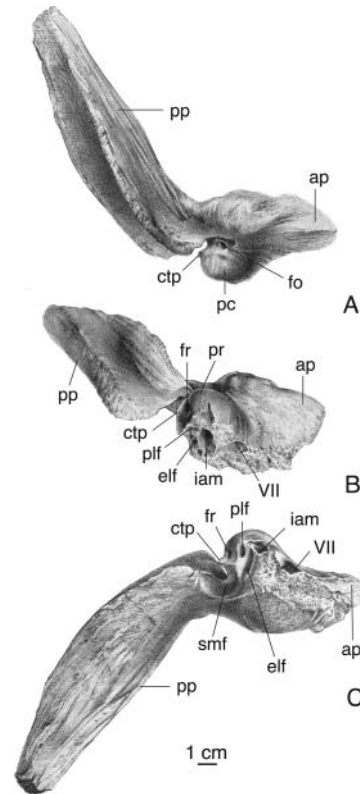
**Remarks.** A syntype periotic (IRScNB CtM 652/Reg 880) is referred to *Aglaoctetus burtinii*. There is no other material that is sufficiently diagnostic to support the species among the syntypes and it is therefore considered a *nomen dubium*.

Family **Diorocetidae** Steeman, 2007  
 Genus ***Amphicetus*** Van Beneden, 1880

**Type species.** *Amphicetus later* Van Beneden, 1880, designated by Kellogg (1931).

**Referred species.** *A. longirostris* (Van Beneden, 1880); *A. sprangii* (Van Beneden, 1886).

**Diagnosis.** Periotic shares the following characters with *Diorocetus* Kellogg, 1968b, *Thinocetus* Kellogg, 1969 and *Uranocetus* Steeman, 2009: promontorium thick and bulges ventral to fenestra rotunda; fenestra rotunda dorsoventrally elongate; caudal tympanic process small; pars cochlearis receding dorsomedially in posterior view; stylomastoid fossa expands laterally onto periotic body and posterior process; endolymphatic foramen lateromedially elongate and slit-shaped. Periotic differs from *Diorocetus* and



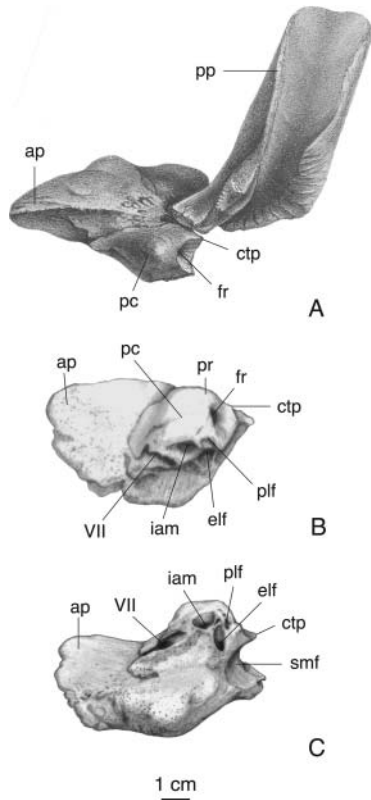
**Figure 8.** Right periotic of *Amphicetus later* Van Beneden, 1880 (IRScNB CtM 575/Reg 313). **A**, ventral view; **B**, medial view; **C**, dorsal view. From Van Beneden (1886). Abbreviations: ap, anterior process; ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; pc, pars cochlearis; pr, promontorium; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

*Thinocetus* in the following: pars cochlearis only slightly laterally compressed; periotic body more massive. It differs from *Uranocetus* in the following: body more slender; coronoid processes anterior on anterior process lacking; aperture of facial nerve canal widely separate from, rather than joint with internal acoustic meatus.

The following combination of characters is unique to *Amphicetus*: periotic body about twice as long as wide; anterior process large and expands ventrally with ventral crest; lateral projection of anterior process a pronounced bulge not extending from body; dorsal foramina for facial nerve canal and internal auditory meatus situated far apart.

***Amphicetus later*** Van Beneden, 1880  
 (Figs 8–10)

**Lectotype.** IRScNB CtM 575/Reg 313, right periotic (Fig. 8).



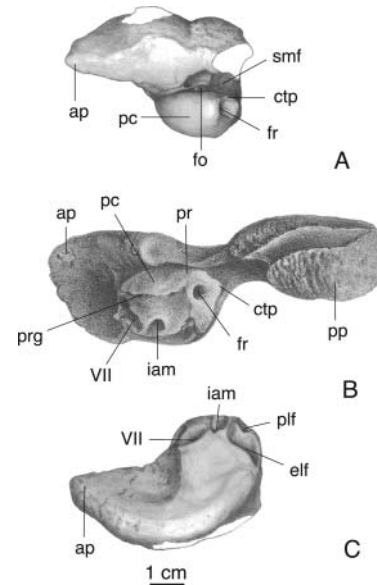
**Figure 9.** Left periotic of *Amphicetus later* Van Beneden, 1880 (referred specimen IRScNB CtM 548 a-b/Reg 1539). **A**, ventral view; **B**, medial view; **C**, dorsal view. Posterior process not included in B and C. A from Van Beneden (1886). Abbreviations: ap, anterior process; ctp, caudal tympanic process; elf, endolymphatic foramen; fr, fenestra rotunda; iam, internal auditory meatus; pc, pars cochlearis; pr, promontorium; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

**Referred specimens.** IRScNB CtM 548 a-b/Reg 1539, left periotic (Fig. 9); IRScNB CtM 622 / Reg 296, left periotic (Fig. 10).

**Diagnosis.** As for genus.

**Locality and age.** Original label: “Anvers, 3<sup>e</sup> section, fossé du ravelin”. The third section of the old inner fortification ring corresponds to the eastern part of the ring road around Antwerp. Possibly from the late Miocene Deurne sands, Diest Formation (O. Lambert pers. comm., 2009).

**Remarks.** Referred specimen IRScNB CtM 548 a-b/Reg 1539 (Antwerp area, late early to middle Miocene Antwerpen Sands, Berchem Formation) was originally a syntype assigned to *Mesocetus longirostris*. Referred specimen IRScNB CtM 622/Reg 296 was a syntype of *Heterocetus sprangii*. The latter originally included a tympanic, but it does not fit the periotic and probably belong a different individual. The bulla is therefore disregarded as part of the



**Figure 10.** Left periotic of *Amphicetus later* Van Beneden, 1880 (referred specimen, IRScNB CtM 622/Reg 296). **A**, ventral view; **B**, medial view; **C**, dorsal view. Posterior process not included in A and C. B from Van Beneden (1886). Abbreviations: ap, anterior process; ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

specimen. The minor differences between the lectotype and the referred specimens are interpreted as being size related.

#### *Amphicetus editus* Van Beneden, 1880

**Remarks.** The syntypes consist of material that is not sufficiently diagnostic to support the species, which is therefore considered a *nomen dubium*.

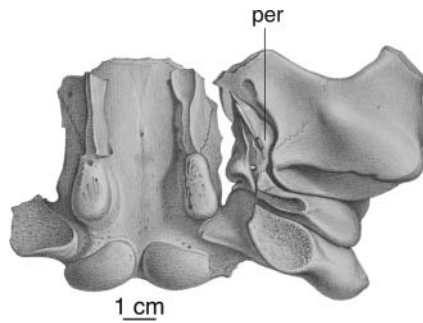
#### *Amphicetus verus* Van Beneden, 1886

**Remarks.** Of the nine syntypes, none are sufficiently diagnostic to support the species, which is therefore considered a *nomen dubium*.

#### Genus *Plesiocetopsis* Brandt, 1873

**Type species.** *Plesiocetopsis hupschii* (Van Beneden, 1859), designated by Kellogg (1931).

**Remarks.** Kellogg (1931) elevated the subgenus *Plesiocetopsis* Brandt, 1873 to genus level and made *P. hupschii* the type species. An accurate diagnosis of the species cannot currently be provided because the type specimen is missing. However, the illustration of the holotype skull shows that the periotic *in situ* resembles that of *Amphicetus*, particularly in having a large anterior process with a prominent ridge on the dorsal aspect. Contrary to the periotic of *Amphicetus* and all other diorocetids, the caudal tympanic process seems



**Figure 11.** Partial skull of *Plesiocetopsis hupschii* (Van Beneden, 1859) in ventral view. From Van Beneden & Gervais (1880). Abbreviation: per, periotic.

to be well developed. Whether *Amphicetus* is congeneric with *Plesiocetopsis* is impossible to tell on the basis of the illustration only. *Plesiocetopsis* will thus have to remain a separate genus for now.

***Plesiocetopsis hupschii*** (Van Beneden, 1859)  
(Fig. 11)

1859 *Plesiocetus hupschii* Van Beneden: p. 140.

1872 *Cetotherium hupschii* (Van Beneden); Van Beneden: p. 17.

1873 *Cetotherium (Plesiocetopsis) hupschii* (Van Beneden); Brandt: p. 144.

1874 *Heterocetus hupschii* (Van Beneden); Vanden Broeck: p. 198.

1887 *Cetotherium hupschi* (Van Beneden); Lydekker: p. 45.

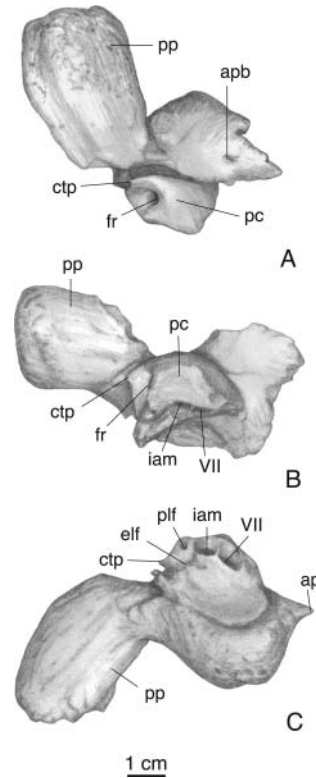
1931 *Plesiocetopsis hupschii* (Van Beneden); Kellogg: p. 309.

**Holotype.** Partial skull including left periotic. Designated by Winge (1909).

**Locality and age.** Between Southwold and Covehithe, Suffolk, UK (Van Beneden & Gervais 1880; Van Beneden 1885).

**Remarks.** Winge (1909) recognized that the skulls illustrated by Van Beneden & Gervais (1880) belonged to different species and he specified the type material of *P. hupschii* to be the partial skull described by Van Beneden & Gervais (1880, pl. 16, fig. 17), supported by the composite material described later (Van Beneden 1885). Kellogg (1934b) noted that the later-described composite material also is from a different species. The type of *P. hupschii* thus comprises only the partial skull described by Van Beneden & Gervais (1880) (Fig. 11). No catalogue number was provided in the original description, and the whereabouts of this specimen is unknown. It is therefore not possible to provide a proper diagnosis for the species.

Family **Pelocetidae** Steeman, 2007  
Genus ***Parietobalaena*** Kellogg, 1924



**Figure 12.** Right periotic of *Parietobalaena palmeri* Kellogg, 1924 (USNM 10668). **A**, ventral view; **B**, medial view; **C**, dorsal view. Abbreviations: ap, anterior process; apb, anterior pedicle for the bulla; ctp, caudal tympanic process; elf, endolymphatic foramen; fr, fenestra rotunda; iam, internal auditory meatus; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; VII, facial nerve canal.

**Type species.** *Parietobalaena palmeri* Kellogg, 1924.

**Referred species.** *P. affinis* (Van Beneden, 1880); *P. laxata* (Van Beneden, 1880); *P. (?) securis* Kellogg, 1931.

**Diagnosis.** Periotic body not dorsally extended, small and thick; lateral surface strongly convex; anterior process small or absent; pars cochlearis set off from body; dorsomedial edge of pars cochlearis situated far ventrally.

***Parietobalaena palmeri*** Kellogg, 1924  
(Fig. 12)

**Holotype.** USNM 10668, partial skull including right (Fig. 12) and left periotics and incomplete left bulla.

**Referred material.** See Kellogg (1968d).

**Diagnosis.** Anterior process of periotic present but small; lateral projection of anterior process small; dorsal surface of body and pars cochlearis smooth and concave; medial edge of dorsal surface pressed down to level ventral to fenestra rotunda; posterior process short and thick.

**Locality and age.** North of Dares Wharf, Calvert Formation, Zone 11, Maryland, USA. Langhian.

**Remarks.** A diagnosis of the remaining material can be found in Kellogg (1968d). Of the 20 specimens Kellogg (1968d) referred to the species, specimens USNM 23203 and USNM 23448 consist of material that is not comparable to the holotype or to other referred material and should be disregarded from the description of this species. The periotic of specimen USNM 11535 does not fit to the skull. The periotics referred to this species seem to represent two different types. The material could be suitable for future detailed studies of intraspecific variation.

*Parietobalaena affinis* (Van Beneden, 1880)  
(Fig. 13)

1880 *Heterocetus affinis* Van Beneden: p. 21.

1887 *Cetotherium affine* (Van Beneden); Lydekker: p. 47.

1931 *Plesiocetus affinis* (Van Beneden); Van Deinsse: p.121.

**Lectotype.** IRScNB CtM 605 a-b/Reg 301, left periotic and bulla.

**Diagnosis.** Differs from *P. palmeri* in the following: periotic body high; lateral projection of anterior process more developed; anterior process reduced; dorsal surface less concave, not smooth; lamellae surround dorsal foramina. Tympanic similar to that of *P. palmeri* except for the following: anterior end slightly less inflated; anteriomedial angle more rounded viewed dorsally; involucrem slightly thicker.

**Locality and age.** Original label: “Anvers, 3<sup>e</sup> section, fossé du ravelin, face gauche de l’ancien fort n°1”. The approximate geographic coordinates of this fort, now destroyed, are N51°12'55"E4°27'. It is located at the boundary of the communes of Deurne and Borgerhout, in the eastern suburbs of Antwerp. Probably from the late Miocene Deurne Sands, Diest Formation (O. Lambert pers. comm., 2009).

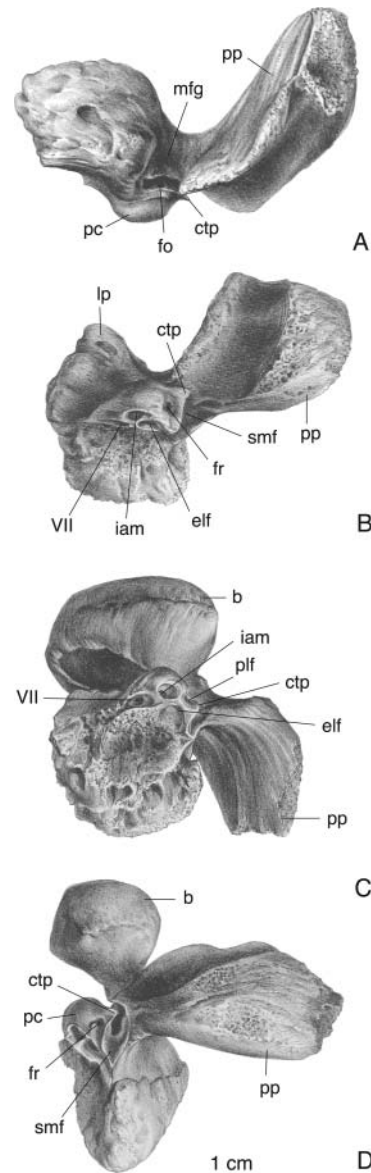
**Remarks.** A thick, elongate body and large wing-like lateral projection are characteristic of *Pelocetus* and *Cophocetus*. *P. affinis* is more developed in these respects than *P. palmeri*, but not nearly as much as *Pelocetus* and *Cophocetus*. The species is therefore closest in morphology to *P. palmeri*, and thus is here referred to *Parietobalaena*, but may eventually prove to belong to a separate group of pelocetids.

*Parietobalaena laxata* (Van Beneden 1880)  
(Fig. 14)

1880 *Mesocetus laxatus* Van Beneden: p. 23.

1886 *Idiocetus laxatus* (Van Beneden); Van Beneden: p. 63.

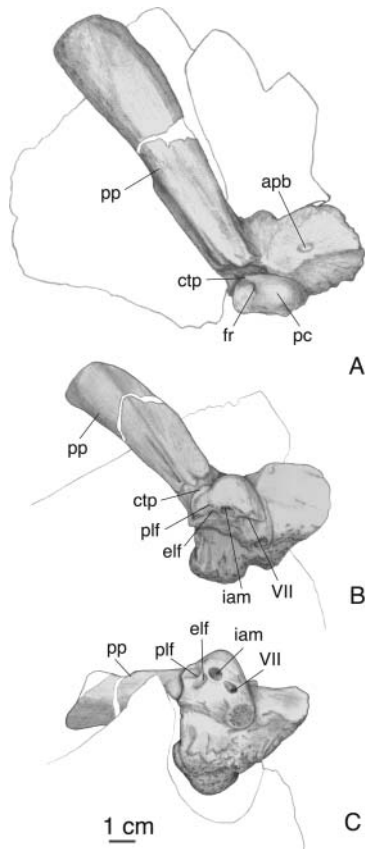
1931 *Plesiocetus laxatus* (Van Beneden); Van Deinsse: p. 140.



**Figure 13.** Left periotic and bulla of *Parietobalaena affinis* (Van Beneden, 1880) (IRScNB CtM 605 a-b/Reg 301). **A**, ventral view; **B**, medial view; **C**, dorsomedial view; **D**, posterior view. Illustrations C and D with bulla in place. From Van Beneden (1886). Abbreviations: b, bulla; ctp, caudal tympanic process; elf, endolymphatic foramen; fo, fenestra ovalis; fr, fenestra rotunda; iam, internal auditory meatus; lp, lateral projection of the anterior process; mfg, malleolar fossa groove; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; smf, stylomastoid fossa; VII, facial nerve canal.

**Lectotype.** Here designated as IRScNB CtM 727/Reg 61, left and right periotics and tympanics, occipital condyle, centra of all cervical and first to seventh thoracic vertebra.

**Diagnosis.** Like *P. palmeri* but with the following exceptions: periotic body extends more dorsally and anteriorly; anterior process reduced; dorsal surface less concave and

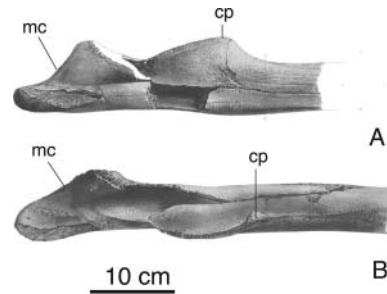


**Figure 14.** Right periotic of *Parietobalaena laxata* (Van Beneden, 1880) (IRScNB CtM 727/Reg 61). **A**, ventral view; **B**, medial view; **C**, dorsal view. Abbreviations: apb, anterior pedicel for the bulla; ctp, caudal tympanic process; elf, endolymphatic foramen; fr, fenestra rotunda; iam, internal auditory meatus; pc, pars cochlearis; plf, perilymphatic foramen; pp, posterior process of the periotic; VII, facial nerve canal.

less smooth; medial edge of dorsal surface situated more dorsally relative to fenestra rotunda; dorsal foramina for facial nerve canal and internal auditory meatus widely separated; posterior process about twice periotic length.

**Locality and age.** “Anvers, partie droite de l’ancien fortin n°1, 3<sup>e</sup> section, fossé du ravelin”. The approximate geographic coordinates of this fort, now destroyed, are N51°12'55"E4°27'. It is located at the boundary of the communes of Deurne and Borgerhout, eastern suburbs of Antwerp. Probably late early to middle Miocene Antwerpen Sands, Berchem Formation (O. Lambert pers. comm., 2009).

**Remarks.** The periotic is still attached to an undiagnostic skull fragment. The syntype series also included two tympanics, an occipital condyle and centra of all cervical and first to seventh thoracic vertebrae. It is, however, uncertain that this material belongs to the same individual as the periotics and is therefore not considered further here.



**Figure 15.** Posterior part of the left mandible of *Herpetocetus scaldiensis* Van Beneden, 1872 (IRScNB CtM 379/Reg 14). **A**, medial view; **B**, dorsal view. From Van Beneden (1882). Abbreviations: cp, coronoid process; mc, mandibular condyle.

Superfamily **Cetotherioidea** Brandt, 1872 *sensu* Steeman, 2007

Family **Cetotheriidae** Brandt, 1872 *sensu* Miller 1923

Subfamily **Herpetocetinae** Steeman, 2007

Genus **Herpetocetus** Van Beneden, 1872

**Type species.** *Herpetocetus scaldiensis* Van Beneden, 1872.

**Referred species.** *H. transatlanticus* Whitmore & Barnes, 2008, *H. bramblei* Whitmore & Barnes, 2008.

**Diagnosis.** See Whitmore & Barnes (2008).

*Herpetocetus scaldiensis* Van Beneden, 1872  
(Fig. 15)

1882 *Erpetocetus scaldiensis* (Van Beneden); Van Beneden: p. 84, pls 103–109 [unjustified emendation, Whitmore & Barnes 2008].

1912 *Plesiocetus scaldiensis* (Van Beneden); True: p. 3.

**Lectotype.** IRScNB CtM 379 a-b/Reg 14, left mandible designated by Abel (1938, p. 22).

**Paralectotypes.** IRScNB CtM 378 a-b/Reg 137, CtM 380/Reg 406, CtM 381/Reg 404, posterior fragments of mandibles (Abel 1938).

**Referred specimens.** A partial cranium, including the right squamosal, part of the parietal, part of the exoccipital, the right occipital condyle, the right periotic, stapes and the posterior part of the right tympanic bulla (USNM 336361), left squamosal IRScNB CtM 382/Reg 405 and an atlas IRScNB CtM 388/Reg 355 (Whitmore & Barnes 2008).

**Locality and age.** According to Whitmore & Barnes (2008), the locality of the lectotype is in Stuyvenberg, Antwerp, approximately 0.3 km east of Stuyvenberg Railroad Station. Whitmore & Barnes report the most likely age

of all specimens known of this species to be Scaldisian (ca 4–2.5 Ma), equivalent to upper Zanclean to Piacenzian.

**Remarks.** The peculiar morphology of the mandibular condyle was noticed by Winge (1909), but True (1912) decided to synonymize the genus with *Plesioceetus* based on cranial material. Later Abel (1938) chose the mandible (IRScNB CtM 379 a-b/Reg 14) as the lectotype. In their monograph on Lee Creek Mine (North Carolina) mysticetes, Whitmore & Barnes (2008) provided a redescription of *H. scaldiensis*, partially based on new material including a periotic, and described two new *Herpetocetus* species. These species have a periotic that can be compared with that of the remaining species revised here. The periotic of *Herpetocetines* differs from that of other mysticetes in having a much smaller body with a thin anterior process and a short, plug-like posterior process with a large flat lateral surface that was exposed on the lateral skull surface. It is therefore unlikely that *Herpetocetus* should be synonymous with either of the other genera revised here.

Superfamily **Balaenoidea** Flower, 1864  
Genus *Idiocetus* Capellini, 1876

**Type species.** *Idiocetus guicciardinii* Capellini, 1876.

**Remarks.** Kellogg (1934b) referred the type specimen of *I. guicciardinii* to *Balaenoptera*. McKenna & Bell (1997) included the genus in Balaenopterinae. According to Michelangelo Bisconti the morphology of the bulla and mandible of *I. guicciardinii* clearly indicates balaenid affinities (M. Bisconti pers. comm., 2003). Because the diagnostic value of this material is questionable, and the specimens were not available for this revision, the genus is only tentatively included in the Balaenidae.

*Idiocetus tsugarensis* Matsumoto, 1926

**Holotype.** The species is described by Matsumoto (1926), but no museum number is given. The specimen consists of a partial skull vertex.

**Remarks.** The morphology of the skull vertex indicates, that the specimen probably belongs to the one of the stem-balaenopterid groups rather than to a Cetotheriidae *sensu stricto*. However, it does not display enough diagnostic value to be able to place this species in a particular genus. Therefore, the species is considered a *nomen dubium*.

#### Genera considered *nomina dubia*

Genus *Burtinopsis* Van Beneden, 1872

**Type species.** *Burtinopsis similis* Van Beneden, 1872.

**Referred species.** *B. minutus* Van Beneden, 1880.

**Remarks.** This genus has been synonymised variously with *Megaptera* (Winge 1909), *Plesiocetus* (True 1912) and *Balaenoptera* (Simpson 1945; Deméré 1986). The described material does not include periotics, but the type series of both species includes several tympanics. These tympanics appear to represent members or close relatives of Balaenopteridae. Possible characters for the genus have been mentioned (an involucral ridge that is higher than the main ridge anteriorly, and an abruptly opening tympanic cavity anteriorly) (Oishi & Hasegawa 1994). However, these characters more likely represent interspecific variation, and neither of these tympanics is sufficiently diagnostic as a type specimen. As none of the included species appear to be based on diagnostic specimens, *Burtinopsis* is considered a *nomen dubium*.

*Burtinopsis similis* Van Beneden, 1872

**Remarks.** Ichishima (1997) considered the skull fragment (IRScNB CtM 683 / Reg 842) as possible representative of this species. The fragment consists of little more than the occipital condyles, and does not contain enough taxonomic information to support the species. Van Beneden (1882) mentioned a periotic, but it is not described, no specimen number is given, it is not figured and it can therefore not be identified. The species is therefore considered a *nomen dubium*.

*Burtinopsis minutus* Van Beneden, 1880

**Remarks.** Van Beneden (1882) mentioned an almost complete braincase among the material. However, this specimen is not described nor figured, and has not been given a museum number. It can therefore not be identified. The species is considered a *nomen dubium*.

Genus *Heterocetus* Capellini, 1877

**Type species.** *Heterocetus brevifrons* (Van Beneden, 1872), designated by Kellogg (1931).

**Referred species.** *H. guiscardii* Capellini, 1877.

*Heterocetus brevifrons* (Van Beneden, 1872)

1872 *Cetotherium brevifrons* Van Beneden: 17.

1873 *Cetotherium (Plesiocetopsis) brevifrons* (Van Beneden); Brandt: 145.

1874 *Heterocetus brevifrons* (Van Beneden); Vanden Broeck: 198.

1931 *Plesiocetus brevifrons* (Van Beneden); Van Deinsen: 125.

**Remarks.** A specimen that includes a periotic and a skull fragment (IRScNB CtM 612a-b/Reg 155) has

tentatively been referred to *Aglaocetus latifrons*. The remaining syntypes are not diagnostic and the species is considered a *nomen dubium*.

*Heterocetus guiscardii* Capellini, 1877

**Remarks.** According to Capellini (1877), the holotype of *H. guiscardii* consists of the right bulla, left stapes and parts of pars cochlearis, right mandible, 3rd-7th cervical, and first dorsal (the material listed by Kellogg (1941, 1968d) is not consistent with that listed by Capellini (1877)). The material is stored in The Museum of Palaeontology in Naples, but was not available for study first hand. However, as assessed from the descriptions, it is from a stem-balaenopterid (Balaenopteroidea), but not diagnostic. The genus is therefore considered a *nomen dubium*.

*Heterocetus sprangii* Van Beneden, 1886

**Remarks.** The syntypes included a left periotic that is referred to *Amphicetus later* (IRScNB CtM 622 b/Reg 296; Fig. 10). None of the other syntypes are sufficiently diagnostic to support the species, and it is therefore considered a *nomen dubium*.

Genus *Isocetus* Van Beneden, 1880

**Type species.** *Isocetus depauwii* Van Beneden, 1880.

*Isocetus depauwii* Van Beneden, 1880

1874 *Mesocetus depauwi* (Van Beneden); Vanden Broeck: 146.

**Holotype.** IRScNB CtM 396 a-t/Reg 370, parts of the mandible, cervical vertebrae, eight thoracic vertebrae, six lumbar vertebrae and several incomplete ribs.

**Paratype.** IRScNB CtM 399 a-c/Reg 4018 skull including a periotic, left mandible, atlas, cervical vertebrae, two thoracic vertebrae (Abel 1938).

**Remarks.** Van Beneden (1886) based this species on a single specimen that consists of most of the postcranial skeleton. However, the specimen is of limited diagnostic value and it is unlikely that new material can be referred with confidence to species or genus based on the original material. The species is therefore considered a *nomen dubium*. The referred specimen is being prepared and redescribed by Michelangelo Bisconti, Olivier Lambert and Mark Bosselaers.

Genus *Mesocetus* Van Beneden, 1880

**Type species.** *M. longirostris* Van Beneden, 1886, designated by Kellogg (1931, p. 308).

**Referred species.** *M. agrami* Van Beneden, 1886; *M. argillarius* Roth, 1978; *M. aquitanicus* Flot, 1896; *M. (?) brachyspondylus* (Brandt, 1873) Pia & Bauml, 1937; *M. hungaricus* Kadic, 1907; *M. latifrons* Van Beneden, 1880; *M. pinguis* Van Beneden 1880; *M. siphunculus* Cope, 1895.

**Remarks.** Junior homonyms of this genus are *Mesocetus* Fraas, 1904 (protocetid) and *Mesocetus* Moreno, 1892 (Physeteridae). The type species and therefore the genus is considered a *nomen dubium* (see below). The species described by Van Beneden (1886) are revised below. However, several other species have subsequently been referred to this genus. Revising these is beyond the scope of this study and individual studies are needed to determine their status and affinities.

*Mesocetus longirostris* Van Beneden, 1880

1931 *Plesiocetus longirostris* (Van Beneden); Van Deinse: 134.

**Remarks.** A periotic among the syntypes (IRScNB CtM 548 a-b/Reg 1539; Fig. 9) has been referred to *Amphicetus*. Another syntype assigned to *M. longirostris*, a skull vertex (IRScNB CtM 33), shows posteriorly projected rostral elements. This type of rostral configuration is, however, present in several extinct mysticete genera. The specimen is therefore not diagnostic or suitable as a lectotype for the species, which is considered a *nomen dubium*.

*Mesocetus pinguis* Van Beneden, 1886

**Remarks.** The nine syntypes do not include a periotic and none them are diagnostic at species level. The species is therefore considered a *nomen dubium*.

## Discussion

### Periotics as diagnostic tools

In the course of revising the material described by Van Beneden (1882, 1885, 1886), it has become evident that the periotic bone shows sufficient diagnostic characters to allow identification at what is believed to be species level. It will thus be possible at a later stage to refer more complete material to these species. It also illustrates the potential for isolated cetacean periotic bones elsewhere to be identified to species level and even to identify the presence of new species within a genus. It should be emphasised, however, that the periotic only represents a small part of an entire animal and that it is not recommended that isolated ear bones or other isolated material be used in the future to establish new scientific names (Barnes 1977). But if used for taxonomic identification purposes, we can dramatically increase the knowledge of species diversity and palaeodistribution of cetaceans. Teeth serve this function in many

**Table 3.** East-west distribution of known extinct mysticete species from the Miocene to Pliocene of the North Atlantic region. Abbreviations: B, Burdigalian; L, Langhian; P, Piacenzian; S, Serravallian; T, Tortonian; Z, Zanclean.

North-East Atlantic Fauna Taxon	Age	North-West Atlantic Fauna Taxon	Age
<b>Aglaocetidae</b>		<b>Aglaocetidae</b>	
<i>Aglaocetus burtinii</i>	T	<i>Aglaocetus patulus</i>	S
<i>Aglaocetus rotundus</i>	T		
<i>Aglaocetus latifrons</i>	B-T		
<i>Aglaocetus ? longifrons</i>	B-S		
<b>Pelocetidae</b>		<b>Pelocetidae</b>	
<i>Parietobalaena affinis</i>	T	<i>Parietobalaena palmeri</i>	L-S
<i>Parietobalaena laxata</i>	B-S	<i>Pelocetus calvertensis</i>	L-S
		<i>Halicetus ignotus</i>	S
<b>Diorocetidae</b>		<b>Diorocetidae</b>	
<i>Amphicetus later</i>	B-T	<i>Diorocetus hiatus</i>	L-S
<i>Plesiocetopsis hupschii</i>	?	<i>Thinocetus arthritus</i>	S
<i>Uranocetus gramensis</i>	T		
<b>Cetotherioidea</b>		<b>Cetotherioidea</b>	
<i>'Mesocetus' argillarius</i>	T	<i>'Cetotherium' megalophysum</i>	T
<b>Cetotheriidae</b>		<b>Cetotheriidae</b>	
<i>Herpetocetus scaldiensis</i>	Z-P	<i>Metopocetus durinasus</i>	S
		<i>Cephalotropis coronatus</i>	T
		<i>Herpetocetus transatlanticus</i>	Z

mammalian groups. In cetaceans, where the mammalian tooth pattern is greatly modified or teeth are absent, the preservation potential and diagnostic value of the periotic makes it an excellent tool for taxonomic identification.

### The extinct Belgian mysticete species

Following this revision of the species described by Van Beneden (1882, 1885, 1886), the genera *Amphicetus* and *Plesiocetus* are retained, with the latter referred to Balaenopteridae. Several species are referred to *Aglaocetus* and *Parietobalaena*, genera that are known from more complete material and for which a broadly defining diagnosis has previously been provided. The material referred to these genera does share important diagnostic characters, but they also present a large variation. This variation clearly exceeds the observed variation in periotic morphology within the recent genus *Balaenoptera*, but for reasons mentioned above, new generic names have not been created on the basis of this material. More complete material is needed to judge if this variation is more consistent with an intergeneric variation among extinct mysticetes. Future studies of more complete material, like the skull referred to *Isocetus* by Abel (1938) and a recently recovered specimen from a temporary exposure of the Deurne Sand in Antwerp (Bosselaers *et al.* 2004), thus holds the potential of shedding more light to these historical species.

### The extinct Belgian mysticete fauna

Despite the problems the Belgian species still present, it is now clear that they encompass a diversity of extinct mysticetes that rivals the fauna from the famous Calvert Formation described mainly by Remington Kellogg (1924,

1965, 1968a, b, c, d, 1969). Interestingly, all the Belgian material could with confidence be placed in existing families of extinct mysticetes and all of these families are represented in the fauna. Comparing the distribution of known species in the Miocene east and west North Atlantic faunas (Table 3), the extinct balaenopteroid families Aglaocetidae, Pelocetidae and Diorocetidae were all well established with an east-west North Atlantic distribution by the Middle Miocene. We therefore have to look to the Early Miocene or the Oligocene for the origin of these groups. The Belgian species extend the range of these families from the Middle to the Late Miocene. The diversity of aglaocetid species in the east North Atlantic fauna is greater than in the west. The species also spans a considerable range of size, as judged from the size of the periotics. Interestingly, only the phylogenetically basal group of relatively small *Parietobalaena* species represents Pelocetidae, while species more closely related to the much larger *Pelocetus* and *Cophocetus* appear to be absent. Diorocetidae is also represented by the phylogenetically basal taxa *Amphicetus* and *Uranocetus* (and perhaps *Plesiocetopsis*, although its phylogenetic position is less certain), while crownward taxa such as *Diorocetus* and *Thinocetus* are confined to the west North Atlantic (phylogeny follows Steeman 2007).

Cetotheriidae (*sensu stricto*) is only represented by *Herpetocetus*. The age of the type material is somewhat uncertain and inferred to be either Late Miocene Deurne Formation or Pliocene Kattendijk Formation. The latter seems most likely, because no *Herpetocetus* material with certainty has subsequently been recovered from the Miocene formations around Antwerp, while the Kattendijk Formation has yielded several specimens referable to

*Herpetocetus* (Whitmore & Barnes 2008) (M. Bosselaers, pers. comm., 2009). In the Miocene, geographically close representatives of Cetotheriidae are *Metopoceetus* and *Cephalotropis* in the northwestern Atlantic, and *Cetotherium rathkei* in the Tethys. This indicates that there was a later extension of members of Cetotheriidae into the northeastern Atlantic Ocean during the Miocene.

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## Note

Supplementary Data can be viewed online.

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